ERP Analyses of Perceiving Emotions and Eye Gaze in Faces: Differential Effects of Motherhood and High Autism Trait

Dissertation

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Abstract

The eye gaze and its direction are important and relevant non-verbal cues for the establishment of social interactions and the perception of others' emotional facial expressions. Gaze direction itself, whether eyes are looking straight at the viewer (direct gaze) or whether they look away (averted gaze), affects our social attention and emotional response. This implies that both emotion and gaze have informational values, which might interact at early or later stages of neurocognitive processing. Despite the suggestion of a theoretical basis for this interaction, the *shared signal hypothesis* (Adams & Kleck, 2003), there is a lack of structured electrophysiological investigations into the interactions between emotion and gaze and their neural correlates, and how they vary across populations. Addressing this need, the present doctoral dissertation used event-related brain potentials (ERPs) to study responses to emotional expressions and gaze direction in a novel paradigm combining static and dynamic gaze with facial expressions. The N170 and EPN were selected as ERP components believed to reflect (among others) gaze perception and reflexive attention, respectively. Three different populations were investigated. Study 1, as a baseline study in a normal sample, investigated the amplitudes of the N170 and EPN components elicited by the initial presentation of faces with different emotional expressions (happy, neutral, angry) plus averted or direct gaze and by subsequent changes of gaze direction in half of the trials. The N170 amplitude was larger to averted than direct gaze for the initial face presentation and – subsequently – larger in response to gaze changes from direct to averted than from averted to direct. In later processing stages (200-400ms), the EPN to happy expressions was larger for direct than for averted gaze. From this finding about the interaction of emotion and gaze, I concluded that happy faces

reflexively attract attention when they look at the observer rather than away. In Study 2, based on the claims about atypical face processing and diminished responses to eye gaze in autism, the N170 and EPN and eye movements were examined in two samples of children varying in the severity of their autism traits; the children were presented with implicit and explicit emotion tasks. The results confirmed the hypothesis of an impaired sensitivity to gaze direction in children with autistic traits, at least for specific emotions. In contrast to the sensitivity impairments going along with high autism trait, Study 3 addressed the putatively increased sensitivity in emotion processing and response to eye gaze in mothers during their postpartum period. In a large sample, I investigated the associations of motherhood with neural signals of the perception of gaze and emotion expressions with a particular focus on infant faces. ERPs were recorded from 59 mothers of infants < 6 months and 55 nulliparous women during a similar gaze change detection task as in Study 1, with the additional inclusion of infant faces. Results replicated the findings of Study 1 that N170 was larger to averted than direct gaze and larger to gaze changes from direct to averted than from averted to direct. In addition, N170 was larger for infant faces than adult faces. As a major new finding, in the initial gaze phase (250-300 ms) I found mothers to show stronger EPN responses to angry infant faces compared to nulliparae, indicating a heightened sensitivity for infant faces during early motherhood.

Taken together, the results from three studies demonstrate that in social interactions, the emotional effects of faces are modulated by dynamic gaze direction. The studies provide insights into the biological correlates and their timing in eye gaze and face perception in normal participants, and populations with impaired and enhanced sensitivity to emotional expressions and eye gaze.

Zusammenfassung

Die Blickrichtung ist ein wichtiges nonverbales Signal für soziale Interaktionen und die Wahrnehmung emotionaler Gesichtsausdrücke. Die Blickrichtung eines Gegenübers, d. h. ob der Betrachter direkt angeschaut wird (direkter Blick) oder ob der Blick abgewandt ist, beeinflusst unsere soziale Aufmerksamkeit und unsere emotionalen Reaktionen. Dies heißt, dass sowohl Emotionen als auch Blicke Informationswert haben, die in frühen oder späteren Phasen der neurokognitiven Verarbeitung interagieren können. Obwohl es eine theoretische Grundlage für diese Interaktion gibt, die *Shared-Signal-Hypothese* von Adams und Kleck (2003), fehlen strukturierte elektrophysiologische Untersuchungen der Interaktion zwischen Emotionen und Blickrichtung und ihrer neuronalen Korrelate, sowie über deren Variation innerhalb der Bevölkerung. Daher wurden in der vorliegenden Dissertation ereigniskorrelierte Hirnpotentiale (EKPs) eingesetzt, um Emotionsausdrücke und Blickrichtungen in einem neu-entwickelten Paradigma mit kombiniertem statischem und dynamischem Blick zu untersuchen. Diese Studien verwendeten die N170 und die EPN Komponente im EKP, von denen angenommen wird, dass sie (unter anderem) die Erfassung der Blickrichtung bzw. die reflexive Aufmerksamkeit auf Emotionsausdrücke widerspiegeln. Die Studien untersuchten drei verschiedene Populationen.

Studie 1, als Basisstudie in einer normalen Stichprobe, untersuchte die Amplitude der N170- und EPN-Komponenten, auf die anfängliche Präsentation von Gesichtern mit verschiedenen emotionalen Ausdrücken (glücklich, neutral, wütend) und abgewandtem oder direktem Blick sowie auf die anschließende Änderung der Blickrichtung. Die N170-Amplitude war bei abgewandtem Blick größer als bei direktem Blick für die anfängliche, statische Gesichtspräsentation und größer bei Blickwechseln von direkt zu abgewandt als von

abgewandt zu direkt in Reaktion auf die Darbietung von dynamischen Blickwechseln. Zwischen 200 und 400 ms nach der Stimulus-Präsentation war die EPN auf glückliche Ausdrücke bei direktem Blick größer als bei abgewandtem Blick. Dies legt nahe, dass glückliche Gesichter mehr reflexartige Aufmerksamkeit auf sich ziehen, wenn sie den Beobachter direkt ansehen, anstatt vorbeizuschauen.

In Studie 2 wurden zwei Stichproben von Kindern untersucht, die sich in der Ausprägung ihrer Autismus-Merkmale unterschieden. Dies erfolgte auf der Grundlage der Hypothese einer atypischen Gesichtsverarbeitung und verminderter Reaktionen auf Blicke Anderer bei Autismus. Untersucht wurden die N170 und EPN sowie Augenbewegungen in impliziten und expliziten Emotionserkennungsaufgaben. Die Ergebnisse bestätigten die Hypothese einer beeinträchtigten Sensibilität für die Blickrichtung bei Kindern mit autistischen Zügen, zumindest für bestimmte Emotionen.

Im Gegensatz zu den Beeinträchtigungen, die mit hohen autistischen Merkmalsausprägungen einhergehen, war das Forschungsziel von Studie 3 die mutmaßlich erhöhte Sensitivität in der Emotionsverarbeitung und für die Blickrichtung bei Müttern während der postpartalen Phase. In einer großen Stichprobe untersuchten wir die Effekte von Mutterschaft auf die neuronalen Signale der Blick- und Emotionswahrnehmung mit einem besonderen Fokus auf Säuglingsgesichter. ERPs wurden von 59 Müttern von Säuglingen unter sechs Monaten und 55 nulliparen Frauen während einer ähnlichen Aufgabe zur Erkennung von Blickwechseln aufgezeichnet wie in Studie 1, wobei zusätzlich Gesichter von Säuglingen miteinbezogen wurden. Wir konnten unsere Ergebnisse aus Studie 1 hinsichtlich der N170 und der EPN weitgehend replizieren. Zudem war die N170 auf Säuglingsgesichter stärker ausgeprägt als auf Erwachsenengesichter. Ein wichtiger neuer Befund ist, dass Mütter zwischen 250 und 300 Millisekunden nach der Darbietung eines Gesichts eine stärkere EPN-

Reaktion auf ärgerliche Säuglingsgesichter zeigen als nulliparae Frauen, was darauf hinweist, dass Mutterschaft eine erhöhte Empfindlichkeit des Emotionserkennungssystems für ärgerliche Säuglingsgesichter mit sich bringt.

Zusammengenommen zeigen die Ergebnisse der verschiedenen Studien meiner Dissertation, dass die emotionalen Effekte von Gesichtern durch die dynamische Blickrichtung moduliert werden. Sie liefern zudem wertvolle Erkenntnisse über die zugrundeliegenden biologischen Korrelate und deren zeitlichen Verlauf in der Blick- und Gesichtswahrnehmung, die sich je nach untersuchter Population unterscheiden

Synopsis

1. Introduction

"Under optimal conditions of interpersonal encounter, the gaze of the other may be experienced as streaming into my whole being - I am filled out and irradiated by it."

(Heron, 1970)

In a world so fundamentally social, other humans have typically been regarded as a special case for the visual system since they are objects in the world that may be looked at or addressed. In dyadic interactions, the sender of an emotional expression (S) directs his gaze to others to not only support their own visual information uptake, but to signal contextual information to the receiver. The receiver of the gaze (R) draws inferences about where the sender's visual attention is directed.

Emotional expressions are relevant to the flow of the interaction as gaze helps to interpret the emotion expressed in the face. In other words, detecting gaze direction in the context of facial expressions may be important in order to better decode the meaning of that emotional expression and plan subsequent action to avoid embarrassing moments or to approach pleasant events. For instance, anger in the face of a person has a very different significance if targeted at an observer (is he angry at ME?) or somewhere else, indicated by where the angry person is looking at. The same holds true for facial expressions of other emotions, such as happiness (if targeted at an observer: is he/she in friendly with ME?), fear (If targeted at somewhere else: Is there a threat in the environment?) or disgust. Worth mentioning, gaze itself can become a part of an emotional display. For instance, one may find himself trying to "stare an opponent down" or embracing him an adoring gaze.

Thus, in order to respond appropriately to other people, as well as to objects that the other is attending to, eye gaze and emotional expression frequently need to interact and be evaluated together.

1.1 Aims and Outline of the Present Work

In this dissertation, I aimed to clarify the interactions between perceiving emotional facial expressions and gaze direction and their underlying neural mechanisms. Specifically, I was interested to study (1) whether the perception of gaze and emotional facial expressions are independent or interactive, and (2) whether any interactions can be functionally localized at the early stages of structural face encoding or later.

To this aim, I measured neural activities during face processing by means of recording and analyzing event-related potentials (ERPs). ERPs have an excellent temporal resolution which is vital when the temporal dynamics of the neural activity is of interest. ERPs are a great tool for parameterizing indicators of neural responses and provide a continuous measure of different stages in cognitive processing. This allows to determine which stages reflect a specific experimental effect (Luck, 2005).

Among ERP components, I focused on the time course and scalp topography of an early stage ERP component (N170) and early posterior negativity (EPN) as a later component. Section 1.3 provides a brief introduction of the N170 and EPN components reflecting the neural bases of perceiving emotional facial expressions and gaze direction.

Following this approach, I addressed several questions which have been controversially discussed from several scientific perspectives. Firstly, I set out to replicate N170 findings for perceiving gaze direction in a nonsocial task. Secondly, I expanded on the findings of the

EPN component for gaze direction effects. In terms of emotion effects, I expected to replicate the standard findings on the EPN. Most importantly, I aimed to assess whether emotional expression and gaze direction would produce additive effects or whether they would interact at certain processing stages as reflected in the ERP components. Finally, I was interested in the differences between presenting different emotional expressions and gaze directions simultaneously at stimulus onset as compared to a gaze change occurring while a face already displays an emotional expression. For this purpose, I used a design which allowed the analysis of ERPs both relative to the initial presentation of the face (initial gaze phase), and also relative to the subsequent gaze change (gaze change phase) with 20 students as participants (Study 1: section 2.1 provides detailed information on the study design).

Further I aimed to expand on the findings of Study 1 and take a relevant step towards investigating the role of emotional facial expressions and gaze direction and their relationship in possible clinical investigations and future applications. Therefore, in Study 2, I investigated the gaze and emotion interaction within a sample of children with different degrees of autistic trait expressions as they are a group with presumably impaired sensitivity in gaze perception and consequently communication complaints (section 1.4 provides a relevant brief literature review). To study the mentioned atypical gaze processing in autism, I addressed several questions using a multimodal approach by measuring both ERPs and eye-movements in two experiments. In Experiment 1 with a sample of 47 children (aged 9–12 years) as participants, I was particularly interested in studying whether the processing of emotion was influenced by gaze direction (or vice versa) when the emotional expression was not task-relevant but an implicit variable, and how this interaction relates to autism trait severity. In Experiment 2, with 44 children (mean age = 13 years) as participants, I investigated the explicit classification of emotional facial expressions, with gaze direction being implicitly manipulated in autism (section 2.2 provides detailed information on the study design). This study includes EEG and eye tracking as measuring modalities and has been conducted in total with 91 participants. However, my report focuses only on the ERP part.

The purpose of Study 3 was to take a complementary step to investigate the heightened sensitivity to eye gaze perception. Evidence has shown that motherhood facilitates the facial expression decoding, especially by increasing the focus on the eye region. For this, I aimed to evaluate the degree to which motherhood influences the emotion and gaze processing plus a secondary aim to replicate the findings of Study 1 with a larger sample of participants. Here, I pursued to utilize the paradigm of Study 1 and measure ERPs in mothers and nulliparae (N=114 in total) to study motherhood effects on emotion and gaze processing. The emotion and gaze interplay and whether this depends on stimulus age (adult versus infant stimuli) were also important questions to capture. Specifically, I asked whether such effects can be functionally localized at the early stage of structural face encoding, as indicated by the N170 component or at a later stage, as indicated by the EPN. In other words, the modulation of N170 and EPN components by emotion, stimulus age, direction of the gaze and motherhood and their interaction in early and late ERP stages could elucidate how information is being differentially integrated into the assessment of face stimuli in mothers and nulliparae. (section 2.3 provides detailed information on the study design). This study includes separate EEG and psychometric sessions and has been conducted with more than 300 participants over a period of 12 months; however, my report focuses only on the ERP part.

1.2 Emotional Facial Expressions and Eye Gaze Perception

Even though facial expressions are effective emotional signals, gaze direction is crucial for indicating the referent of an expression and, consequently, the attended object of the elicited emotion (George & Conty, 2008). Therefore, gaze direction, that is, whether a person's eyes are fixed straight at the viewer (direct gaze) or averted (averted gaze), influences our emotional response and capacity to make inferences about emotional states of other's, as well as social attention (for a review, see Itier & Batty, 2009). Consequently, eye gaze is a core component of communication theories which explains how everyday theory of mind works (e.g. Baron-Cohen & Cross, 1992; Readinger, 2002). The hypothesis stating that eye gaze processing draws on the same neural networks as inferring mental states is supported by two investigations that found the brain activity induced in theory of mind research and eye gaze processing experiments is similar (Calder et al., 2002; Conty et al., 2007).

One of the most compelling evidence for the connection between eye gaze processing and theory of mind is that certain populations (e.g. with autism spectrum disorder, schizophrenia, and social anxiety disorder) who present with altered theory of mind, also show altered eye gaze processing (Weeks et al., 2013; Weiser et al., 2009).

Similar to eye gaze, emotional expressions are changeable features of the face that permit inferences about internal states and intentions of others. Together with gaze direction that provides information about the spatial location of another person's attention, facial expressions provide information about the communication partner's attitude towards the observer that is looked at. Thus, the integration of gaze and emotional expression information is necessary for higher order social perception.

Multiple studies have investigated how the perceived emotional expression is dependent on eye gaze direction, particularly for static emotional expressions (Adams & Kleck, 2003, 2005; McCrackin & Itier, 2019; Sander, 2007). As a classical view, Haxby et al. (2002) propose a specialized neuronal face recognition system which has a hierarchical organization of face processing. In this theory, invariant aspects of the face are processed first, followed by the changeable aspects, such as eye gaze and emotional expressions in superior temporal regions, in particular, the superior temporal sulcus (STS) (Haxby et al., 2002). Its posterior part (pSTS) is a major component of 'core' networks subserving face perception. It is consistently modulated not only by facial expressions of emotion (Kujala et al., 2009) but also by perceived eye gaze shifts (Allison et al., 2000; Calder et al., 2007)

A more specific theoretical basis for understanding interactions between gaze and emotion, the *shared signal hypothesis (SSH),* is provided by R. B. Adams and R. E. Kleck (2003). This hypothesis takes a motivational approach-avoidance stance and suggests that emotion perception is enhanced when gaze direction matches the expression of the face in terms of implied approach or avoidance. Specifically, the processing of emotional expressions that are related to approach (e.g. joy, anger) is facilitated by direct gaze, whereas expectations related to avoidance (e.g. fear, sadness) are facilitated by averted gaze. Hence, according to Adams and Kleck (2003), matching gaze direction enhances perceptual processing of emotional expressions. Worthy to mention, this hypothesis concentrates on how approach-avoidance behavioral motivations are perceived by an observer. For instance, although observers are likely to move away from another person with an angry face, they will also likely expect the expressor to approach them.

Another proposed common mechanism of gaze and emotional processing is affective arousal model (Senju & Johnson, 2009). The model suggests that gaze direction can influence arousal level and that processing of direct versus averted gaze may alter due to differing arousal level. In line with this idea, direct gaze perception is associated with increased awareness of the perceiver's own emotional state (Baltazar et al., 2014) and arousal (Conty et al., 2010; Helminen et al., 2011; McCrackin & Itier, 2018; Nichols & Champness, 1971) In this regard, specific amygdala activation reflecting the arousal level in response to direct gaze has been previously reported (Kawashima et al., 1999).

Additionally, research on the level of electrophysiological correlates demonstrates that the processing of emotion and gaze might overlap, meaning that emotions are processed in a similar time window as gaze (Rellecke et al., 2011; Schacht & Sommer, 2009). Thus, the processing of interaction is a complex issue comprising many different influential factors in cues, context, and cognitive processes.

Speaking of influential factors and context, altered processing of eye gaze and emotional facial expressions has been associated with population variations in various domains of enhanced healthy functioning (e.g. pregnancy hormones and birth giving in mothers) (section 1.5 elaborates on the topic), as well as with symptoms of affective eye gaze deficits, including autism (see section 1.4 for more elaboration on the topic). In autism, the ability to follow the other's gaze is impaired (Emery, 2000), which goes along with impairment of interpersonal coordination. In this regard, autism is characterized by a lack of spontaneous mentalizing and/or behavioral adaptation. Individuals with autism still struggle greatly in real-time social interactions despite having a healthy capacity for conscious reflection on others' mental states (Schilbach et al., 2013).

Consequently, one can say that the interaction of eye gaze and emotional facial expression can modulate cognitive processing as well as social features of human life. Since the interaction of these facial features is important for social communication, identifying the spatial and temporal patterns of these changeable features is an important object of investigation in order to know how emotion and gaze play along and how they are processed by the observer.

1.3 Electrophysiological Indicators of Emotional Facial Expressions and Eye Gaze Perception

Due to the high temporal resolution of noninvasive electrophysiological techniques, ERPs provide great methods to elucidate the underlying neural processes for face perception. Several ERP studies have revealed ERP components that are related to different stages in face processing (e.g. Bentin et al., 1996; Rossion et al., 2000; Pourtois et al., 2005; see Schweinberger & Neumann, 2016 for a review). The most commonly studied face-related ERP component is the negative-going N170, which occurs around 170 ms after stimulus onset at occipito-temporal region (e.g. Bentin et al., 1996; Bötzel et al., 1995). The neural generators of the N170 have been traced to visual processing in areas sensitive to faces, such as the fusiform gyrus (Eimer & Holmes, 2002; Gao et al., 2019). Many studies have shown that N170 reflects structural encoding of facial features (e.g. Bentin et al., 1996; Carmel & Bentin, 2002; Eimer, 2011), and can be modulated by emotional expressions (e.g. Rellecke et al., 2011, Hinojosa et al., 2015; Stephani et al., 2020). For example, Itier et al. (2007) found that the N170 is substantially smaller when the eyes are removed from the face image.

Larger amplitudes for N170 have been found in a number of studies in response to faces with averted gaze as compared to direct gaze, that is, when eyes appear to look directly at the participant/observer (Caruana et al., 2014; Itier et al., 2007; Latinus et al., 2015; Puce et al., 2000; Rossi et al., 2015). There are also reports of larger N170 amplitudes for direct as compared to averted gaze (Conty et al., 2007, 2012; Watanabe et al., 2006). On the other hand, several studies found no modulation of the N170 by gaze direction (Brefczynski-Lewis et al., 2011; Myllyneva & Hietanen, 2015; Ponkanen et al., 2011; Schweinberger et al., 2007; Taylor et al., 2001; for a recent review see Tautvydaite et al., 2022). Some of these inconsistencies may be explained by properties of the task (Latinus et al., 2015). As suggested by Latinus et al. (2015), social tasks, in which the participant indicates whether or not the face makes eye contact, may attenuate gaze impact on the N170 in contrast to emotional tasks, where expressions are classified for emotion, or spatial tasks, when gaze direction has to be judged. In addition to task requirements, head and face orientation plus static versus dynamic gaze have been discussed as causing inconsistencies in the gaze perception literature (Conty et al., 2007; Itier et al., 2007; Puce et al., 2000).

Multiple ERP studies have examined the processing of emotions (Kissler et al., 2009; Schacht & Sommer, 2009a; Schupp et al., 2004). The most prominent emotion-sensitive ERP components are EPN and the late positive complex (LPC). Both components occur for emotional relative to neutral stimuli in different domains, for example, faces and words (Schacht & Sommer, 2009b). The LPC consists in an increased parietal positivity around 350-500 ms post stimulus in response to emotional relative to neutral stimuli. The LPC component is observed mainly when stimulus emotion is task-relevant rather than implicit (Rellecke et al., 2011); therefore, it has been linked to motivated attention towards the stimuli (Schupp et al., 2006). Because in the present study, emotional facial expressions were not task-relevant, I did not expect any effects on the LPC. This is in line with the findings of some prior studies (e.g. Rellecke et al., 2011; Schacht and Sommer., 2009). For this reason, I have not assessed effects on the LPC component.

The EPN component appears at occipito-temporal scalp sites and, if elicited by facial expressions, can start as early as around 150 ms (Rellecke et al., 2011) reaching its maximum around 260 - 280 ms after stimulus onset (Schupp et al., 2006). Whereas to words and emotional pictures, EPN latency is usually longer (Bayer & Schacht, 2014; Schacht & Sommer, 2009a; for a review see Schindler & Bublatzky, 2020). Some studies (Holmes et al., 2009; Schupp et al., 2006) indicate a larger negativity for emotional, especially happy and fearful faces, than neutral ones. EPN amplitude to facial expressions increases with the intensity of the emotional expression (Recio et al., 2014), and has also been observed for non-emotional facial movements, such as jaw movements versus eye blinks (Recio et al., 2014). This is in line with the suggestion of Schupp et al. (2006) that the EPN indicates the reflexive attention elicited by a stimulus. In most studies affective stimuli are used to elicit the EPN (Schindler & Bublatzky, 2020), but according to findings of Recio et al. (2014), this can also be the case for non-affective visual stimuli (attention catching). It should be noted that there is also evidence for early effects of emotional expressions in the time range of the N170 (Hinojosa et al., 2015; Rellecke et al., 2011; Stephani et al., 2020) although some of these effects might be due to overlap by early onset EPN and not to modulations of the N170 component itself (Rellecke et al., 2013).

First evidence for a possible interaction between gaze and emotional expression was reported by Klucharev and Sams (2004), who presented static pictures of angry and happy faces with different gaze directions. They reported a modulation of the ERPs between 300 and 330 ms after stimulus onset to both happy and angry faces due to the face's gaze direction (Klucharev & Sams, 2004). The findings suggest that angry expressions directed at an individual are rapidly detected. The authors, specifically, proposed that gaze direction and emotion are processed independently before 270 ms but interact thereafter. In addition, Rigato et al., (2010) found an interaction between gaze and emotion on the latency of the face-sensitive occipito-temporal P2 component. In this study, the P2 was smaller for fearful faces with direct gaze than for both fearful faces with averted gaze and happy faces with direct gaze (Rigato et al., 2010). This fining is in contrast to the *shared signal hypothesis* by Adams and Kleck (2003) suggesting an association between averted gaze and fearful expressions. Moreover, in a complex study design, Conty et al. (2012) manipulated gaze direction together with head and body posture, emotional expression (neutral versus anger) and presence or absence of hand pointing. The P2 was larger to angry than to neutral expressions and – independently – larger to direct than to averted gaze; emotion and gaze interacted after 200 ms. However, in this study, gaze was not studied in isolation but confounded with head and body orientation and there was only one emotion included.

As a conclusion from previous studies (Conty et al., 2007, 2012; Rigato & Farroni, 2013), it seems that interactions of gaze and emotions emerge only after the N170 component, that is, after the structural encoding of facial features. Otherwise, it is hard to discern a consistent picture from these studies. It remains unclear (1) for which components or cognitive processes these interactions take place and (2) what is their specific electrophysiological pattern. Because existing studies are heterogenous in terms of the stimulus material (isolated and static gaze or in combination with other properties) and with regard to the inclusion of neutral faces as a reference condition.

1.4 Impairments of Emotional Facial Expressions and Eye Gaze Perception

The interaction framework also holds that gaze should be investigated in relation to the characteristics of the observer, the interaction's content, and the interactive context. For instance, impairments in social, emotional and communicative abilities are core symptoms of autism spectrum disorder (ASD; American Psychiatric Association, 2013). These abilities are closely related to eye gaze and emotional facial expression processing (Adams and Kleck, 2003). Many studies have shown that gaze processing deficits in autism may be due to impairments in using eye gaze as a proxy to understand facial expressions, intentions, and mental states of others (Baron-Cohen, 1995; Baron-Cohen et al., 1997, 2001; Leekam et al., 2000). The struggle to recognize emotions from facial expressions is one of the earliest identifiable markers of ASD (Dawson et al., 2005).

ERP studies indicate difficulties of individuals with ASD in orienting to social stimuli. This was demonstrated by a reduced or delayed N170 response to faces, which may indicate impaired structural processing of faces (Samaey et al., 2020) or diminished emotion recognition (Chronaki, 2016). The N170 is therefore of great interest for investigating altered face processing in autism (for reviews see Kang et al., 2018, and Monteiro et al., 2017). In individuals with ASD, compared to typically developing (TD) individuals, longer N170 latencies to faces and smaller amplitudes to emotional facial stimuli have been found (Batty et al., 2011; de Jong et al., 2008; Tye et al., 2014). For example, Webb et al. (2006) reported longer N170 latencies to faces in children with ASD compared to TD individuals, indicating a deviant pattern of brain responses to faces at an early age. With respect to specific emotions, previous studies demonstrated stronger increases of N170 amplitudes to fearful versus neutral expressions in a control group compared to an ASD group. In contrast, N170 amplitudes to neutral faces did not significantly differ between these groups (de Jong et al., 2008; Faja et al., 2016). Faja et al. (2016) and Wagner et al. (2013) reported increased N170 amplitudes to happy and angry faces, only for a TD group but not for an ASD group.

However, Tye et al. (2014) found larger N170 amplitudes for neutral as compared to fearful expressions only in ASD participants.

Evidence of unusual eye gaze direction processing among children with ASD was found in two ERP studies. Grice et al. (2005) recorded high-density ERPs from children (aged 3.5–7 years) with ASD while passively viewing faces with different gaze directions. The occipito-parietal negativity was larger in a direct than an averted gaze condition in children with ASD, resembling data collected from 4-month-old infants (Farroni et al., 2002). In contrast, ERPs of age-matched TD children and adults were not sensitive to perceived gaze direction (Grice et al., 2005), suggesting a developmental delay in the ASD group. The absence of gaze direction effects in TD individuals reported by Grice et al. (2005) is surprising and at variance with findings of Senju et al. (2005) who investigated ERP correlates in an active gaze direction detection task in children with ASD and TD children (M = 12 years). Given the sensitivity to perceived eye gaze direction, N170 to direct gaze was larger than to averted gaze in controls but not in the ASD group. After gaze direction changes, the N170 was followed by an enhanced occipito-temporal negativity (N2), which was lateralized to the right hemisphere. N2 component was larger for direct than averted gaze for TD children but not for children with ASD. Similar problems with gaze processing have been also reported on the performance level. Unlike children with ASD, TD children showed an advantage in detecting direct gaze over averted gaze (Senju et al., 2005; Senju & Johnson, 2009).

Regarding the EPN component, one study found that adults with ASD had different hemispheric distribution of EPN in response to facial expression, compared to neurotypical adults (e.g. Faja et al., 2016). Faja et al. (2016) found that adults with ASD differed from neurotypical participants by showing a reduced sensitivity to emotional information in the

EPN but not in the preceding P1 or N170 components. The authors concluded that the N170, which is associated with perceiving information to distinguish faces from other object categories (Bentin et al., 1996), is not modulated differentially by emotional expressions in adults with ASD relative to neurotypical adults.

Interactive aspects of emotional facial expression perception and eye gaze processing are often emphasized as crucial issues in autism (Akechi et al., 2010; de Jong et al., 2008; Grice et al., 2005; Senju et al., 2005; Tye et al., 2013). Akechi et al. (2010) investigated the neural correlates of processing facial expressions with different gaze directions. Approach-oriented expressions (e.g. anger) combined with direct gaze elicited a larger N170 than avoidance-oriented expressions (e.g. fear) combined with averted gaze in both TD and ASD children groups. However, this effect was smaller in the ASD group. This finding suggests that gaze direction modulates the effect of emotional facial expressions. In an attention cueing task, de Jong et al. (2008) presented fearful and neutral faces with different gaze directions either in static and dynamic conditions. Children with ASD processed gaze cues typically when static neutral faces were presented, exhibiting larger N200 amplitudes and shorter RTs in validly cued conditions. However, in the dynamic condition, attention orienting was influenced by emotion only in the control group but not in the ASD group. These effects were taken to suggest an impairment of processing social information in individuals with ASD. Emotional expression and gaze direction interact, and jointly contribute to approach- or avoidance-related basic behavioral motivations.

Importantly, as mentioned before, children with ASD have difficulties in recognizing other's facial expressions, especially anger (Bal et al., 2010). It was therefore of great interest to study whether autistic individuals can benefit from this interaction of emotional expression and gaze direction in the same way as normal controls do, and to see whether the *shared* *signal hypothesis* (mentioned on section 1.2) relates to other concepts of how ASD individuals process facial expressions and eye gaze. For example, the *"eye avoidance hypothesis"* proposes that atypical gaze behavior in autistic individuals is due to a lack of social interest (Tanaka & Sung, 2016). Tanaka and Sung (2016) consider avoidance of the eye region as an adaptive strategy for autistic individuals, as they often perceive eye gaze as socially threatening and unpleasant. However, avoiding the eyes severely limits the possibility of recognizing a person's identity, emotional expressions and intentions from his/her face. Tanaka and Sung (2016) believed that this avoidance behavior is the most plausible explanation for the autistic deficits found so far. In conclusion, referring to a second-person neuroscience, introduced by Schilbach et al. (2013), autism goes along with an impairment of interpersonal coordination. That means gaze can modulate cognitive processing as well as social features of human life.

1.5 Enhancement of Emotional Facial Expressions and Eye Gaze Perception

Hormones modulate brain activity in areas associated with social cognition and thus appear to be central neuromodulators for interpersonal perception and communication (Febo et al., 2005). Previous research indicates that higher levels of hormones such as oxytocin in mothers facilitate the decoding of facially expressed emotions, enhance facial processing by increasing the focus on the eye region of human faces, and increase the orienting of attention according to gaze cues (Guastella et al., 2008; Kanat et al., 2015; Theodoridou et al., 2009). Likewise, the direct gaze of mothers enhances facial recognition and processing by infants and increases engagement in mother-infant interaction (Farroni et al., 2007; Rigato et al., 2010). Infant faces have distinct features that attract the observer's attention such as large head and eyes, chubby cheeks and a small nose (DeBruine et al., 2016; Glocker et al., 2009;

Luo et al., 2015; Thompson-Booth et al., 2014). In this context, mother-infant interaction including mutual gaze is positively associated to the development of infant attentional control (Niedźwiecka et al., 2018), language (Topping et al., 2013) and socio-emotional development (Abraham et al., 2016; Cerezo et al., 2008; MacLean et al., 2014), as well as learning (Wu et al., 2014). Therefore, infant's facial cues and eye gaze seem to be especially important elicitors of caregiver responses, prompting mothers to employ a range of soothing behaviors for the infants.

A deeper understanding of face processing by mothers (and more general in parents) can be achieved by considering the time course of neurocognitive processing of infant faces using ERPs. Some studies have reported neural responses to infant stimuli (see Maupin et al., 2015 and Vuoriainen et al., 2022 for a review) and variously tested whether becoming a parent and the experience of parenting, modulates neural responses to children's faces as compared to adult faces. Noll et al. (2012) and Peltola et al. (2014) found no difference in processing infant faces between mothers and nulliparous women. Other studies investigated whether parental ERP responses are augmented to images of one's own versus other's children and found that parents typically respond stronger to the face of their own child (Bernard et al., 2018; Grasso et al., 2009; Kuzava and Bernard, 2018; Weisman et al., 2012). Others addressed whether variations in mothers' ERP responses to their own child's face is associated with parenting quality. Thus, Bernard et al. (2015) reported that larger responses to emotional infant faces were associated with greater parental sensitivity. Groh and Haydone (2018) and Leyh et al. (2016) found that insecure attachment style of mothers was associated with larger ERP responses specifically only to distressed infant stimuli (negative stimuli), whereas in securely attached mothers, responses to positive and negative infant stimuli were indistinguishable.

During pregnancy, women show increased N170 amplitudes when looking at faces, indicating that their ability to structurally analyze faces is enhanced (Raz, 2014). Also after birth, mothers show larger N170 responses to their own infant's faces as opposed to the faces of other infants (Weisman et al., 2012), indicating heightened perceptual sensitivity for their own infant's face.

Concerning the sensitivity to faces, emotional facial expressions also affect the perceptual and attentional processing. As compared to nulliparae, larger N170 amplitudes were observed in pregnant women when looking at angry faces compared to neutral faces (Raz, 2014) and in a sample of mothers when looking at happy compared to neutral infant faces (Rutherford et al., 2017). Likewise, complementary results indicate increased sensitivity of N170 amplitude to emotional facial expressions in non-neglectful mothers, such as significantly larger amplitudes to crying than to neutral or laughing infant faces compared to neglectful mothers who showed attenuated N170 amplitudes across all three emotional expressions (Rodrigo et al., 2011). These findings indicate the special role of the interaction of mothers with infants in terms of early face processing.

Structural encoding of eyes and their importance is also reflected in mothers' more frequent and longer gaze fixation behavior toward their infant's eyes (De Pascalis et al., 2017). Doi and Shinohara (2012) extended this work by evaluating maternal sensitivity to children's gaze directions as an element of dyadic relationship between mothers and infants. In this study, mothers showed larger N170 amplitudes when viewing their own child's face (familiar face) with direct rather than averted gaze, which was not the case for the faces of unfamiliar children. The authors suggested that gaze information from a mother's own child with direct gaze induces differential neural responses at early perceptual stages of face processing concerning the interaction of facial identity and gaze direction (Doi & Shinohara, 2012).

The processing stages following structural encoding are associated with more elaborate processing (Recio et al., 2014; Schacht & Sommer, 2009). There is some evidence that compared to nulliparae, mothers show greater attentional engagement with emotional facial expressions and infant faces, which are thought to be biologically salient to the mother while also generating an incentive for their caregiving behavior (e.g. Ferrey et al., 2016; Thompson-Booth et al., 2014). This maternal bias towards infant emotions has also been found at a neurobiological level using functional magnetic resonance (fMRI), with stronger maternal responses to crying compared to laughing infants (Seifritz et al., 2003). Regarding EEG research for mothers, Peltola et al. (2014) reported larger EPN amplitudes in response to distress compared to happy infant faces when the task required focusing attention on these faces, which was not the case for non-mothers.

Altogether, these findings indicate pervasive (albeit not entirely consistent) effects of motherhood on the neural correlates of emotional facial expression and eye gaze processing. Here, identifying the level at which eye gaze and facial emotion perception in mothers differs from nulliparae is important to understand the degree to which motherhood affects socio-emotional abilities.

2. Summary of the Present Studies

2.1 Study 1: The Time Course of Emotional Facial Expressions and Eye Gaze Perception (Bagherzadeh-Azbari et al. 2022a)

The emotional expression and gaze direction of a face are important cues for human social interactions. However, the interplay of emotional expression and gaze direction factors and their neural correlates are only partially understood. The meaning of emotional expression on a face may vary depending on the direction of the observer's gaze. In Study 1, I investigated ERP correlates of gaze and emotion processing following the initial presentation of gaze as well as the subsequent change of gaze direction. The study design included faces with different emotional expressions (happy, neutral, angry) and an averted or direct gaze direction. Each trial began with a fixation cross on a white screen shown for 800 ms. Then, the first image of a face appeared for 1000 ms, showing one of three emotional expressions and either a direct gaze or an averted gaze. The presentation of the first image was seamlessly followed by the second image for another 1000 ms. In 50 % of the trials, the second image was identical to the first one (no change). In the other half of trials, the same facial identity and emotional expression was shown but with a different gaze direction. In other words, in these trials, the person's gaze direction changed.

In the following, we will distinguish between the initial gaze phase, lasting from the onset of face presentation until the onset of the gaze change phase. In the initial gaze phase, happy, neutral, and angry expressions appeared equally often and were orthogonally combined with direct, left, and right averted gaze. The probabilities of gaze change to any of the other gaze directions at the onset of the gaze change phase were the same, except that no changes from an averted position to another averted position (e.g. left-averted to right-averted) occurred. The second face image was followed by a blank screen, during which participants should indicate by button presses with their left or right hand whether or not a gaze change had occurred during the trial. Participants were told to focus on response accuracy.

As introduced in Section 1.3, the most important components for present purposes are the N170 and the EPN. Based on previous reports (see review by Dolcos et al., 2020) it was argued that both gaze and emotion are properties that provoke attention, giving rise to interactions at both early (N170) and late (EPN) stages. Thus, we focused on the time course of the N170 and EPN components.

The N170 amplitude was larger to averted than to direct gaze for the initial face presentation and larger to gaze changes from direct to averted than from averted to direct gaze. In line with previous findings, such as by Itier et al. (2007) for both initial gaze position and change gazes, by Latinus et al. (2015) for dynamic gaze changes, and by Stephani et al. (2020) for gaze-contingent stimulus presentations, N170 amplitude was larger when the eyes were looking away from the observers than when aiming at them. The N170 is interpreted as reflecting the structural encoding of faces (Eimer, 2000). Therefore, the increased N170 to averted (or averting) gaze may indicate additional neural activity required to structurally encode faces with non-canonical (i.e. averted) gaze directions. This holds for the initial gaze phase where all facial features, including expression and gaze direction appear all at once on the screen and have to be structurally encoded. But it would also hold for the gaze change phase, where all facial features, including the emotional expression, are already present on the screen and then just the gaze direction changes. Gaze direction changes in the gaze change phase elicited an astonishingly large N170, presumably due to the challenges to structurally encode the altered face configuration, which may be even more challenging when gaze averts rather than aims at the observer.

For the gaze change phase, we found significant main effects of gaze as well as hemisphere. Although the interaction of gaze and hemisphere did not reach significance, scalp topographies showed that a larger N170 for gaze aversion was observed in the right than in the left hemisphere. This resembles the findings of Latinus et al. (2015) in a social task and several other studies (for review see Eimer, 2011), which found a larger gaze effect in the right hemisphere.

Emotional expression modulated the N170 in the initial gaze phase, where angry and happy faces elicited a more negative-going amplitude compared to neutral faces. Similar effects on the N170 have been reported by Rellecke et al. (2011) who suggested that such effects may be due to overlap of the N170 with the onset of the subsequent and similarly distributed EPN. Alternatively, emotion effects on the N170 may be due to differences in structural encoding processes in emotional and non-emotional faces. With the same stimulus material as used here but with continuous presentation of faces displaying multiple successive gaze changes, a modestly enlarged N170 had been seen for angry faces (Stephani et al., 2020), which is at variance with the lack of such an effect in Study 1. This discrepancy may be due to the display mode or to a higher number of change trials in the experiment of Stephani et al (2020).

For the EPN component in response to the initial face presentation, we replicate classic effects of emotion, which did not interact with gaze direction. In the initial gaze phase, we observed the expected emotion effects in the EPN ROI and time windows. The emotion effects correspond to reports from many studies (e.g. Itier & Neath-Tavares, 2017; Rellecke et al., 2011; Schacht & Sommer, 2009b) and show the typical posterior negativity, especially for the expression of happiness. Interestingly, in this phase, the EPN with its occipito-temporal negativity appeared to be very long-lasting for happy expressions, covering even the 400-600 ms interval. As a major new finding, changes from direct to averted gaze elicited an EPN-like effect only when the face showed a happy expression. No such effect was seen for angry expressions. We conclude that happy faces reflexively attract attention when they look at the observer rather than away. These results for happy expressions are in line with the *shared signal hypothesis* of Adams and Kleck (2003) that posits a better processing of expressions if their approach or avoidance tendency is consistent with gaze direction. However, the *shared signal hypothesis* is not supported by the present results for angry faces.

2.2 Study 2: Influences of Autism Trait and Autism on Processing of Emotional Facial Expressions and Eye Gaze Perception (Bagherzadeh-Azbari et al. 2022b)

According to the *shared signal hypothesis* (Adams & Kleck., 2003) the impact of facial expressions on emotion processing partially depends on whether the gaze is directed towards or away from the observer. In autism spectrum disorder (ASD) several aspects of face processing have been found to be atypical, including attention to eye gaze and the identification of emotional expressions. However, there is little research on how gaze direction affects emotional expression processing in typically developing (TD) individuals and in those with ASD. Recently, the Research Domain Criteria (RDoC) approach advocates a shift from treating mental disorders as categories to examining the continuum of symptom severity and diversity, spanning the entire population (Insel et al., 2010; Cuthbert, 2015). In line with this approach, a growing body of studies has investigated autism-associated social, emotional and communicative traits in the population, involving a broad range of individuals within or outside the autism spectrum (Abu-Akel et al., 2019; Giambattista et al., 2021). In line with RDoC, adaptive and maladaptive traits need to be characterized from a multimodal perspective, involving neural correlates and behavioral manifestations. Therefore, describing behavioral and neural correlates and associations of facial expression processing and their interactions with gaze direction and how they relate with continuous autism traits and clinical manifestations may contribute to better understanding of autism at a mechanistic level. Toward these aims, we report two experiments investigating the interactions between facial expressions and gaze direction and their relationship to social, emotional and communicative impairments in children with different degrees of autistic trait expressions.

Experiment 1 required processing eye gaze direction while faces differed in emotional expressions. For each emotional expression, two gaze changes (from left or right averted to direct gaze and vice versa) and a condition without gaze change were created, with 20% non-change trials in total to prevent expectation effects. Half of all change-trials involved a gaze change from an averted to a direct gaze direction, whereas the other half was a change from direct to averted direction. Children's pictures of angry or neutral faces with or without gaze direction change were presented. After 1000 ms in most trials, the gaze direction changed from direct to averted or vice versa. After the disappearance of the second image, a blank screen was shown, during which participants should indicate by pressing a left or right button whether the gaze had changed or not. Forty-seven children (aged 9-12 years) participated. Their Autism Diagnostic Observation Schedule (ADOS) scores ranged from 0 to 6 in the experiment. ADOS-2 score was treated as a continuous variable, where a higher score indicates a higher level of autistic trait. Two distinct time windows (150–190 and 220–270 ms) were extracted from this broad window to make the N170 amplitude easier to observe and score within individuals.

The ERPs to the initial gaze phase (START interval) showed a significant effect of emotion on N170 amplitudes during the 220–270 ms interval. In the following gaze change interval (CHANGE interval), there was a main effect of gaze change on N170 amplitudes at the time window of 220–270 ms but emotion processing did not depend on gaze direction. However, for angry faces the gaze direction effect on the N170 amplitude, as typically observed in TD individuals, diminished with increasing ADOS score. Within the early interval (150–190 ms) of N170 in the gaze change phase, there was a significant correlation of ADOS and the individual gaze change effect for angry faces (ERPs in the direct to averted condition minus the averted to direct condition). The positive correlation indicated that participants with low ADOS scores tended to show the commonly observed larger N170 amplitudes to dynamic gaze changes from direct to averted than for averted to direct. As ADOS scores increased, the gaze effect on the N170 diminished, yielding a positive relationship for angry faces. For neutral expressions this correlation was not significant.

Experiment 2 required explicit emotion classifications in a facial emotion composite task while eye gaze was manipulated incidentally. Here, in addition to measuring classification accuracy, we tracked the eye gaze behavior of the participants. We used an emotional composite task (classification of facial emotions) where faces where presented that expressed different emotions in the upper and lower half but only one half was relevant for the classification. Each trial began with a fixation cross presented for 200 ms in the middle of the screen, followed by a composite face together with six color-framed labels for the six emotions and a prompt ("TOP" or "BOTTOM") placed above the composite face, cueing which face half was to be categorized. Emotion labels and the face remained on the screen until a decision was made about the displayed emotion by clicking one of the emotion labels with the mouse. In total, 72 experimental trials were presented in random order.

A group of 22 children with ASD was compared to a propensity score-matched group of 22 TD children (mean age = 13 years). The same comparison was carried out for an additional subgroup of nine children with ASD who were less trained in social cognition, according to the clinician's report. The ASD group performed overall worse in emotion recognition than the TD group, independent of type of emotion or gaze direction. However, for disgust expressions, eye tracking data revealed that TD children fixated relatively longer on the eyes of the stimulus face with a direct gaze as compared with averted gaze. In children with ASD we observed no such modulation of fixation behavior as a function of gaze direction.

Overall, the present findings from ERPs and eye tracking confirm the hypothesis of an impaired sensitivity to gaze direction in children with ASD or elevated autistic traits, at least for specific emotions. Therefore, we concluded that multimodal investigations of the interaction between emotional processing and stimulus gaze direction are promising to understand the characteristics of individuals differing along the autism trait dimension.

2.3 Study 3: Influences of Motherhood on Processing of Emotional Facial Expressions and Eye Gaze Perception (Baherzadeh-Azbari et al. in prep.)

The post-partum period in mothers has been suggested to be special for eye contact behavior and facial expression decoding; however, the neural correlates of motherhood in these signals are poorly understood. In the present study we recorded ERPs from 59 mothers of infants and 55 nulliparous women. The experimental task resembled Study 1 with some changes. Faces of adults and infants with happy, angry and neutral expressions were presented with direct or averted gaze. Each trial began with a fixation cross shown for 800 ms on a white screen. Then, the first image of a face appeared for 1000 ms, displaying one of three emotional expressions and either a direct, left- or right-averted gaze. The presentation of the first image was seamlessly followed by the second image for another 1000 ms. In 20

% of the trials, the second image was identical to the first one (no change). In the other 80 % of trials, the second image changed gaze direction but retained exactly the same emotional expression.

We replicated previous findings about gaze direction and emotion as in Study 1. Infant faces elicited larger N170 amplitudes and larger early posterior negativities (EPN) than adult faces, especially when they showed angry expressions. Both effects were more pronounced in mothers than nulliparae, and particularly so, when the angry infant face dynamically directed its gaze on a mother. For the N170 component of the ERP, we obtained larger responses to infants than adult face stimuli. In line with previous reports of increased neural responses to infant stimuli reviewed by Maupin et al. (2015) and Vuoriainen et al. (2022), this finding indicates increased neural activity required to structurally encode infant faces. Similarly, infant faces have been previously found to activate brain regions involved in face perception like fusiform gyrus as a likely generator of N170; these activities have been suggested to reflect the encoding of "baby schema" meaning facial features that are indicators of infant faces such as round face, big eyes etc. (Glocker et al., 2009; Luo et al., 2015). These features are typically perceived as cuter and more attractive, prompting a different response than to adult faces (e.g. Endendijk et al., 2018; Glocker et al., 2009; Lobmaier et al., 2010). Therefore, the increased response to infant faces during the early visual processing might reflect increased encoding of distinct infant facial features. Alternatively, the increased N170 to infant faces might reflect an increased difficulty of structural encoding or, more specifically, configural processing, as compared to adult faces, resembling the effects of face inversion, which frequently increase the N170.

In line with Weisman et al. (2012), who compared the responses to infant stimulus in mothers and non-mothers and found no effect in the N170 amplitude, the present increase of

N170 amplitude to infant faces was not significantly modulated by motherhood. Considering the relatively large sample size in our study, motherhood does not seem to modulate the structural encoding of faces – whether of adults or infants.

Altogether, Study 3 suggests that (1) mothers show an enhanced structural encoding of infant faces and (2) stronger reflexive attention to the emotions expressed in infant faces together with dynamic gaze movements. Hence, mothers can be characterized by greater sensitivity to emotional children faces at the level of structural face encoding and reflexive attention.

All in all, many results of Study 1 and Study 3 overlap. However, a few discrepant findings deserve to be discussed, as will be done in Section 3.1.

3. General Discussion

Depending on the gaze direction of a face, emotional expressions may differ in their significance for the observer. Thus, gaze and emotional properties of faces are essential for an effective social interaction. The present dissertation investigated the neurobiological correlates of the interplay between emotion and gaze and their variations in specific subgroups of the population. To this aim, ERPs were measured both during the initial presentation of a face and in response to a subsequent gaze change in a normal sample, in individuals with autism or high on the autistic trait, and in mothers of young infants.

Study 1 examined the time course of N170 and EPN as well-established ERP components indicating the gaze and emotion at the neural level within a nonsocial task. Our findings disentangled the effect of gaze on N170 and emotion effect on EPN. A substantial interaction between gaze and emotion was seen in response to the subsequent gaze change of the face despite the fact that the emotional expression of the face remained invariant during the change. Study 2 extended the investigation of the emotion and gaze interaction to the population of children with autism traits to take one step toward studying impaired sensitivity to eye gaze perception and its interplay with emotion. Although no interaction of emotion and gaze per se was observed, a correlation between autism severity and the gaze effect in the N170 amplitude elicited by angry faces, was found. This correlation indicated diminished gaze effects on N170 amplitude with increasing autism trait scores. Study 3 confirmed the interplay of emotion and gaze in the direction of gaze change -as observed in Study 1- in a large sample of mothers and nulliparae (N= 114). By adding age of the presented stimulus face as a new factor to the paradigm, in comparison to adult expressions, infant faces elicited a larger N170 and EPN amplitude, particularly when they exhibited an angry facial expression. Both effects were more noticeable in mothers than in nulliparae. This effect was especially true when the baby's angry face dynamically turned to look at the mother.

In the following I will first discuss the neural markers of emotion and gaze as reflected by the N170 and EPN and discuss similarities and discrepancies (section 3.1). In this section I will further focus on the interplay of emotion and gaze as reflected by the EPN. Thereafter, I will comment on differential effects of emotion and gaze interaction in autism trait and motherhood (section 3.2). Finally, I will outline a proposal about the interplay of emotion and gaze in face processing (section 3.3). Open questions and suggestions for further research are discussed along the way.

3.1 Neural Markers of Emotional Facial Expressions and Eye Gaze Perception

By analyzing ERPs in three studies, I examined the different stages of information processing in response to the short-lived and dynamic nature of eye gaze and emotional facial expressions. In particular, the excellent temporal resolution of ERPs allowed to test whether emotion and gaze interaction take place within the early structural processing of faces (as reflected in N170) or rather during later stages of face processing (as reflected in EPN), which involve the allocation of reflexive attention and the assignment of significance to a face. Importantly I evaluated both the initial gaze as well as changing gaze in one consistent paradigm (with the exception of Experiment 2 of Study 2).

In the gaze change phase, main effects of gaze for the N170 were obtained by all three studies. The N170 amplitude was consistently larger when the eyes turned the gaze away from the observers than when they were aiming at them. This is in line with earlier findings by Latinus et al. (2015) for dynamic gaze changes, and Stephani et al. (2020) for gaze-contingent stimulus presentations.

Consistent with the study by Itier et al. (2007), in Study 1, we also replicated the gaze effect on N170 for the initial gaze phase, when the task requires to structurally encode all facial features at once, including emotional expression and gaze direction. Therefore, the higher neural activity needed to structurally encode faces with non-canonical (i.e. averted) gaze direction is indicated by the increased N170 to averted (i.e. avoiding) gaze. However, no main effect of gaze was significant in the initial gaze phase in Studies 2 and 3. In Study 2, all children, showed a very large right-lateralized P1 to the onset of visual stimuli not only pushing N170 latency toward larger values, but also possibly obscuring or overlapping this component (see Batty et al., 2011 and Burra et al., 2018 for further discussion). Such evidence highlights the role of neurodevelopmental conditions such as autism on early modulations of electrophysiological markers as well as its impact at an early stage of visual processing, even prior to the N170 component. Considering the role of autism, de Jong et al. (2008) and Akechi et al. (2010) also found differences between ASD and TD groups at P1 and N170. They showed that in ASD individuals, integrating emotional facial expressions and gaze direction is impaired at the level of visual analysis which corresponds to the initial gaze phase in our study. In Study 3, also regardless of motherhood, the increased neural activity required to structurally encode infant faces could potentially explain the absence of gaze effect in the initial gaze phase. There is evidence for increased neural activity required to structurally encode infant faces (Maupin et al., 2015). Infant faces have features that are typically perceived as cute and attractive (such as round face, big eyes) and have been previously found to activate brain regions involved in face perception like fusiform gyrus, a likely generator of N170 (Vuoriainen et al., 2022). This evidence could reflect an increased difficulty of structural encoding or, more specifically configural processing, resembling the effects of face inversion, which can obscure this component (e.g. Endendijk et al., 2018; Glocker et al., 2009; Lobmaier et al., 2010). Thus the absence of a gaze effect on the N170 in initial gaze phase for Study 3, does not necessarily question the results of Study 1.

In all three studies, emotional expression modulated the N170 in the initial gaze phase, where angry and happy faces elicited a more negative-going amplitude compared to neutral faces. Similar effects on the N170 have been reported by Rellecke et al. (2011) who suggested that such effects may be due to overlap of the N170 with the onset of the subsequent and similarly distributed EPN. Alternatively, emotion effects on the N170 may be due to differences in structural encoding processes in emotional and non-emotional faces. Thus, one can argue that the emotion effect in the N170 is rather due to structural encoding processes, and emotion is evaluated semantically in later stages, such as the following EPN. In terms of structural encoding, this would mean that an emotional face is more difficult to analyze structurally than a neutral face.

Importantly, irrespective of the interpretation of the emotion effects on the N170 and together with prior research (Conty et al., 2012; Conty et al., 2007; Rigato & Farroni, 2013) summarized in section 1.3, there was no interaction of emotion and gaze on N170 and EPN despite their main effects in the initial gaze phase.

For the gaze change phase, we found significant main effects of gaze in all three studies with larger N170 amplitudes for direct to averted gaze changes than averted to direct gaze changes. Difficulties in structural encoding in averted gaze can be an explanation for this gaze effects in the N170. Another interpretation of the N170 gaze effects could be the spatial mode of the brain. This is in line with the ideas of Latinus et al. (2015) who suggested that there is a spatial and a social mode in the processing of stimuli and that the spatial one is the default mode. According to Latinus et al. (2015), the spatial mode should be relevant here fitting a higher amplitude of the N170 in averted gaze. Thus, besides structural encoding, the spatial mode of the brain, influenced by task effects, can be an explanation of N170 gaze effects. Regarding "spatial mode", Taylor et al. (2001) argue in favor of a dissociation between the processing of averted versus direct gaze by posing the questions "What is he looking at?" with a spatially motivated focus of attention or "Why is he looking at me?", with a self-referential locus of attention. In this respect, Latinus et al. (2015) state that the brain`s default mode is a spatial one and the social mode has to be triggered specifically. Thus, there may be several reasons for differences in N170 amplitude concerning gaze. These are essentially due to differences in task and stimuli.

As outlined in section 1.3, the EPN is robustly sensitive to emotional contents that reflexively catch the attention of the observer. These effects may occur for different qualities (valence) of emotional content and sometimes even for non-emotional factors such as large versus small non-emotional facial movements. In the initial gaze phase, we observed the expected emotion effects across all three studies. Here, the emotion effects correspond to reports from many studies (e.g. Itier & Neath-Tavares, 2017; Rellecke et al., 2011; Schacht & Sommer, 2009b). In Study 1, the posterior negativity was more present for the expression of happiness than anger while in Study 3 more pronounced for angry expression. It is possible that presenting different types of stimulus age (infants and adults) in Study 3, may have triggered the sensitivity to negative emotions. The effect directions of findings in mothers and nulliparae are discussed in the next sections (3.2 & 3.3).

The results were markedly different in the gaze change phase as compared to the initial phase in Studies 1 and 3. Here, the emotional expressions remained the same but gaze direction changed. Hence, as to be expected, in Study 1, there was no main effect of emotion in the EPN in the gaze change phase. However, in Study 3, we observed similar emotion effects in the EPN of the change phase as in the initial gaze phase. Given that in the change phase only the gaze moved but emotion remained constant, to find an EPN may seem to be counterintuitive. However, as discussed earlier, in the context of emotion effects in the N170, it may indicate the close relationship of gaze and emotional expression. Thus, in Study 3 the gaze change may have rekindled the emotional analysis of the – unchanged – facial expression; this analysis has been modulated by stimulus age in this paradigm (having different mixture of stimuli than Study 1) and by the presence of rather early effects of angry emotion.

Based on the findings of both Study 1 and Study 3, there were clear interactions of gaze and emotion in EPN on the gaze change phases. Closer inspection of Study 1 revealed an EPN-like posterior negativity but only when the gaze in happy faces changed from averted to directed at the observer. No other condition combination elicited a significant emotion effect. Thus, a gaze change in an invariantly (happy) facial expression can trigger an EPN. Notably and in contrast to Study 1, in Study 3, a three-way interaction of emotion and gaze and stimulus age was observed within the time window of 300-400 ms. EPN to angry infant faces was larger when gaze was directed toward the observer and it was larger to happy adult faces when the gaze was averted. This means, the emotion by gaze interaction results in Study 3 for the adult faces is opposite to the results from Study 1. Given that Study 3 had replicated many results of the Study 1 and involved a considerably higher number of participants, I consider it unlikely that the discrepancy of these particular results is due to a lack of power or otherwise faulty procedural details. Instead, I suggest that the discrepancy is due to using only adult faces in Study 1 and a randomized mixture of adult and infant faces with different emotional expressions in Study 3. This procedural difference may have induced different emotion by gaze interactions regarding the adult phases, corresponding to differential “range effects” in the repeated measures designs of studies 1 and 3 (Poulton, 1973).

3.2 Diminished and Enhanced Responses

Our starting point was that according to the *shared signal hypothesis* (Adams and Kleck, 2003), approach-related emotions, for example, happiness and anger, are more easily recognized when the observer is directly looked at. In contrast, avoidance-related emotions, such as sadness and disgust, are supposedly better recognized with averted gaze. We expected that these benefits would be less pronounced or even absent in children with ASD compared to TD children. Study 2 provided some further support of the SSH in its original form. In

Experiment 1, the facial emotion expression was implicit and the gaze direction was incidental to the task. Yet, we did not find an interaction between emotion and gaze in the ERPs. In Experiment 2, when participants were required to explicitly categorize emotion expressions, performance was indeed best when gaze was direct. This effect was most pronounced for smiles and anger, which are both considered approach-related emotions. However, the avoidance-related emotion, sadness, revealed a similar effect as anger, and disgust recognition was facilitated by direct compared to averted gaze, albeit with a relatively small effect. Although the whole pattern of effects revealed by the present data in TD children can not be fully explained by the SSH, we found some evidence that autistic trait is related to diminished sensitivity to gaze in the context of processing facial emotions. Although there was no interaction of gaze direction and emotion at the group level in Experiment 1, the gaze effect in the N170 amplitude elicited by angry faces correlated positively with the ADOS score. This correlation is broadly in line with the SSH, which assumes an interaction between eye gaze and emotion. Thus, when gaze direction (from direct to averted in our experiment) was combined with the intent communicated by a specific expression (anger in our study), the perceptual analysis of that emotion was enhanced. Therefore, the observed correlation between the N170 gaze effect in angry faces and its attenuation with increasing ADOS seems to fit the hypothesis: avoiding/averting gaze is a signal shared with the non-affiliative emotion of anger in neurotypical (low ADOS) individuals. Besides the loosening or reversal of this association at higher ADOS scores is in line with what one might expect for higher autistic trait expression. Hence, these data are consistent with the observation that in a naturalistic setup, in which dynamic emotional gaze cues require the integration of emotional information and gaze information, individuals with ASD differ from TD individuals in their responses to eye gaze in emotional faces.

In line with prior ERP literature (e.g. Maupin et al., 2015), ERP responses to infant face stimuli may provide useful information for assessing the parental neurocognitive system. In Study 3, we investigated motherhood ERP responses to infant's faces to elucidate whether infant faces in general and emotional infant face in particular elicit larger perceptual and attentional brain responses in mothers than in nulliparae.

The findings in this large sample study suggest that ERPs in the later (EPN) processing stage could be relevant indicators for assessing attentional-reflexes factors related to motherhood, since these responses were found to be consistently larger for infant faces and they were also associated with motherhood in the initial gaze phase. Moreover, our findings suggest that increased attentional allocation to infant distress may be an essential part of the parent-child interaction, as it allows the mother to prioritize relevant infant signals and subsequently react in a sensitive and appropriate way to resolve the source of distress. Attention to distress and sensitivity to negative emotion is important not only in the immediate moment of caregiving, but also in the formation of long-term mother-infant attachment and overall development of the infant. As an example, another study from our lab conducted with the same participants using a facial Stroop paradigm, has also suggested that especially in mothers, negative deliberate facial expressions like frowning when facing infants is offset by an automatic caregiving response (Recio et al., 2022).

3.3 The Interplay of Emotion and Gaze

Given the *shared-signal hypothesis*, which states that gaze can influence the processing of an emotional content (Adams & Kleck, 2003), I put an emphasis on the investigation of emotion and gaze interaction in all 3 studies mentioned in this dissertation with an aim to study the cognitive processes these interactions take place and what their specific electrophysiological pattern is.

In Study 1, we observed an interaction between facial expression and gaze direction, indicating stronger reflexive attention elicited by a happy face that is directing its gaze at the observer. Here one question is of special interest; Why did we not obtain an interaction of emotion and gaze direction in the initial gaze phase? Several previous studies have reported a superiority of dynamic changes over static presentation. Recio et al. (2014) have shown that the EPN is larger when facial expressions are dynamic compared to static presentation. Eye gaze effects have been also shown to be larger in gaze change phase with shifts of gaze (Latinus et al., 2015). Therefore, it is conceivable that in the gaze change phase, there was a stronger involvement of the dorsal visual system. Besides, in all three experiments, motion consisted of very similar eye movements in smile versus anger and in moving from averted to direct versus direct to averted. Therefore, based on the emotion and gaze interaction in Study 1, when a happy face turns its gaze towards the observer, stronger attention is reflexively elicited as compared to when gaze averts. This is in partial contrast with Klucharev and Sams (2004) who reported an ERP modulation around 300 ms to both happy and angry faces due to gaze direction. However, due to the absence of a neutral emotional condition, their study is hard to interpret in terms of the EPN component.

In line with the standard interpretation of the EPN (Schupp et al., 2006), its elicitation by a gaze change of a smiling face towards the observer might indicate that such an event triggers reflexive attention towards the face. A gaze change away from the observer does not trigger a comparable EPN. Therefore, the direct gaze at the observer might act as a social cue for the self-relevance of the face. This idea matches with the *shared-signal hypothesis* which states that gaze can influence the processing of an emotional content (Adams & Kleck, 2003).

Based on the emotion and gaze interaction in Study 3, averted-to-direct gaze shifts in angry infant face stimuli elicited larger EPN amplitudes in comparison to adult faces. Thus, a gaze change in an invariant (angry) facial expression of infant faces can trigger an EPN, that is, reflexive attention. Therefore, it seems that when an angry infant face turns its gaze towards the observer, stronger attention is reflexively elicited as compared to when gaze is averted or when the stimulus is an adult face. The presence of the infant faces that strongly attract attention, especially when displaying negative emotions may have provided a very different context for the adult faces compared to Study 1 where only adult faces were shown (Poulton, 1973).

However as explained before, because of impaired integration of emotion and gaze in autism at the level of visual analysis no interaction was obtained in Study 2. Here, the existence of impairments in emotional and gaze processing has implications for the understanding of the relationship between emotional and social deficits in ASD.

Notably, the emotion and gaze interactions obtained in Study 1 and Study 3 clearly indicate that the gaze effect in terms of gaze change can elicit an emotional re-evaluation of facial stimuli. Importantly, irrespective of the interpretation of the emotion effects on the N170, for present purposes it is relevant that despite main effects of both gaze direction as well as emotional expression on the N170 in the initial gaze phase and gaze change phase, these factors did not interact. This is in line with findings by Klucharev and Sams (2004). Hence, in the time range of the N170, both emotion and gaze seem to be processed independently and (possibly) in parallel. The interaction in the late time window factor (EPN) means that the connection on gaze and emotion only elicits reflexive attention in the later stages as reflected by the EPN component.

In conclusion my studies would be fruitful to identify the neural mechanisms underlying gaze processing, and its impact on social interaction and communication as well as the physiological status like motherhood and neurodevelopmental conditions as autism affecting these domains. Understanding gaze direction processing effects has a wide implication for social and cognitive neuroscience, in which gaze-related ERPs have a potential to be used as an endophenotype of clinical symptoms or diagnosis of atypical social development (e.g. Elsabbagh et al., 2012).

4. Limitations and Future Outlook

Though the present studies extended our knowledge about interactions of gaze and emotions and its variation across the population, there were some limitations which are mentioned in this section and solutions are suggested for improvements in following studies.

In Study 1, we included a gaze change but not an emotion change between picture one and two. Although we consider our findings as relevant steps towards investigating everyday social interactions, one important next step would be to implement a paradigm in which dynamic eye gaze changes are combined with dynamic facial expressions to take one further step toward more natural and mutual human interactions. Following up on the contrast between the eye gaze interaction on the EPN to smiling faces but its absence to other expressions, it would also be very interesting to investigate the interaction for other emotions, especially fear.

As findings of Study 2 indicate the diminished sensitivity in processing gaze direction in emotional faces, it would be promising to increase the spectrum of emotions investigated while combining eye tracking in unrestrained viewing conditions in stimuli with varying gaze behavior. Recent methodological advances, such as the co-registration of EEG and eye movements (Dimigen et al., 2011) and the employment of dynamic stimuli in gaze-contingent display situations (Stephani et al., 2020) already make such an approach feasible.

In Study 3, associations are derived from the repeated measure observations and may not be reliable indicators of causal effects and for causal inferences about motherhood. Pre and post motherhood (longitudinal) data and covariates that might trigger the effects should be investigated. In addition, the presence of the infant faces that strongly attract attention, especially when displaying negative emotions may have provided a very different context for the adult faces as compared to the Study 1 where adult faces were the only ones. Future research using e.g. blocked presentation - a condition is presented continuously for an extended time interval (block) to maintain cognitive engagement, - of adult and infant faces may assess this suggestion.

5. Conclusions

The present dissertation helped to elucidate the electrophysiological correlates of the interplay between eye contact and emotion, both during the initial presentation of a face and in response to a subsequent gaze change. (1) I showed the consistency of N170 findings for perceiving gaze direction in a nonsocial task. (2) Not only the replication of emotion effect on the EPN but also the effect of gaze direction on EPN was observed. (3) The interaction of gaze and emotion only elicits reflexive attention in the later stage (EPN) and in dynamic gaze change conditions. (4) Autistic trait is related to diminished sensitivity to gaze in the context of processing facial emotions. (5) Infant faces pose higher demands on structural face encoding than adult faces (6) mothers show greater sensitivity to emotional children faces at the level of structural face encoding and reflexive attention.

In conclusion, the integrated results from different studies in my dissertation demonstrate an interaction between facial expression and gaze direction, indicating stronger reflexive attention elicited by an emotional face that is either directing or averting its gaze based on the observed context. The perception and processing of facial expression and gaze direction strongly depends on experience and is highly context specific. Context involves the interdependency of stimuli age, emotional expression and gaze direction, and it includes aspects of the expressor, the observer and the neurodevelopmental condition.

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Eidesstattliche Erklärung

Hiermit erkläre ich an Eides statt,

1. dass ich die vorliegende Arbeit selbständig und ohne unerlaubte Hilfe verfasst habe,

2. dass ich mich nicht anderwärts um einen Doktorgrad beworben habe und noch keinen Doktorgrad der Psychologie besitze,

3. dass mir die zugrunde liegende Promotionsordnung vom 3. August 2006 bekannt ist.

Berlin, den 11. November, 2022
Shadi Bagherzadeh Azbari

Original Articles

I.

Bagherzadeh-Azbari, S., Lion, C. J., Stephani, T., Dimigen, O., & Sommer, W. (2022). The impact of emotional facial expressions on reflexive attention depends on the aim of dynamic gaze changes: An ERP Study. *Psychophysiology*, e14202. https://doi.org/10.1111/psyp.14202

II.

Bagherzadeh-Azbari, S., Lau, G. K. B., Ouyang, G., Zhou, C., Hildebrandt, A., Sommer, W., & Lui, M. (2022). Multimodal Evidence of Atypical Processing of Eye Gaze and Facial Emotion in Children with Autistic Traits. *Frontiers in Human Neuroscience,* 16, 733852. https://doi.org/10.3389/fnhum.2022.733852

III.

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ORIGINAL ARTICLE

The impact of emotional facial expressions on reflexive attention depends on the aim of dynamic gaze changes: An ERP study

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Abstract

The emotional expression and gaze direction of a face are important cues for human social interactions. However, the interplay of these factors and their neural correlates are only partially understood. In the current study, we investigated ERP correlates of gaze and emotion processing following the initial presentation of faces with different emotional expressions (happy, neutral, angry) and an averted or direct gaze direction as well as following a subsequent change in gaze direction that occurred in half of the trials. We focused on the time course and scalp topography of the N170 and EPN components. The N170 amplitude was larger to averted than direct gaze for the initial face presentation and larger to gaze changes from direct to averted than from averted to direct in response to the gaze change. For the EPN component in response to the initial face presentation, we replicate classic effects of emotion, which did not interact with gaze direction. As a major new finding, changes from direct to averted gaze elicited an EPN-like effect when the face showed a happy expression. No such effect was seen for angry expressions. We conclude that happy faces reflexively attract attention when they look at the observer rather than away from the observer. These results for happy expressions are in line with the shared signal hypothesis that posits a better processing of expressions if their approach or avoidance tendency is consistent with gaze direction. However, the shared signal hypothesis is not supported by the present results for angry faces.

KEYWORDS

emotion processing, EPN, face recognition, gaze direction, N170, scalp topography

1 | INTRODUCTION

Anger in the face of a person has a very different significance if targeted at the observer or somewhere else, indicated by what the angry person is looking at. The same holds true for facial expressions of other emotions, such as happiness, fear, or disgust. A direct gaze at an observer is a strong cue delivering different messages to a communication partner depending on the facial expression and social context, whereas averted gaze can indicate dis-attending the communication partner or attending at something in the peripheral space. Both, the production and perception of emotional expressions, as well as the direction of gaze and its perception have been widely studied (McCrackin & Itier, 2019; Adams & Kleck, 2003, 2005; Sander et al., 2007). However, how gaze direction interacts with emotional expression, amplifying or attenuating its effect during face perception, has found much less attention and is the focus of the present study.

A theoretical basis for understanding interactions between gaze and emotion is provided by the shared signal hypothesis of Adams and Kleck (2003). This hypothesis takes a motivational approach-avoidance stance and states that emotion perception is enhanced when gaze direction matches the expression of the face in terms of implied approach or avoidance. Specifically, the processing of emotional expressions that are related to approach (e.g., joy, anger) is facilitated by direct gaze, whereas expressions related to avoidance (fear, sadness) are facilitated by averted gaze. Hence, according to Adams and Kleck (2003), matching gaze direction enhances perceptual processing of emotional expressions.

In response to perception of eye gaze, the components of the human social brain network such as superior temporal sulcus (STS) and amygdala are activated (for review see Adolphs, 2009). In their affective arousal model, Senju and Johnson (2009) suggested that relative to averted gaze emotional arousal increases in response to direct gaze because it signals the intention to communicate. This is consistent with the self-referential impression that the awareness of being looked at is associated with physiological arousal. Senju and Johnson (2009) argue that particularly the amygdala plays a central role in mediating the affective arousal response and attentional allocation to direct gaze.

Conversely, some studies have investigated whether emotional facial expressions influence the interpretation of gaze direction. Lobmaier et al. (2008) reported that participants most strongly believed to be directly gazed at by faces with happy expressions, followed by angry and fearful expressions and least when the face was neutral. These findings were discussed within the approach-avoidance stance of the shared signal hypothesis (Adams & Kleck, 2003) and in terms of a self-referential positivity bias, that is, observers more likely judge happy faces to be as looking at them than angry or neutral faces (Lobmaier et al., 2008). In addition, Ewbank et al., 2009 also reported that angry faces were perceived as looking at the observers more directly than fearful or neutral faces. Thus, faces with angry or happy expressions are more likely to be categorized as looking at the observer.

To the best of our knowledge, previous behavioral studies on the modulation of cognitive processing following the perception of eye gaze have not directly addressed the interaction between eye gaze and emotional facial expressions. Therefore, the present study investigated the interplay of gaze direction with the emotional expressions by measuring event-related brain potentials (ERPs) as will be explained next.

1.1 | Electrophysiological correlates of eye gaze

One of the most useful methods to study the processing of short-lived and dynamic events such as eye gaze and emotional expressions are ERPs derived from the EEG. The most important components for present purposes are the N170 and the EPN. The N170 is an occipito-temporal negativity peaking around 170 ms after stimulus onset that, as compared to other objects, is greatly enhanced and typically lateralized to the right hemisphere for face stimuli (Eimer, 2011). Commonly, the N170 is interpreted to reflect the structural encoding of faces or other objects and is increased by attention directed at the stimuli, for example, when participants respond to faces rather than non-face targets (Eimer, 2000).

Larger amplitudes for N170 have been found in a number of studies in response to faces with averted gaze as compared to direct gaze, that is, when eyes appear to look directly at the participant (Caruana et al., 2014; Itier et al., 2007; Latinus et al., 2015; Puce et al., 2000; Rossi et al., 2015). Yet, there are also reports of larger N170 amplitudes for direct as compared to averted gaze (Conty et al., 2007, 2012; Watanabe et al., 2006), and several studies found no modulation of the N170 by gaze direction (Brefczynski-Lewis et al., 2011; Myllyneva & Hietanen, 2015; Ponkanen et al., 2011; Schweinberger et al., 2007; Taylor et al., 2001). Some of these inconsistencies may be explained by the properties of the task (Latinus et al., 2015). As suggested by Latinus et al. (2015), social tasks, in which the participant indicates whether or not the face makes eye contact, may attenuate gaze effects on the N170 in contrast to emotional tasks, where expressions are classified for emotion, or spatial tasks, when gaze direction has to be judged. In addition to task requirements, also head orientation, gaze deviations, and static versus dynamic gaze have been discussed as causing inconsistencies in the gaze perception literature (Conty et al., 2007; Itier et al., 2007; Puce et al., 2000, for a recent review see Tautvydaitė et al., 2022).

1.2 | Electrophysiological correlates of perceiving facial expressions

There are many ERP studies examining the processing of emotions (Kissler et al., 2009; Schacht & Sommer, 2009a; Schupp et al., 2004). The most prominent emotion-sensitive ERP components are the early posterior negativity (EPN) and the following late positive complex (LPC). Both components occur for emotional relative to neutral stimuli in different domains, for example, faces and words (Schacht & Sommer, 2009b). The LPC consists in an increased parietal positivity around 350–500 ms poststimulus in response to emotional relative to neutral stimuli and is observed mainly when stimulus emotion is task-relevant rather than implicit (Rellecke et al., 2011); therefore, the LPC has been linked to motivated attention to the stimuli (Schupp et al., 2006). Because in the present study, emotion facial expressions were not task-relevant, we did not expect effects on the LPC, in line with, for example, Rellecke et al. (2011) and Schacht and Sommer (2009a). Therefore, we assessed effects on the LPC only on an explorative basis with the results provided in Figure S5.

The EPN component appears at occipito-temporal scalp sites and, if elicited by facial expressions, can start as early as around 150 ms (Rellecke et al., 2011) reaching its maximum around 260–280 ms after stimulus onset (Schupp et al., 2006), whereas to words and emotional pictures, EPN latency is usually longer (Bayer & Schacht, 2014; Schacht & Sommer, 2009a; for review see Schindler & Bublatzky, 2020). Some studies indicate a larger negativity for emotional, especially happy faces than fearful and neutral ones (Holmes et al., 2009). EPN amplitude to facial expressions increases with the intensity of the emotional expression (Recio et al., 2014), but has also been observed for non-emotional facial movements, such as jaw movements versus eye blinks (Recio et al., 2014). This is in line with the suggestion of Schupp et al. (2006) that the EPN indicates the reflexive attention elicited by a stimulus. In most studies, affective stimuli are used to elicit the EPN, but according to the findings of Recio et al. (2014), this can also be the case for (attention catching) non-affective visual stimuli.

It should be noted that there is also evidence for early effects of emotional expressions in the time range of the N170 (Hinojosa et al., 2015; Rellecke et al., 2011; Stephani et al., 2020) although some of these effects might be due to overlap by early onset EPN and not to modulations of the N170 component itself (Rellecke et al., 2013).

1.3 | Interplay of gaze and emotion in ERP studies

First evidence for a possible interaction between gaze and emotional expression was reported by Klucharev and Sams (2004), who presented static pictures of angry and happy faces with different gaze directions and reported a modulation of the ERPs between 300 and 330 ms after stimulus onset to both happy and angry faces due to the face's gaze direction (Klucharev & Sams, 2004). The results led the authors to suggest that angry expressions directed at an individual are rapidly detected. Specifically, the authors proposed that gaze direction and emotion are processed independently before 270 ms but interact thereafter. In addition, Rigato et al. (2010) found an interaction between gaze and emotion on the latency of the face-sensitive occipito-temporal P2 component. In contrast with the shared signal hypothesis by Adams and Kleck (2003)—suggesting an association between averted gaze and fearful expressions—the P2 was smaller for fearful faces with direct gaze than for both fearful faces with averted gaze and happy faces with direct gaze (Rigato et al., 2010). Moreover, in a complex study, Conty et al. (2012) manipulated gaze direction together with head and body posture, emotional expression (neutral vs. anger), and presence or absence of hand pointing. The P2 was larger to angry than to neutral expressions and—independently—larger to direct than to averted gaze; emotion and gaze interacted after 200 ms. However, in this study, gaze was not studied in isolation but confounded with head and body orientation and there was only one emotion included.

As a conclusion from previous studies (Conty et al., 2007, 2012; Rigato & Farroni, 2013) it seems that interactions of gaze and emotions emerge only after the N170 component, that is, after the structural encoding of facial features. Otherwise, it is hard to discern a consistent picture from these studies. Because existing studies are heterogenous in terms of the stimulus material (isolated and static gaze or in combination with other properties) and with the regard to the inclusion of neutral faces as a reference condition, it remains unclear for which components or cognitive processes these interactions take place and what their specific electrophysiological pattern is.

1.4 | Aims and hypotheses

In the present study, we aimed to clarify the interactions between perceiving emotional facial expressions and gaze direction by both the initial gaze presentation and gaze change phases in the same paradigm. Specifically, we addressed whether the perception of gaze and emotional facial expressions are dissociated or interactive, and whether any interactions can be functionally localized at the early stages of structural face encoding, as indicated by the N170 component or at later stages, as indicated by the EPN. Based on previous reports (see review by Dolcos et al., 2020) it might be argued that both gaze and emotion are properties that provoke attention (Dolcos et al., 2020), giving rise to interactions at both early (N170) and late (EPN) stages. However, if different lead-in processes are involved in gaze and emotion, they might interact only at later stages of processing.

Specifically, we addressed the following questions; Firstly, we wanted to replicate the N170 findings for gaze direction in a nonsocial task. Furthermore, we tried to expand on the findings of later components for gaze direction effects. In terms of emotion effects, we expected to replicate the standard emotion effects on the EPN. Most importantly, we aimed to assess whether emotional expression and gaze direction would produce additive effects or whether they would interact at certain processing stages as reflected in the different ERP components. Finally, we were interested in the differences between presenting emotional expression and gaze direction together at stimulus onset as compared to a phase where the gaze change happens in a face that already shows an existent emotional expression.

In order to address these questions, we presented faces that displayed a happy, angry, or neutral expressions in combination with direct or averted gaze directions (see Figure 1). After 1 s, in half of the trials, the gaze direction changed, while the emotional expression always remained the same. This design allows an analysis of ERPs both relative to the initial presentation of the face (in the following termed *initial gaze phase*) and also relative to the subsequent gaze change (*gaze change phase*). Important to mention, we chose a simple non-social task in which participants simply had to detect whether the gaze had changed direction during the trial or not.

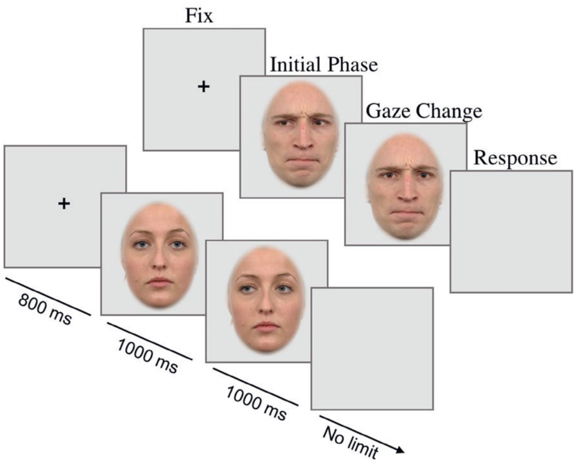

FIGURE 1 Trial structure, illustrated with two examples. A fixation cross (fix) was presented for 800 ms, followed by a first face image (initial gaze phase) for 1000 ms, and a second image (gaze change phase) for another 1000 ms. the second image involved a gaze change in 50% of the trials (as shown here). It was followed by a blank screen interval during which the participants indicated by a button press whether a change had occurred or not (response).

1.4.1 | N170

For the N170, we expected a larger amplitude for averted relative to direct gaze in both initial gaze and gaze change phases; based on Itier et al. (2007) who observed larger N170 amplitudes for averted gaze in static images and the studies by Latinus et al. (2015) and Puce et al. (2000) who found the same effect in changing gaze. In a previous study using our change detection task, we observed larger N170 amplitudes in response to averting gaze than to gaze that turns toward observer (Stephani et al., 2020). Based on Eimer (2011), we expected larger N170 amplitude in the right hemisphere than left hemisphere.

In terms of emotion effects, we expected larger N170 amplitudes for emotional faces, relative to neutral faces in the initial gaze phase than the gaze change phase. We base this assumption on Rellecke et al. (2011) who reported such early emotion effects with static face presentations and similar effects were also reported by Conty et al. (2012).

Along with the findings of Klucharev and Sams (2004) which were taken to indicate an independent processing of gaze effects and emotion effects before 200 ms, we expected additivity of gaze and emotion effects if both are present in the initial gaze phase. On the other hand, the N170 is sensitive to both structural properties of faces (Eimer, 2011) and, at least in some studies, to emotional expressions (Rellecke et al., 2013; Stephani et al., 2020). If the sensitivity of the N170 to facial expression reflects sensitivity to structural face properties, one should expect an interaction of gaze direction and expression. However, if the emotion effects on the N170 are related to an overlap with the early EPN component, it is a different process from structural analysis and should therefore be independent from and additive with gaze effects.

In the gaze change phase, only the gaze direction changed, which should elicit an N170. However, it remains unclear whether a gaze change in an otherwise immobile emotional face would also trigger a renewed emotion effect in the N170, that is, whether the N170 triggered by a gaze change would depend on the (static) emotional expression of the face. This might be the case if gaze change is integrated differently into static faces with different emotional expressions. Such a finding would represent strong evidence for an interaction, in fact interdependence, of emotion perception and gaze changes.

1.4.2 | EPN

In the time window of the EPN, in the initial gaze phase, we expected the classic EPN finding, that is, more negative amplitudes for happy and angry faces relative to neutral expressions (e.g., Schacht & Sommer, 2009a). For gaze effects on the EPN in the initial gaze phase, we expected a larger (i.e., more negative) amplitude for averted as compared to direct initial gaze (e.g., Caruana et al., 2014). We expected a similar effect also for gaze change phase (when comparing gaze aversion relative to directing gaze) based on the findings of Latinus et al. (2015) for the time range up to 260 ms. For the gaze change phase, changes in faces showing different emotional expressions, we did not expect an EPN as a main effect, because the expression was invariant during this time. To contrast the differential predictions arising from previous empirical research on the EPN (Klucharev & Sams, 2004) on the one hand, and the shared signal hypothesis (Adam & Kleck, 2003) on the other—suggesting a larger EPN for directing gaze than for gaze aversion for both anger and happiness emotions (as both are considered approach-oriented emotions and so are usually accompanied by a direct gaze). We aimed at defining the specific locus of interaction between gaze and emotion Adams and Kleck (2003). It was therefore crucial to study the locus of this interaction in our experiment. In other words, modulation of these components by emotion and direction of the gaze and their interaction in early and late ERP components could reflect how information is being integrated into the cognitive assessment of the face stimuli.

2 | MATERIALS AND METHOD

2.1 | Participants

Twenty German-speaking students[1] took part in the experiment. Participants provided written informed consent as approved by the institutional ethics review board of the Department of Psychology of the Humboldt-University at Berlin and received monetary remuneration or course credits. The mean age of the sample was 24.40 years (*SD* = 6.02, Range [18;44]), and 60% of the participants were female. All participants, but one, were right-handed (*M* = +91.40, *SD* = 24.57), as assessed by the German version of the Edinburgh Handedness Inventory (Oldfield, 1971).

[1]A power analysis conducted in G*Power (Faul et al., 2009) using the N170 effect sizes from Stephani et al. (Stephani et al., 2020), a power of 0.80 and alpha = 0.05 indicated that 20 participants would provide sufficient power for a two-tailed test.

2.2 | Materials

Face stimuli were extracted from the Radboud Database (Langner et al., 2010) and edited with Adobe Photoshop (version CC 2015, Adobe Systems, San Jose, CA). A total of 36 face identities (18 female, 18 male) were selected from the frontal-view pictures database with three different expressions (neutral, angry, and happy) and with either a direct or an averted gaze (averted to the left or right). All images were edited such that the eyes were always located at the same horizontal and vertical positions within the picture. Furthermore, all external features of the face (such as the hair, neck, or visible clothing) were removed. Because gaze motion was created from static images by presenting two images with different gaze direction sequentially (see Figure 1), we wanted to ensure that only eye gaze (but no other facial feature) would change between the subsequently and seamlessly presented pictures with different gaze directions. Therefore, we edited the stimuli as follows: For each individual and for each emotional expression of that individual, the eye region of the picture with an averted gaze was copied and carefully pasted into the eye region of the corresponding picture with direct gaze using Photoshop (see Figure 1 for an example). Thus, for each identity and emotion, we had images showing an averted gaze (to the left or right) or a direct gaze (looking at the observer).

2.3 | Procedure

Before the experiment proper, during a 7-min session, we collected prototypical eye-movement and blink artifacts from each participant that were later used in the ocular artifact correction procedure. Afterward, 12 practice trials were administered to familiarize the participants with the trial structure and task demands of the actual experiment. The experiment was implemented using *Presentation* software (version 18.10, Neurobehavioral Systems Inc, Albany, CA) and consisted of a total of 864 trials, which were presented in a random order, with a short break after every 108 trials.

As shown in Figure 1, each trial began with a fixation cross on a white screen shown for 800 ms. Then, the first image of a face appeared for 1000 ms, showing one of three emotional expressions and either a direct gaze or an averted gaze. The presentation of the first image was seamlessly followed by the second image for another 1000 ms. In 50% of the trials, the second image was identical to the first one (no change). In the other half of trials, the same facial identity and emotional expression were shown but with a different gaze direction. In other words, in these trials, the person's gaze direction changed. In the following we will distinguish between the *initial gaze phase*, lasting from the onset of face presentation until the onset of the *gaze change phase*. In the initial gaze phase, happy, neutral, and angry expressions appeared equally often and were orthogonally combined with direct, left, and right averted gaze. The probabilities of gaze change to any of the other gaze directions at the onset of the gaze change phase were the same, except that no changes from an averted position to another averted position occurred.

The second face image was followed by a blank screen, during which participants should indicate by button presses with their left or right hand whether or not a gaze change had occurred during the trial. Participants were told to focus on response accuracy. In case of a premature or incorrect response, feedback was given via a written statement in red ("Fehler," *error*) for 500 ms. After the button-press, the next trial began, starting again with the fixation cross. Participants were instructed to sit calmly, to fixate the fixation cross while visible, and to avoid blinking their eyes during the presentation of the faces. Instead, they were encouraged to blink at the end of the trial, after the offset of the second image.

2.4 | Data acquisition

Participants were seated in an electrically and acoustically shielded recording chamber. The EEG was recorded from 47 Ag/AgCl electrodes using a BrainAmp DC amplifier (BrainProducts GmbH, Gilching, Germany). Most electrodes were placed inside an elastic electrode cap (Easycap, Herrsching, Germany) at standard positions of the International 10–10 System. Four electrodes were placed at the outer canthus and infraorbital ridge of each eye to record the electrooculogram. An additional electrode at position FCz was used as ground. Electrode impedances were kept below 10 kΩ. Data were recorded with respect to the left mastoid and digitized at a sampling rate of 500 Hz and with an amplitude resolution of 0.1 μV. During recording, the data were high-pass filtered at 0.1 Hz and low-pass filtered at 250 Hz.

Stimuli were presented on a 22-inch CRT monitor (IIyama Vision Master Pro 512, vertical refresh: 160 Hz, resolution: 1024 × 768 pixel). The face stimuli subtended 7.07 (vertically) × 9.41° (horizontally) of visual angle (or 280 × 210 pixel) and were presented in the center of the screen using Presentation Software (Neurobehavioral Systems, Berkely, USA). In order to control for the fixation on the eye region and objectively detect blinks in the data, the participants' eye movements were simultaneously recorded at a rate of 500 Hz with an IView X Hi-Speed eye tracker (Sensomotoric Systems GmbH, Teltow, Germany). Analysis of the eye tracking data indicated that participants tended to make small saccades toward the eye region of the presented faces, as one would expect in a gaze change detection task, in which the eyes are task-relevant. Note that the ocular EEG artifacts generated by these small saccades were effectively removed by our ocular correction algorithm (described further below). No additional analyses of the eye tracking data are presented here, as fall outside of the scope of the present paper.

2.5 | Data analysis

2.5.1 | Response accuracy

Behavioral response data, collected by the Presentation software, were imported for analysis into the R Software for Statistical Computing (Version 3.2.2). Mean accuracy was calculated for each participant and condition and analyzed descriptively. Because the task was unspeeded, response times were not analyzed.

Overall response accuracy in the change detection task was high with a mean of 97.81% (SD = 0.02) correct responses. No participant gave less than 92.82% correct responses. Accuracy was statistically tested with a repeated-measures ANOVA with factors gaze and emotion; there was a significant effect of gaze, $F(1,20) = 6.32$, $p = .005$, $\eta^2 = 0.057$, with averted to direct gaze being less accurately recognized than direct to averted gaze and the no gaze change condition (see Table 1 for full statistical details).

2.5.2 | EEG data preprocessing

EEG data preprocessing was performed in MATLAB R2019a (The MathWorks Inc., Natick, MA) and EEGLAB v14.1.1b (Delorme & Makeig, 2004). In a first step, the EEG data were high- and low-pass filtered at passband edges of 0.03 and 30 Hz, respectively, using EEGLAB's windowed sinc FIR filter (pop_eegfiltnew.m) with default transition bandwidth settings. Afterward, the data were digitally re-referenced to an average reference.

TABLE 1 Mean (*SD*) accuracy of gaze change detection performance per condition

Gaze	Emotion: Neutral	Angry	Happy
Averted to direct	0.96 (0.13)	0.97 (0.11)	0.96 (0.13)
Direct to averted	0.98 (0.13)	0.97 (0.13)	0.98 (0.12)
No change	0.98 (0.11)	0.98 (0.11)	0.98 (0.09)

Eye movement and blink artifacts were corrected using the surrogate variant of the Multiple Source Eye Correction procedure (MSEC; Berg & Scherg, 1994; Ille et al., 2002) as implemented in the software BESA (version 6.0, BESA GmbH, Gräfeling, Germany). The procedure followed for the MSEC correction followed the steps outlined in the Supplementary Materials of Dimigen (2020).

Following ocular correction, the continuous EEG was then segmented into 1.4 s epochs (lasting from −0.2 s to 1.2 s relative to the time-locking event). For the initial gaze phase, the time-locking event was the onset of the face stimulus; a total of 864 epochs per participant resulted from 144 epochs per combination of gaze direction (averted, direct) and emotion (happy, angry, neutral). For the gaze change phase, the time-locking event was the gaze change (taking place in 50% of all trials), yielding a total of 432 epochs per participant, or 72 epochs for each of the six combinations of gaze change direction (averted to direct, direct to averted) and emotion.

All epochs were baseline-corrected using a 100 ms pre-stimulus baseline interval. To exclude epochs with remaining non-ocular artifacts (e.g., drifts or EMG bursts), we then removed all epochs which contained voltages exceeding ±80 μV in any of the channels. On average, 82.7% of all epochs (M = 1072.3 per participant, SD = 145.5) remained for analysis.

As a last step, an average ERP was calculated for each participant both for the initial eye gaze phase (aligned to face-stimulus onsets) and the gaze change phase (aligned to the onset of gaze changes). In both phases, ERPs were averaged according to the factors emotion (happy, neutral, angry) and gaze direction; for the initial gaze phase the latter factor distinguished direct gaze and averted gaze (averaging left- and right-averted conditions) and for the gaze change phase it distinguished between the *averted to direct* condition (i.e., averaged over both changes from left- or right-averted to direct) and the *direct to averted* condition (i.e., averaged over both changes from direct to left- or right-averted).

2.5.3 | Component peak detection (N170 and EPN)

The N170 component was quantified using an occipito-temporal region of interest (ROI) consisting of four electrodes, separated into two bilateral electrode pairs: P7/PO7 (left hemisphere) and P8/PO8 (right hemisphere), allowing to assess hemispheric differences. These electrodes have been frequently used in previous studies of emotion and gaze effects on the N170 component (Conty et al., 2007; Latinus et al., 2015; Rellecke et al., 2011; Stephani et al., 2020). To estimate the peak of the N170 component, we searched for the minimum (most negative) voltage in a time window from 150 to 200 ms after stimulus onset (face onset or gaze change onset) in the subject-level ERP averages for each condition. The minimal amplitude in this time range was then defined as the N170 peak amplitude. The N170 latencies were not included in the analysis.

For the EPN component, the ROI comprised the following 10 electrodes: P7 / P8, PO9 / PO10, PO7 / PO8, O1 / O2, Oz, and Iz, as previously used, for example, by Rellecke et al. (2011) and Bublatzky et al. (2017). The mean EPN amplitude was quantified by averaging across the voltages of four time windows after stimulus onset (200–250 ms, 250–300 ms, 300–350 ms, 350–400 ms, and 400–600 ms), separately for the initial gaze and the gaze change phases.

Since the EPN may last up to 600 ms (Rellecke et al., 2011), we considered it appropriate to analyze a wider time window than in the classic studies (e.g., Schupp et al., 2006). Therefore, we analyzed four 50-ms intervals, starting from 200 ms (providing high time resolution) in the interval from 400 to 600 ms.

2.6 | Statistical analysis

Statistical analyses of ERP peak amplitudes and accuracy data were performed in R Software for Statistical Computing (version 3.5.3, R Core Team, 2018) using the "ez" package (version 4.4-0, Lawrence, 2016).

2.6.1 | Event-related potentials

Repeated measures analyses of variance (ANOVA) were performed on ERP amplitudes on the within-subject factors emotion (happy, angry, neutral) and gaze direction. In the ANOVAs for the initial gaze phase the levels for factor gaze direction were direct versus averted; in the gaze change phase the levels were direct to averted versus averted to direct (i.e., we averaged over left and right gaze in the averted conditions). For the EPN component, from 200 to 400 ms, we included an additional factor time window (200–250, 250–300, 300–350, 350–400 ms), in order to assess any changes in the emotion effect during this time range.

Based on the previously mentioned hypothesis, hemisphere (left vs. right) was included as an additional factor

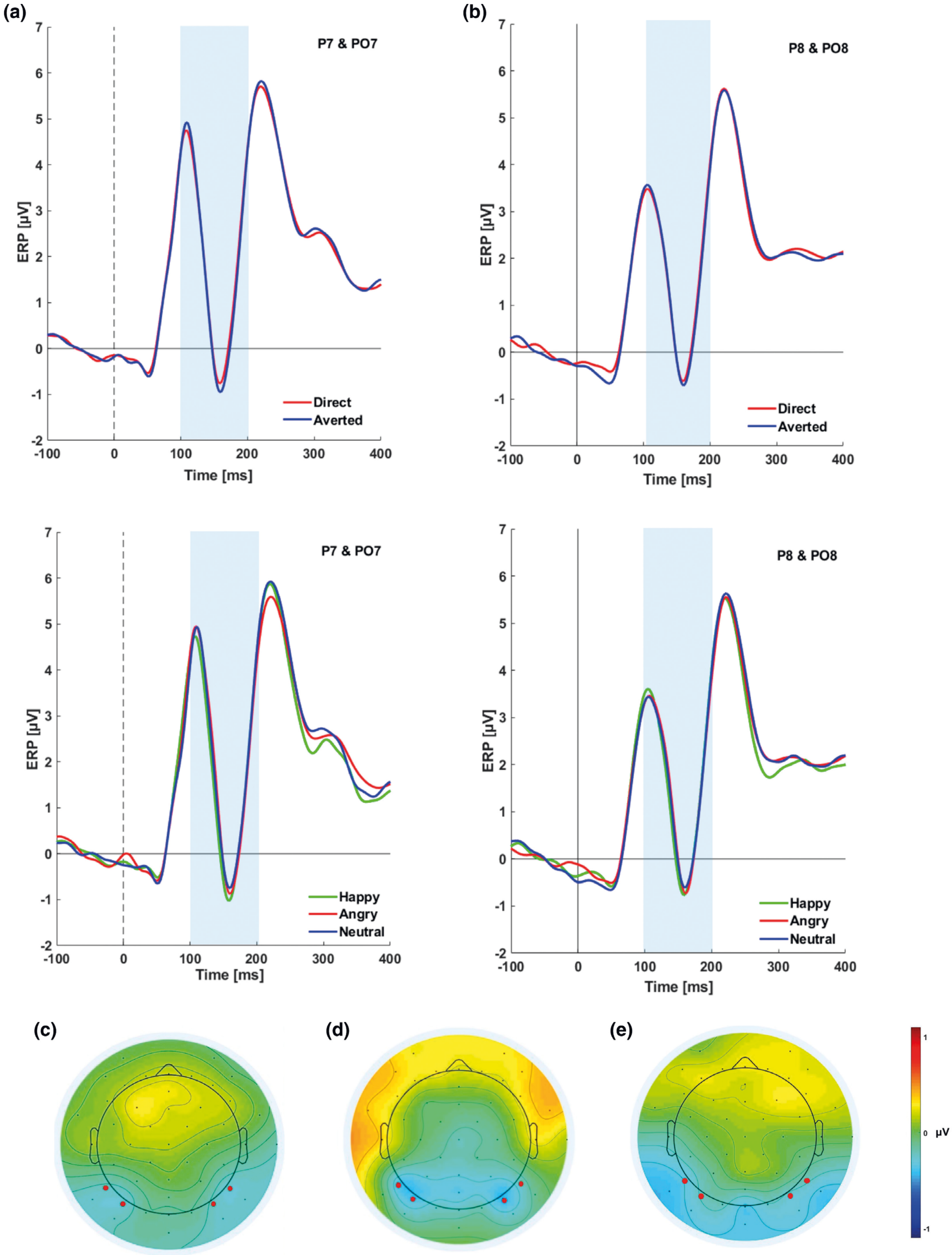
(a)
(b)
P7 & PO7
P8 & PO8
ERP [µV]
Time [ms]
Direct
Averted
Happy
Angry
Neutral
(c)
(d)
(e)
µV

FIGURE 2 Effects of gaze direction and emotion on the N170 component in the initial gaze phase. Top: Grand mean ERPs for the N170 region of interest (consisting of left hemisphere electrodes P7 and PO7 and right-hemisphere electrodes P8 and PO8); the time window during which the N170 was analyzed is shaded. (a) Effect of gaze direction. (b) Effect of emotion. Bottom: Difference topographies for the N170 time window highlighted above; (c) N170 gaze effect (averted minus direct gaze), (d) Emotion effect (happy minus neutral expression). (e) Emotion effect (angry minus neutral expression).

for the N170 component, for both the initial gaze phase and the gaze change phase. For all statistical analyses, the significance level was set to $p<.05$. The sphericity assumption was assessed using Mauchly's test and, if needed, adjustments were made by applying the Huynh–Feldt correction. Effects sizes for ANOVAs are reported as eta squared (η^2). Post-hoc pairwise comparisons were performed between the three levels of the factor Emotion, with *p*-values adjusted according to the Bonferroni method. Below, we report the unstandardized effects sizes (in μV) together with their between-subject confidence intervals (95%*CI*). In addition, we also report standardized effect sizes (Cohen's *d*).

3 | RESULTS

In the following, we first report the results for the initial gaze phase (ERPs locked to stimulus onset) and then for the gaze change phase (ERPs locked to gaze change). Within each of these phases, we first report the effects on the N170 and then on the EPN component.

3.1 | Initial gaze phase

3.1.1 | N170

Figure 2 shows the ERPs in the N170 ROI in the initial gaze phase, where the N170 ANOVA revealed a significant main effect of gaze direction, $F(1, 19) = 5.20$, $p = .034$, $\eta^2 = 0.02$, with faces showing an averted gaze ($M = 0.17$ μV, $SD = 3.34$) eliciting a more negative-going N170 amplitude than faces showing a direct gaze ($M = 0.40$ μV, $SD = 3.25$) (single subject data showing effects of gaze direction on the N170 component are provided in the Figure S1). In addition, we observed a significant main effect of emotion, $F(1, 19) = 7.77$, $p = .002$, $\eta^2 = 0.08$. Paired t-tests indicated that as compared to neutral faces ($M = 0.55$ μV, $SD = 3.21$), both angry faces ($M = 0.26$ μV, $SD = 3.29$) and happy faces ($M = 0.04$ μV, $SD = 3.37$) showed more negative-going N170 amplitudes. Moreover, the contrasts of neutral versus angry and neutral versus happy faces were significant. No significant difference was observed between angry and happy faces (see Table 2 for full statistical details and effect sizes for the post hoc comparisons). Importantly, N170 amplitude showed no interaction between gaze direction and emotion $F(2, 38) = 0.41$, $p = .666$, $\eta^2 = 0.001$.

3.1.2 | EPN

Figure 3 shows the waveshapes and Figure 4 illustrates the topographies of the EPN in the initial gaze phase. An overall ANOVA of EPN amplitude with the factors time window, emotion and gaze direction revealed main effects of emotion, $F(2, 38) = 17.22$, $p = < .001$, $\eta^2 = 0.11$, and time window $F(2, 38) = 27.75$, $p = < .001$, $\eta^2 = 0.06$. Importantly, there was also an emotion by time window interaction, $F(2, 38) = 6.99$, $p = < .001$, $\eta^2 = 0.05$. Post hoc analysis of emotion was then conducted for each time windows, yielding the following results:

ANOVAs of EPN amplitude revealed main effects of emotion in all four time windows: 200–250 ms: $F(2, 38) = 8.57$, $p = .008$, $\eta^2 = 0.02$; 250–300 ms: $F(2, 38) = 2.81$, $p < .001$, $\eta^2 = 0.01$; 300–350 ms: $F(2, 38) = 13.34$, $p = .001$, $\eta^2 = 0.08$; 350–400 ms: $F(2, 38) = 9.72$, $p = .005$, $\eta^2 = 0.03$; 400–600 ms: $F(2, 38) = 12.98$, $p = .001$, $\eta^2 = 0.07$ (see Table 2 for full statistical details and effect sizes for the post hoc comparisons).

For the time window 200–250 ms, post hoc pairwise comparisons between emotion levels revealed a significant difference between neutral faces ($M = 7.08$ μV, $SD = 4.46$) and angry faces ($M = 6.75$ μV, $SD = 4.62$). A significant difference was also found between neutral and happy faces ($M = 6.68$ μV, $SD = 4.58$). In contrast, the EPN amplitude to happy and angry faces was not significantly different. Importantly, in none of the time windows for the EPN, did we observed a main effect of gaze direction ($F < 1$) or an interaction between gaze direction and emotion ($p > .05$).

For the time window 250–300 ms, all emotions differed significantly from each other. That is, neutral faces ($M = 4.98$ μV, $SD = 3.71$) differed from both angry ($M = 4.60$ μV, $SD = 3.86$) and happy faces ($M = 4.15$ μV, $SD = 3.80$), as well as happy from angry faces.

For the time window 300–350 ms, the contrast between happy ($M = 4.21$ μV, $SD = 3.74$) and neutral faces ($M = 4.81$ μV, $SD = 3.75$), was significant. In contrast, the EPN amplitude to neutral and angry faces was not significant. Also, the contrast between happy and angry faces ($M = 4.75$ μV, $SD = 3.84$) was significant.

For the time window 350–400 ms, the contrast between happy ($M = 2.82$ μV, $SD = 3.29$), and neutral faces

TABLE 2 Test statistics of post hoc pairwise comparisons of emotion effects on the N170 and EPN components in the initial gaze phase

	Emotion effects—initial gaze phase					
	Condition effect	**Effect size (μV)**	***95% CI***	***t*-test (*df* = 19)**	***p***	**Cohen's *d***
N170						
150–200 ms	Angry–Neutral	−0.28	[−0.54, −0.03]	2.38*	.028	0.09
	Happy–Neutral	−0.51	[−0.77, −0.25]	4.14*	<.001	0.15
	Happy–Angry	−0.22	[−0.52, 0.07]	1.55	.14	0.06
EPN						
200–250 ms	Angry–Neutral	−0.33	[−0.55, −0.11]	3.15*	.005	0.07
	Happy–Neutral	−0.39	[−0.60, −0.19]	4.17*	<.001	0.11
	Happy–Angry	−0.06	[−0.28, 0.16]	0.59	.57	0.01
250–300 ms	Angry–Neutral	−0.38	[−0.63, −0.14]	3.28*	.003	0.11
	Happy–Neutral	−0.82	[−1.11, −0.54]	6.14*	<.001	0.22
	Happy–Angry	−0.44	[−0.58, −0.30]	6.57*	<.001	0.12
300–350 ms	Angry–Neutral	−0.05	[−0.31, 0.19]	0.48	.63	0.01
	Happy–Neutral	−0.61	[−0.87, −0.34]	4.87*	<.001	0.16
	Happy–Angry	−0.54	[−0.84, −0.25]	3.89*	<.001	0.14
350–400 ms	Angry–Neutral	−0.01	[−0.28, 0.31]	0.11	.91	0.00
	Happy–Neutral	−0.54	[−0.80, −0.29]	4.51*	<.001	0.15
	Happy–Angry	−0.56	[−0.91, −0.21]	3.36*	.003	0.11
400–600 ms	Angry–Neutral	−0.15	[−0.41, 0.92]	1.32	.21	0.05
	Happy–Neutral	−0.56	[−0.79, −0.32]	5.01*	<.001	0.21
	Happy–Angry	−0.41	[−0.63, −0.17]	3.69*	.002	0.14

*$p < .05$.

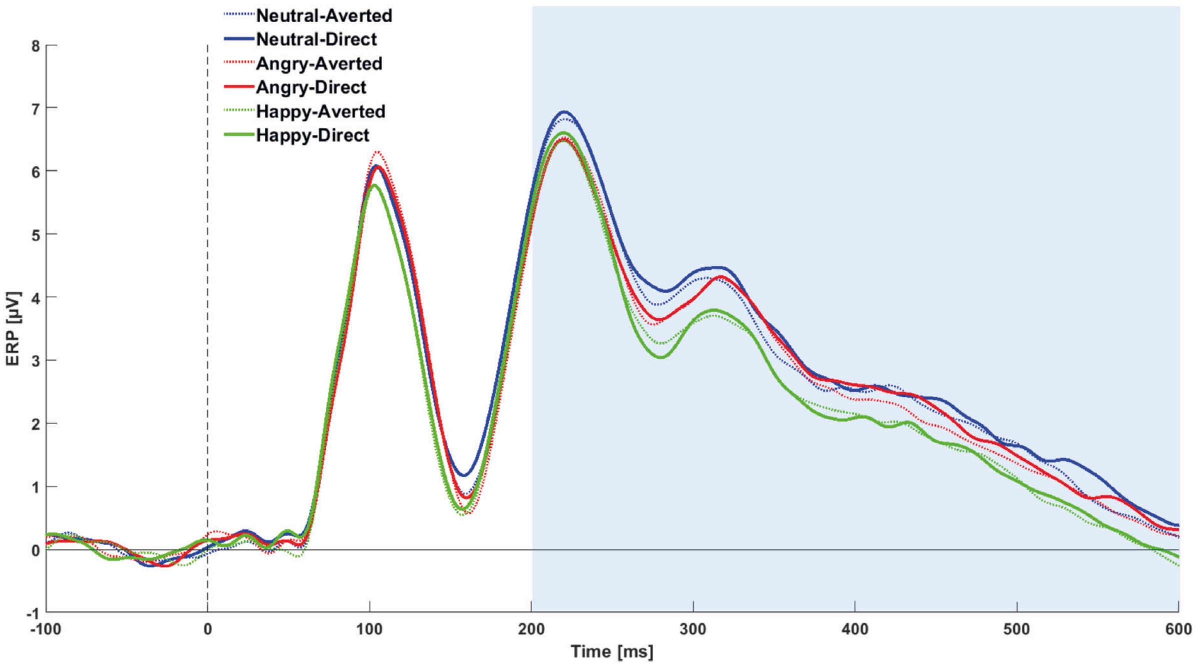

FIGURE 3 Effects of gaze and emotion on the EPN component for the initial gaze phase. ERPs are averaged across the electrodes of the EPN region of interest (P7, PO7, P8, PO8, PO9, PO10, O1, oz, O2, Iz). Shading indicates the time window that was defined for the EPN analysis. (effects of gaze and emotion on the EPN component are provided individually for EPN ROI electrodes in Figure S3).

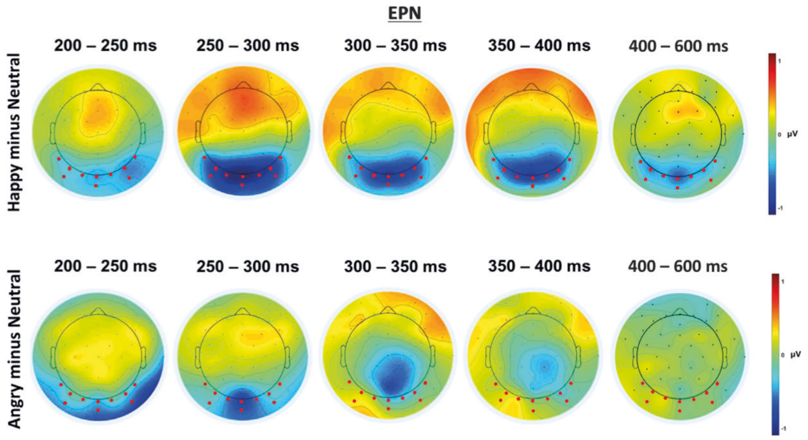

FIGURE 4 Difference topographies of the emotion effects in the initial gaze phase between 200 and 600 ms after face onset for the EPN component. The electrodes for the EPN ROIs are marked as thick red dots.

($M = 3.37\,\mu$V, $SD = 3.71$) was significant, as was the contrast between happy and angry faces ($M = 3.39\,\mu$V, $SD = 3.45$). As in the preceding time window, the contrast between neutral and angry faces did not reach significance ($p > .05$).

For the time window 400–600 ms, the contrast between happy ($M = 1.41\,\mu$V, $SD = 2.72$), and neutral faces ($M = 1.96\,\mu$V, $SD = 2.75$) was significant. However, the EPN amplitude to neutral and angry ($M = 1.81\,\mu$V, $SD = 2.83$) faces was not significant ($p > .05$). Also, the contrast between happy and angry faces was significance.

3.2 | Gaze change phase

3.2.1 | N170

Figure 5 shows the grand average ERPs in the gaze change phase for the N170 region-of-interest. For N170 amplitude, we observed a significant main effect of hemisphere, $F(1, 19) = 4.53$, $p = .047$, $\eta^2 = 0.05$, with more negative amplitudes over the right hemisphere (Figure 6) (M $= -5.29\,\mu$V, $SD = 3.38$) than over the left hemisphere ($M = -4.08\,\mu$V, $SD = 3.75$). Also, for gaze direction, there was a significant main effect, $F(1, 19) = 8.18$, $p = .010$, $\eta^2 = 0.09$, with larger amplitudes for direct-to-averted gaze changes ($M = -4.88\,\mu$V, $SD = 3.78$) than for averted-to-direct changes ($M = -4.51\,\mu$V, $SD = 3.45$) (single subject data showing effects of gaze direction on the N170 component are provided in Figure S2). Emotion did not yield a main effect ($F < 1$) nor was there an interaction between emotion and gaze direction ($p > .05$).

3.2.2 | EPN

Figure 7 shows the grand average ERPs in the EPN ROI for the gaze change phase. Figure 8 visualizes the EPN topographies. An overall ANOVA of the EPN amplitude with factors time window, emotion and gaze direction revealed a main effect of time window: $F(2, 38) = 28.26$, $p = < .001$, $\eta^2 = 0.14$. Importantly, we also observed an interaction of emotion and gaze $F(2, 38) = 7.11$, $p = <.001$, $\eta^2 = 0.08$, although there was no significant interaction of emotion and time window. In order to show that the emotion by gaze interaction is robust in each time window, post hoc analyses of emotion were conducted for each time windows as follows.

Significant interactions of emotion and gaze were obtained in all time windows between 200 and 400 ms: 200–250 ms: $F(2, 38) = 3.79$, $p = .031$, $\eta^2 = 0.01$; 250–300 ms: $F(2, 38) = 4.06$, $p = .025$, $\eta^2 = 0.01$; 300–350 ms: $F(2, 38) = 3.71$, $p = .033$, $\eta^2 = 0.01$; 350–400 ms: $F(2, 38) = 7.45$, $p = .001$, $\eta^2 = 0.02$; 400–600 ms: $F(2, 38) = 4.26$, $p = .02$, $\eta^2 = 0.01$. Post hoc tests showed that for the time window from 200 to 400 ms, happy faces ($M = -1.24\,\mu$V, $SD = 2.72$) differed significantly from neutral faces ($M = -0.68\,\mu$V, $SD = 2.73$), when the gaze changed from averted to direct. The contrast between neutral and angry faces ($M = -0.96\,\mu$V, $SD = 2.74$) was not significant ($p > .05$). For the time window 400–600 ms, the contrast between happy ($M = 0.45\,\mu$V, $SD = 2.09$) and neutral faces ($M = 0.75\,\mu$V, $SD = 2.17$) was significant. However, the amplitude difference between neutral and angry faces was not significant. Also, the contrast between happy and angry faces ($M = 0.71\,\mu$V, $SD = 2.18$) was significant (see Table 3 for full statistical details and effect sizes for the post hoc comparisons). It is worth to mention that due to the similarity of the effects across the time windows, we averaged the difference topographies across time windows from 200 to 400 for the visualization in Figure 8. For the sake of simplicity, only this averaged version is shown for the gaze change phase.

4 | DISCUSSION

Depending on the gaze direction of a face, emotional expressions may differ in their significance to the observer. In the current study, we therefore investigated the

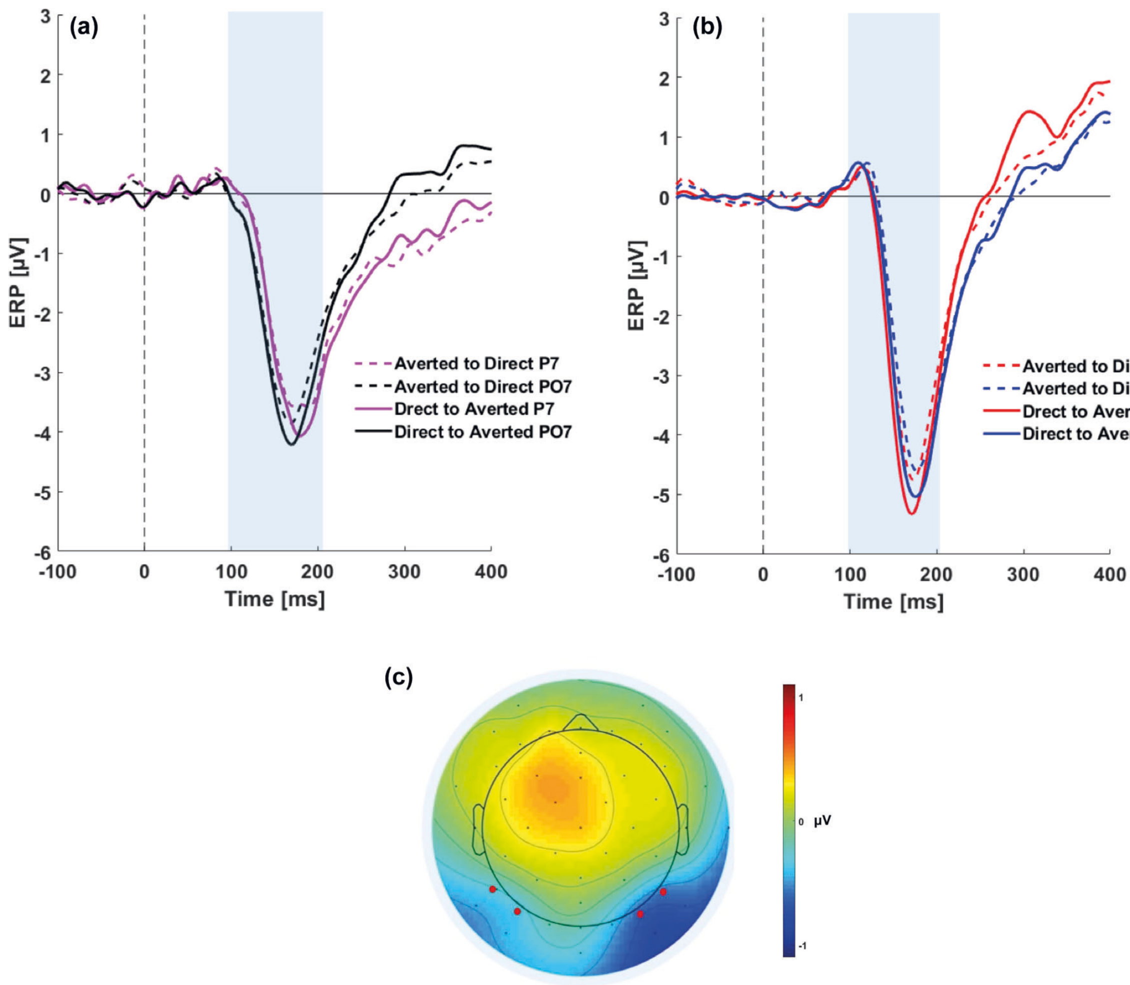

FIGURE 5 Effects of gaze and hemisphere on the N170 component in the gaze change phase. ERP waveforms of gaze effects for the (a) left hemisphere (electrodes P7 and PO7), and (b) right hemisphere (electrodes P8 and PO8). (c) Grand average ERP scalp map in the interval from 125 to 225 ms after the gaze change shows a typical N170 topography elicited by the change in gaze direction.

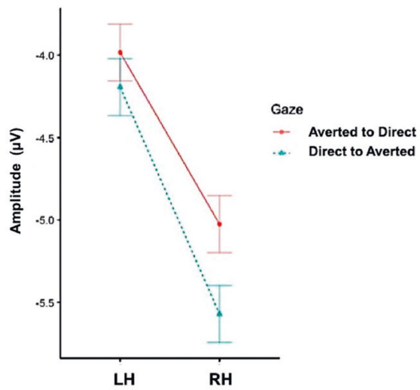

FIGURE 6 Effects of gaze direction and hemisphere on N170 amplitudes in the gaze change phase. Levels of the *x*-axis: Hemisphere (LH = left hemisphere, RH = right hemisphere). Error bars indicate Fisher's least significant difference.

electrophysiological correlates of the interplay between eye contact and emotion, both during the initial presentation of a face and in response to a subsequent gaze change. For the N170 component of the ERP, we confirmed larger responses to averted than direct gaze in both phases. In response to the initial presentation of the face, we also obtained an effect of emotion, but there was no interaction with gaze direction. Importantly, however, such an interaction between gaze and emotion was seen in response to the subsequent gaze change in the face, despite the fact that the emotional expression of the face remained invariant during the change.

4.1 | N170

For the N170, we found main effects of gaze, both in the initial gaze phase, as well as in the gaze change phase. In

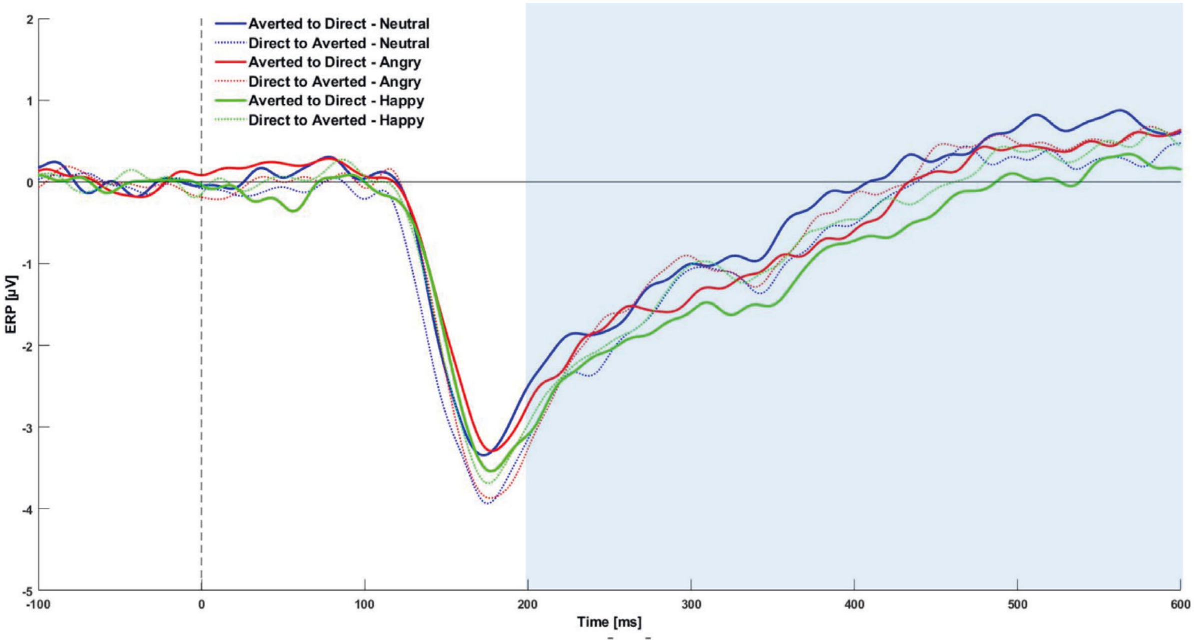

FIGURE 7 Effects of gaze change direction and emotion on the EPN component in the gaze change phase, averaged across the electrodes of the EPN region-of-interest. The shading indicates the time window pre-defined for the analysis. Thick lines indicate the significant emotion effect of happy faces in the averted-to-direct condition.

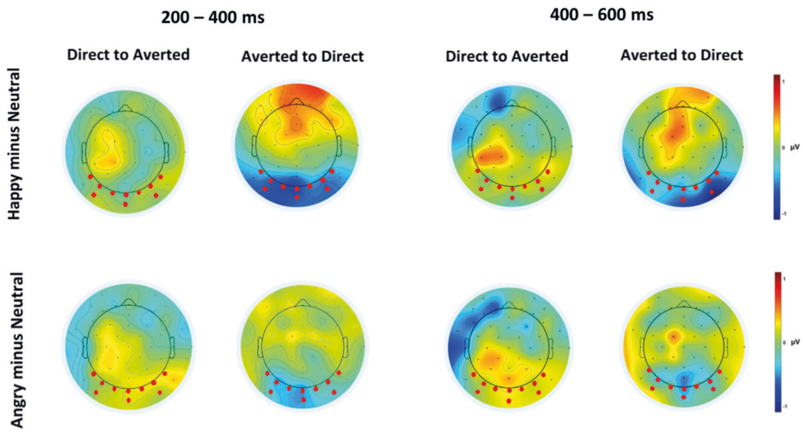

FIGURE 8 Scalp topographies of the emotion effects as a function of gaze change direction in the 200–400 ms and 400–600 ms time window for the EPN component.

line with previous findings, such as by Itier et al. (2007) for both initial gaze position and gaze changes, by Latinus et al. (2015) for dynamic gaze changes, and by Stephani et al. (2020) for gaze-contingent stimulus presentations, N170 amplitude was larger when the eyes were looking away from the observers than when aiming at them.

The N170 is interpreted as reflecting the structural encoding of faces (Eimer, 2000). Therefore, the increased N170 to averted (or averting) gaze may indicate increased neural activity required to structurally encode faces with non-canonical (i.e., averted) gaze direction. This holds for the initial gaze phase where all facial features, including expression and gaze direction appear all at once and have to be structurally encoded. But it would also hold for the gaze change phase, where all facial features, including the emotional expression, are present on the screen and then just the gaze direction changes. Gaze direction changes in the gaze change phase elicited an astonishingly large N170, presumably due to the challenges to structurally encode the altered face configuration, which may be even more challenging when gaze averts rather than aims at the observer.

For the gaze change phase, we found significant main effects of gaze as well as hemisphere. Although the interaction of gaze and hemisphere did not reach significance, scalp topographies showed that a larger N170 for

TABLE 3 Test statistics of effects of gaze change direction (averted gaze-to-direct gaze) and emotion on the EPN component in the gaze change phase

	Emotion × gaze effect – gaze change phase					
	Condition effect	**Effect size (μV)**	***95% CI***	***t*-test (*df* = *19*)**	***p***	**Cohen's *d***
EPN (gaze change: averted to direct)						
200–400 ms	Angry–Neutral	−0.27	[−0.64, 0.09]	1.57	.13	0.11
	Happy–Neutral	−0.55	[−0.88, −0.22]	3.56*	.002	0.21
	Happy–Angry	−0.27	[−0.55, −0.00]	2.11*	.43	0.11
400–600 ms	Angry–Neutral	−0.04	[−0.33, 0.24]	0.31	.75	0.01
	Happy–Neutral	−0.31	[−0.65, −0.04]	2.44*	.02	0.14
	Happy–Angry	−0.26	[−0.45, −0.06]	2.85*	.01	0.12

*$p < .05$.

gaze aversion was observed in the right than in the left hemisphere (see, Figure 5C). This resembles the findings of Latinus et al. (2015) in a social task and several other studies (for review see Eimer, 2011), which found a larger gaze effect in the right hemisphere.

Emotional expression modulated the N170 in the initial gaze phase, where angry and happy faces elicited a more negative-going amplitude compared to neutral faces. Similar effects on the N170 have been reported by Rellecke et al. (2011) who suggested that such effects may be due to overlap of the N170 with the onset of the subsequent and similarly distributed EPN. Alternatively, emotion effects on the N170 may be due to differences in structural encoding processes in emotional and non-emotional faces. With the same stimulus material as used here but with continuous presentation of faces displaying multiple successive gaze changes, a modestly enlarged N170 had been seen for angry faces (Stephani et al., 2020), which is at variance with the lack of such an effect in the present study. This discrepancy is maybe due to the display mode or to higher number of change trials in the experiment of Stephani et al. (2020).

Importantly, irrespective of the interpretation of the emotion effects on the N170, for present purposes it is relevant that despite main effects of both gaze direction as well as emotional expression on the N170 in the initial gaze phase, these factors did not interact. This is in line with findings by Klucharev and Sams (2004). Hence, in the time range of the N170, both emotion and gaze seem to be processed independently and (possibly) in parallel.

4.2 | Later effects

In the initial gaze phase, we observed the expected emotion effects in the EPN ROI and time windows. The emotion effects correspond to reports from many studies (e.g., Itier & Neath-Tavares, 2017; Rellecke et al., 2011; Schacht & Sommer, 2009b) and show the typical posterior negativity, especially for the expression of happiness. Interestingly, in this phase, the EPN with its occipito-temporal negativity appeared to be very long-lasting for happy expressions, covering even the 400–600 ms interval. The absence of a positive-going parietal LPC in this interval may be due to the task, which was not emotion-centered (see Rellecke et al., 2011; Schacht & Sommer, 2009a). Possibly, the long-lasting EPN in the present study may have been due to the ongoing monitoring of the face for a gaze change. This question could be addressed in future research that possible topographic changes in the emotion effects across time with micro-state analysis (see Murray et al., 2008 for a review).

Importantly, in the initial gaze phase, we observed no effects of gaze in the EPN ROI and interval, nor were there interactions of these factors. This may be seen to contrast with the findings of Caruana et al. (2014) of a larger intracranial activity around 250 ms for gaze aversion compared to direct gaze in epileptic patients; it remains unclear, however, whether this effect has a counterpart in scalp-recordable ERPs. Conty et al. (2012) found an interaction of gaze, pointing, and emotion in a frontal P200 component, which was largest when an actor pointed and looked at the observer with an angry expression. Although this frontal P200 may be a partial counterpart of the EPN, it is unclear from their report whether an interaction of eye gaze and emotion held when there was no pointing, as in the present study. In a similar study as the present one with dynamic gaze changes but without manipulating emotional expressions, Latinus et al. (2015) observed effects of gaze changes between 300 and 450 ms mainly over central and temporo-frontal areas. In the ROI used in our study, the topographies showed no central effect as the EPN is typically found at occipito-parietal locations (Rellecke et al., 2011).

The results were markedly different in the gaze change phase. Here, the emotional expression remained the same but gaze direction changed; hence, as to be expected, there was no main effect of emotion in the EPN ROI in this phase. However, there were clear interactions of gaze and emotion from 200 to 400 ms. Closer inspection revealed a similar emotion effect as initial gaze phase, consisting in an EPN-like posterior negativity but only when the gaze in happy faces changed from being averted from to being directed at the observer. No other condition combination elicited a significant emotion effect. Thus, a gaze change in an invariant (happy) facial expression can trigger an EPN (single subject data showing effects of emotion on the EPN component are provided separately for the initial gaze phase and gaze change phase in Figure S4).

The effect is hard to explain as an effect of motion per se, as had been observed in dynamic faces by Recio et al. (2014). In their study large non-emotional facial (chewing) movements elicited an EPN-like activity relative to a small non-emotional movement (eye blink), which was explained by the attention attracting power of motion. However, in the present study motion consisted of very similar eye movements in smile and anger and even in moving from averted to direct versus direct to averted. Therefore, it seems that when a happy face turns its gaze toward the observer, stronger attention is reflexively elicited as compared to when gaze averts. This is in partial contrast with Klucharev and Sams (2004) who reported an ERP modulation around 300 ms to both happy and angry faces due to gaze direction. However, due to the absence of a neutral emotional condition, their study is hard to interpret in terms of the EPN component.

In line with the standard interpretation of the EPN (Schupp et al., 2006), its elicitation by a gaze change in a smiling face toward the observer might indicate that such an event triggers the attention toward the face. A gaze change away from the observer does not trigger a comparable EPN. Therefore, the direct gaze at the observer might act as a social cue for the self-relevance of the face. This idea matches with the shared-signal hypothesis which states that gaze can influence the processing of an emotional content (Adams & Kleck, 2003).

Alternatively, the EPN triggered by direct gaze might be interpreted as a global effect of a stimulus (or face) change. However, this account can be ruled out because the EPN was not elicited by the same change in neutral faces or in angry faces. And it was not elicited by gaze aversion. Therefore, the effect seems to be highly specific for smiling faces looking at the observer.

A very interesting question in this context is, why we did not see the EPN for angry faces. This may be due to the fact that the EPN in the gaze change phase was weak in both gaze phases. This, in turn, might relate to the stimulus material. As in many ERP studies on expression effects, our faces with happy expressions showed open mouths while this was not the case for angry expressions. For isolated mouths, daSilva et al. (2016) have shown the effects of mouth open versus closed for early ERP components. Of more direct relevance for the present study, Langeslag et al. (2018) showed that open mouths significantly increased the EPN. Hence our relatively weak EPN to angry as compared to happy faces may relate to the confound of emotional expression with mouths opened or closed.

Why did we not obtain the interaction of emotion and gaze direction in the initial gaze phase? Several previous studies have reported a superiority of dynamic changes over static presentation. Thus Recio et al. (2014) have shown that the EPN is larger when facial expressions are dynamic as compared to static presentation. Also, eye gaze effects have been shown to be larger in gaze change phase (Latinus et al., 2015). Therefore, it is conceivable that in the gaze change phase, there was a stronger involvement of the dorsal visual system.

4.3 | Perspectives

This current study also had some limitations, which offer opportunities for further research. For example, we included a gaze change but not an emotion change between picture one and two. Although we consider our findings as relevant steps toward investigating everyday social interactions, one important next step would be to implement a paradigm in which dynamic eye gaze changes are combined with dynamic facial expressions to take one further step toward more natural and mutual human interactions. Following up on the contrast between the eye gaze interaction on the EPN to smiling faces but its absence to other expressions, it would also be very interesting to investigate the interaction for other emotions, especially fear.

Furthermore, clinical applications of this paradigm might be possible. Akechi et al. (2010) reported differences in eye gaze and the processing of gaze in autistic children. Applying the present paradigm, it could be interesting to investigate whether the emotional EPN—which interacted here with gaze change—can also be found in autistic children. This might provide further insight into the neural correlates and mechanisms of autism.

In conclusion, we confirmed the enhancement of the N170 component by averted relative to direct gaze, which may be due to increased demands on structural face encoding in gaze aversion. Importantly, we observed an interaction between facial expression and gaze direction, indicating stronger reflexive attention elicited by a happy face that is directing its gaze at the observer. Interestingly, this was only observed during the gaze change phase, emphasizing the importance of dynamic movements for the interplay of emotional expression and gaze direction, at least for happy faces.

AUTHOR CONTRIBUTIONS

Charlotte J. Lion: Conceptualization; investigation; writing – review and editing. **Olaf Dimigen:** Conceptualization; methodology; writing – review and editing. **Shadi Bagherzadeh-Azbari:** Conceptualization; formal analysis; investigation; methodology; writing – original draft. **Tilman Stephani:** Conceptualization; investigation; writing – review and editing. **Werner Sommer:** Conceptualization; resources; supervision; writing – review and editing.

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CONFLICT OF INTEREST

We have no known conflict of interest to disclose.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1

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Multimodal Evidence of Atypical Processing of Eye Gaze and Facial Emotion in Children With Autistic Traits

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According to the shared signal hypothesis (SSH) the impact of facial expressions on emotion processing partially depends on whether the gaze is directed toward or away from the observer. In autism spectrum disorder (ASD) several aspects of face processing have been found to be atypical, including attention to eye gaze and the identification of emotional expressions. However, there is little research on how gaze direction affects emotional expression processing in typically developing (TD) individuals and in those with ASD. This question is investigated here in two multimodal experiments. Experiment 1 required processing eye gaze direction while faces differed in emotional expression. Forty-seven children (aged 9–12 years) participated. Their Autism Diagnostic Observation Schedule (ADOS) scores ranged from 0 to 6 in the experiment. Event-related potentials (ERPs) were sensitive to gaze direction and emotion, but emotion processing did not depend on gaze direction. However, for angry faces the gaze direction effect on the N170 amplitude, as typically observed in TD individuals, diminished with increasing ADOS score. For neutral expressions this correlation was not significant. Experiment 2 required explicit emotion classifications in a facial emotion composite task while eye gaze was manipulated incidentally. A group of 22 children with ASD was compared to a propensity score-matched group of TD children (mean age = 13 years). The same comparison was carried out for a subgroup of nine children with ASD who were less trained in social cognition, according to clinician's report. The ASD group performed overall worse in emotion recognition than the TD group, independently of emotion or gaze direction. However, for disgust expressions, eye tracking data revealed that TD children fixated relatively longer on the eyes of the stimulus face with a direct gaze as compared with averted gaze. In children with ASD we observed no such modulation of fixation behavior as a function of gaze direction.

Overall, the present findings from ERPs and eye tracking confirm the hypothesis of an impaired sensitivity to gaze direction in children with ASD or elevated autistic traits, at least for specific emotions. Therefore, we conclude that multimodal investigations of the interaction between emotional processing and stimulus gaze direction are promising to understand the characteristics of individuals differing along the autism trait dimension.

Keywords: gaze direction, emotion processing, face recognition, N170, EPN, autism spectrum disorder, ADOS

INTRODUCTION

Impairments in social, emotional and communicative abilities are core symptoms of autism spectrum disorder (ASD; American Psychiatric Association, 2013). These abilities are closely related to eye gaze and facial emotional expression processing (Adams and Kleck, 2003). Many studies have shown that gaze processing deficits in autism may be due to impairments in using eye gaze as a proxy to understand facial expressions, intentions, and mental states of others (Baron-Cohen, 1995; Baron-Cohen et al., 1997, 2001; Leekam et al., 2000). The struggle to recognize emotions from facial expressions is one of the earliest identifiable markers of ASD (Dawson et al., 2005). In a large sample Reed et al. (2020) have found behavioral and genetic evidence for poorer emotion recognition with increasing autistic traits. In neuroimaging studies using facial emotion recognition tasks (Harms et al., 2010), individuals with ASD demonstrated altered processing (Johnson et al., 2015) in the amygdala (Dalton et al., 2005), fusiform gyri (Pierce et al., 2004; Pierce and Redcay, 2008), and posterior superior temporal gyri (Pelphrey et al., 2005). On the behavioral level, individuals with ASD have shown altered emotion recognition of positive and negative facial expressions with larger impairments in processing fear, anger, sadness, and disgust emotions as compared to happy emotions (Wong et al., 2008). However, in some previous studies there were no performance differences between individuals with ASD and typically developing (TD) children in facial emotion recognition tasks (Castelli, 2005; Jones et al., 2011; Fink et al., 2014).

Event-Related Potential Studies on Face and Eye Gaze Processing in Autism Spectrum Disorder

Event-related potential (ERP) studies indicate difficulties of individuals with ASD in orienting to social stimuli. This was demonstrated by a reduced or delayed N170 response to faces, which may indicate impaired structural processing of faces (Samaey et al., 2020) or diminished emotion recognition (Chronaki, 2016). The N170 is one of the most frequently investigated face-sensitive ERP components, and is also associated with eye gaze processing (Pelphrey et al., 2005; Senju et al., 2005b; Webb et al., 2006). The N170 is therefore of great interest for investigating altered face processing in autism [for reviews see Monteiro et al. (2017) and Kang et al. (2018)]. In individuals with ASD, as compared to TD, longer N170 latencies to faces and smaller amplitudes to emotional facial stimuli have been found (de Jong et al., 2008; Batty et al., 2011; Tye et al., 2014). For example, Webb et al. (2006) reported longer N170 latencies to faces in children with ASD as compared with TD individuals, indicating a deviant pattern of brain responses to faces at an early age. With respect to specific emotions, previous studies demonstrated stronger increases of N170 amplitudes to fearful over neutral expressions in a control group as compared to an ASD group; in contrast, the N170 amplitudes to neutral faces did not significantly differ between these groups (de Jong et al., 2008; Faja et al., 2016). Wagner et al. (2013) and Faja et al. (2016) reported increased N170 amplitudes to happy and angry faces, only for a TD group but not for an ASD group. However, Tye et al. (2014) found larger N170 amplitudes for neutral as compared to fearful expressions only in ASD participants.

Evidence of unusual eye gaze direction processing among children with ASD was found in two ERP studies. Grice et al. (2005) recorded high-density ERPs from children (aged 3.5–7 years) with ASD while passively viewing faces with different gaze directions. The occipito-parietal negativity was larger in a direct than an averted gaze condition in children with ASD, resembling data collected from 4 months-old infants (Farroni et al., 2002). In contrast, ERPs of age-matched TD children and adults were not sensitive to perceived gaze direction (Grice et al., 2005), suggesting a developmental delay in the ASD group. The absence of gaze direction effects in TD individuals reported by Grice et al. (2005) is surprising, given the sensitivity to perceived eye gaze direction in other ERP studies. This is also at variance with findings of Senju et al. (2005a) who investigated ERP correlates in an active gaze direction detection task in children with ASD and TD children (M = 12 years). N170 to direct gaze was larger than to averted gaze in controls but not in the ASD group. After gaze direction changes, the N170 was followed by an enhanced occipito-temporal negativity (N2), which was lateralized to the right hemisphere and larger for direct than averted gaze for TD children but not for children with ASD. Similar problems with gaze processing have been reported on the performance level, unlike children with ASD, TD children showed an advantage in detecting direct gaze over averted gaze (Senju et al., 2005a; Senju and Johnson, 2009).

A later ERP component, the early posterior negativity (EPN) is considered to indicate reflexive visual attention to emotional stimuli, facilitating sensory encoding. Thus, both negative and positive emotional stimuli enhance EPN amplitudes as compared to neutral stimuli (Schupp et al., 2003; Foti et al., 2009; Holmes et al., 2009; Schacht and Sommer, 2009). A study found that adults with ASD had different hemispheric distribution of EPN in response to facial expression, as compared to neurotypical adults (e.g., Faja et al., 2016). Faja et al. (2016) found that adults with ASD differed from neurotypical participants by showing a reduced sensitivity to emotional information in the EPN but not in the preceding P1 or N170 components. The authors concluded that the N170, which is associated with perceiving information that is needed to distinguish faces from other object categories (Bentin et al., 1996), is not modulated differentially by emotional expressions in adults with ASD relative to neurotypical adults. All in all, a diminished EPN in adults with ASD suggests that emotional cues are perceived or attended less than in normotypical individuals. However, to the best of our knowledge, there are no such studies on children with a diagnosis of autism or high on autistic traits. It remains to be seen, however, whether this is also the case in children with high autistic traits.

Interactive aspects of facial emotion expression perception and eye gaze processing are often emphasized as crucial issues in autism (Grice et al., 2005; Senju et al., 2005b; de Jong et al., 2008; Akechi et al., 2010; Tye et al., 2013). Akechi et al. (2010) investigated the neural correlates of processing facial expressions with different gaze directions. Approach-oriented expressions (e.g., anger) combined with direct gaze elicited a larger N170 than avoidance-oriented expressions (e.g., fear) combined with averted gaze in TD children but less so in the ASD group. This finding suggests that gaze direction modulates the effect of emotional facial expressions. In an attention cueing task, de Jong et al. (2008) presented fearful and neutral faces with different gaze directions either in static and dynamic conditions. Children with ASD processed gaze cues typically when static neutral faces were presented, exhibiting larger N200 amplitudes and shorter RTs in validly cued conditions. However, in the dynamic condition, attention orienting was influenced by emotion only in the control group but not in the ASD group. These effects were taken to suggest an impairment of processing social information in individuals with ASD. Emotional expression and gaze direction interact, and jointly contribute to approach- or avoidance-related basic behavioral motivations.

The interaction of face and eye gaze processing is in line with the "shared signal hypothesis" (SSH; Adams and Kleck, 2003), which postulates that when gaze direction matches the intent communicated by a specific expression, it enhances the perception of that emotion. For example, happy and angry expressions are both categorized as "approach-oriented emotions," and hence are usually better recognized in faces that look directly at the observer. In contrast, disgusted and sad expressions are categorized as "avoidance-oriented emotions," and are more easily recognized when accompanied by an averted gaze. Importantly, it is suggested that children with ASD have difficulties in recognizing other's facial expressions, especially anger (Bal et al., 2010). It is therefore of great interest to study, whether autistic individuals can benefit from this interaction of emotional expression and gaze direction in the same way as normal controls do, and to see if the SSH relates to other concepts about how ASD individuals processes facial expressions and eye gaze. For example, the "eye avoidance hypothesis" proposes that atypical gaze behavior in autistic individuals is due to a lack of social interest (Tanaka and Sung, 2016). Tanaka and Sung (2016) consider avoidance of the eye region as an adaptive strategy for autistic individuals, as they often perceive eye gaze as socially threatening and unpleasant. However, avoiding the eyes severely limits the possibility of recognizing a person's identity, emotional expression and intentions from his/her face. Tanaka and Sung (2016) believed that this avoidance behavior is the most plausible explanation for the autistic deficits found so far. To investigate such interaction strategies, methodologies such as eye-tracking provide valuable behavioral measures of individuals with ASD.

Eye-Tracking Studies on Face and Eye Gaze Processing in Autism Spectrum Disorder

Eye-tracking technology has been adopted in autism research for studying atypical gaze fixation on primary facial regions, such as the eyes. Chita-Tegmark (2016) conducted a meta-analysis of 68 studies on the allocation of attention in autistic individuals, inferred from fixation durations on faces, specific face regions (eyes, mouth), the body and non-social stimulus elements. The findings confirmed the commonly assumed atypical gaze patterns in autism. Across all studies, gaze times on the eyes, mouth, and face were reduced in autistic individuals as they looked more at the body and less at social details. According to the author, although effect sizes are small, gaze behaviors of autistic individuals consistently differ from healthy controls (also see Papagiannopoulou et al., 2014).

The findings on eye avoidance, a critical feature of face perception in individuals with ASD, suggest that recognition of basic emotions in autism is deficient, especially when the eye region is relevant. Individuals with ASD are less able to understand the "language of the eyes" and often cannot clearly assign subtle information from eye signals (Baron-Cohen et al., 1997). Song et al. (2012) examined the ability to recognize emotions in autistic children aged 6–12 with regard to looking at eye regions. They observed that it was easier for autistic children to look into another person's eyes while processing positive emotions than negative emotions. In emotion recognition for happiness, autistic individuals were able to assess facial expressions using the eye region as competently as TDs. This seems to contradict the "eye avoidance hypothesis." However, the authors suggested that atypical gaze behavior in autism is more likely to result in recognition of negative emotions, such as an angry facial. Later, Song et al. (2016) found that autistic individuals show a remarkable reduction in the processing of the eye region and an increased processing of the mouth region in fearful faces, when compared to their TD group. The authors suggested that autistic individuals may look less in the eyes of fearful faces because they experience a higher level of arousal, making them feel uncomfortable.

Support for differences in gaze behavior and its influence on the ability of autistic individuals to recognize emotions is not universal. Thus, Hernandez et al. (2009) examined the gaze behavior of autistic and healthy adults during the exploration of neutral and emotional facial expressions by means of eye tracking. In contrast to previous work assuming that individuals with ASD show a general disinterest in the eye region, both autistic and TD adults looked more frequently at the eye region than at other areas of the face. However, this study with only 11 adults with ASD was low powered. In an emotion 1-back task, Leung et al. (2013) studied fixation behavior in autistic children and TD children when they looked at pictures of disintegrated faces (with eyes separated) and normal faces. The results showed no difference between the groups with regard to the ability to recognize emotions and the number of fixations. Since both groups fixated the eyes more often and performed better when the eyes were presented together, the authors argued that also for individuals with ASD the eyes are the most important source of information during emotion recognition. However, since the autistic group showed increased fixation durations, recognizing emotions from the eyes may have been more effortful for them. Matsuda et al. (2015) also failed to find group differences between children with ASD and TD children in their fixation behavior at static emotional facial expressions (including surprise, happiness, anger, and sadness). Participants in both groups fixated longer on the eye regions of angry and sad than surprised faces but fixated longer on the mouth region in surprised and happy than angry and sad faces. According to the authors, this complements prior findings, showing the key role of the eye region in recognizing angry and sad expressions, and the importance of the mouth region for the recognition of surprised and happy faces.

Together, the findings on the influence of gaze behavior on facial perception and emotion recognition from facial expressions are inconsistent. Atypical gaze patterns seem to be generally well documented for autistic children and adolescents (Papagiannopoulou et al., 2014) but the effects of these differences and their manifestations in the preference or avoidance of certain facial regions are still unclear. However, the atypical avoidance of the eye region could explain autistic deficits regarding the processing of fear expressions (Lozier et al., 2014; Tell et al., 2014). In the few existing studies on the ability to recognize emotions from facial expressions, priority was given to facial stimuli of adults for selected emotions. As a result, there is a lack of research into the relationships of processing facial expressions and gaze perception and eye movements in autism, especially in children.

Recently, the Research Domain Criteria (RDoC) approach advocates a shift from treating mental disorders as categories to examining the continuum of symptom severity and diversity spanning the entire population (Insel et al., 2010; Cuthbert, 2015). In line with this approach, a growing body of studies investigated autism-associated social, emotional and communicative traits in the population, involving a broad range of individuals within or outside the autism spectrum (Abu-Akel et al., 2019). In line with RDoC, adaptive and maladaptive traits need to be characterized from a multimodal perspective, involving neural correlates and behavioral manifestations. Therefore, describing behavioral and neural correlates and associations of facial expression processing and their interactions with gaze direction and how they relate with continuous autism traits and clinical manifestations may contribute to better understanding of autism at a mechanistic level. The results of such an approach have the potential to explain hitherto reported mixed findings in neuro-typical and clinical populations.

Toward these aims, we report two experiments investigating the interactions between facial expressions and gaze direction and their relationship to social, emotional and communicative impairments in children with different degrees of autistic trait expressions. Experiment 1 recorded ERPs in response to angry and neutral facial expressions in children with varying degrees of autism traits. We were particularly interested in studying whether the processing of emotion was influenced by gaze direction (or vice versa), and how this interaction relates with autism trait. Experiment 2 compared two groups of children with and without diagnosis of ASD, matched in age, sex, and cognitive abilities, in an emotion classification task with faces of different expressions and gaze directions, while eye movements were recorded.

EXPERIMENT 1

In Experiment 1 we investigated whether autistic traits in children modulate ERPs related to emotion and gaze processing. Based on the SSH, we studied the interaction between emotional expression and static and dynamic gaze directions. We presented angry and neutral faces with direct and averted gaze, requiring the detection of occasional gaze changes. Based on the findings from the general populations (Latinus et al., 2015), we expected individuals with low autistic traits to show larger N170 amplitudes to faces with averted gaze or changing from direct to averted gaze, compared to the opposite direction. In line with the reported atypical orienting to social stimuli in individuals with ASD (Senju et al., 2005b), we expected this effect to become smaller with higher autistic traits. Moreover, in line with studies using comparable stimulus materials (Senju et al., 2005a; Akechi et al., 2010; Tye et al., 2013, 2014), we expected the gaze effect on the N170 should be stronger for emotional than for neutral faces. Such an interaction of emotion and gaze should diminish with increasing autism trait.

Methods

Participants

Forty-seven Chinese children from the Hong Kong region participated in the study; 16 were excluded because of technical electroencephalography (EEG) issues ($n = 4$), termination of the session prior to completion ($n = 1$), noisy EEG data ($n = 5$), or excessive data loss after EEG preprocessing ($n = 7$), resulting in a final sample of 30 children (19 boys, 11 girls with range 9–12 years, $M_{\mathrm{Age}} = 10$; $M_{\mathrm{IQ}} = 100$). All children had been tested with the Autism Diagnostic Observation Schedule – Second Edition (ADOS-2; Hus and Lord, 2014; see details below/$\mathrm{Min}_{\mathrm{score}} = 1$, $M_{\mathrm{score}} = 3.72$, $\mathrm{Max}_{\mathrm{score}} = 12$). Both the participant and his/her parent or caretaker signed informed consent, as approved by the institutional ethics review board of the Hong Kong Baptist University.

Autism Diagnostic Observation Schedule

The ADOS-2 (Hus and Lord, 2014) is a standardized, semi-structured observational assessment tool used to diagnose ASD and is considered a "gold standard" diagnostic instrument. The ADOS-2 is considered more objective as compared to self-report autistic measures, such as the autism-spectrum quotient (AQ). In particular, the ADOS-2 score is not affected by response biases, individual differences in introspective ability, and honesty of the respondents. The ADOS-2 comprises of four modules designed for different age and language fluency levels. For the present study, Module 4 of the ADOS-2 was used, including the communication and social interaction domains and taking approximately 45 min. The interview was administered and scored by a licensed clinical psychologist according to the diagnostic algorithm outlined in the manual, which can be categorized into non-spectrum, autism spectrum, or autism. In the present study ADOS-2 score was treated as a continuous variable, where a higher score indicates a higher level of autistic trait.

Face Stimuli

A total of 16 frontal view faces (10 females, 6 males) were selected from the child affective facial expression (CAFE) database (LoBue, 2014; LoBue and Thrasher, 2015) with two different expressions (neutral, angry) and with direct and averted gaze. Gaze direction was photo-edited and the size and position of the faces on the screen was standardized. The eyes were placed at the same horizontal and vertical positions of the screen for every facial picture; and external facial features, such as hair or visible clothing were removed by placing the image into an oval mask. Apparent gaze motion was created from static images by sequentially presenting images with different gaze direction (**Figure 1**). Therefore, it was important to ascertain that only eye gaze changed between the seamlessly presented pictures with different gaze directions. We manipulated the stimuli as follows: for each individual and emotional expression, the eye region of a picture of the same individual in the data base with averted gaze was copied and carefully pasted into the eye region of the corresponding picture with direct gaze by means of Adobe Photoshop software (version CC 2015, Adobe Systems, San Jose, CA, United States). For each emotion, two gaze changes (from left or right averted to direct gaze and vice versa) and a condition without gaze change were created, with 20% non-change trials in total to prevent expectation effects. Half of all change-trials involved a gaze change from an averted to a direct gaze direction, whereas the other half was a change from direct to averted direction. The emotional type and intensity of the face stimuli were rated by 33 Hong Kong Chinese children aged between 8 and 12 years. The face emotions were correctly identified by 78–100% of the raters.

Experimental Design

Figure 1 provides a visualization of the trial structure. Pictures of angry or neutral faces with or without gaze direction change were presented. In most trials, the gaze direction changed after 1000 ms from direct to averted or vice versa. After the disappearance of the second image, a blank screen was shown, during which participants should indicate by pressing a left or right button whether the gaze had changed or not.

Electroencephalography Recording

Upon arrival, the parent or caretaker was asked to leave the room during EEG preparation and the experiment. Participants were seated approximately 60 cm away facing an LCD monitor in a dimly lit, sound-attenuated room. The EEG was sampled at a rate of 1000 Hz from 38 Ag/AgCl electrodes mounted in a cap (Waveguard^{TM}original) plus one nose reference and connected to an amplifier (eego^{TM}mylab, ANT Neuro). Electrode

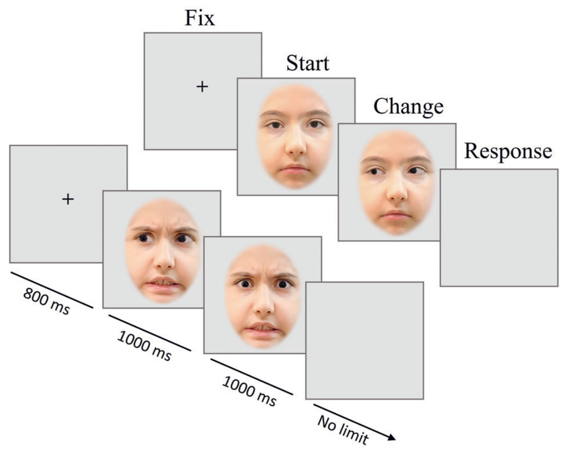

FIGURE 1 | Trial scheme of Experiment 1. Presentation of the fixation cross (FIX) for 800 ms, followed by the first picture with one of two emotional expressions and one of three gaze directions (START) for 1 s, and (in most trials) the gaze change (CHANGE) shown for 1 s; a blank screen prompted a button-press decision, whether a change had occurred or not (RESPONSE). The pictures are for illustration only and were neither taken from the CAFE database nor used in the experiment.

impedances were kept below 20 kΩ using ECI Electro-Gel^{TM}. Common reference electrode during recording was CPz. Four additional Kendall^{TM} H124SG ECG electrodes were placed above and below the left eye and at the outer side of each eye to record eye movement.

Data Analysis

Participants' responses were recorded by EPrime software (version 2.0). Mean accuracy data of each participant and condition were analyzed. Overall response accuracy in the change detection task was high with a mean of 96.81% (SD = 0.03) correct responses. No participant gave less than 92.82% correct responses. Response times were not included in the analyses because the task was unspeeded. There were a total of 378 trials per participant. Each trial consists of two intervals, START (the initial face presentation) and CHANGE (gaze change). In the change interval, those cases without changes were dropped from the analysis, leaving 210 trials for START interval and 168 trials for the CHANGE interval. To examine ERP effects of direct eye gaze compared to gaze aversion, the ERPs in the START interval were pooled for the gaze conditions left averted and right averted. Thus, there were just two gaze categories per interval: direct and averted. As a result, for START intervals, each emotion condition (i.e., neutral and angry) had 49 direct trials and 56 averted trials. For the CHANGE intervals, we pooled direct to left averted and direct to right averted trials plus pooling left-averted to direct and right-averted to direct trials, yielding 42 trials for each combination of gaze direction and emotion.

Electroencephalography data were preprocessed in MATLAB R2019a (The MathWorks Inc., Natick, MA, United States) and EEGlab v14.1.1b (Delorme and Makeig, 2004). High- and low-pass filters were set to 0.02 and 30 Hz, respectively. Continuous data was re-calculated to average reference and cut into 1.4-s epochs, including a 100 ms pre-stimulus segment, used for baseline corrections from 50 ms to stimulus onset. On average, 75.2% (M = 286.0 intervals out of 378 total intervals, SD = 44.8) of all epochs per participant remained for analysis (START: 128 epochs; CHANGE: 158 epochs). Epochs were removed if they contained extreme values exceeding ±80 μV in any channel. A total of 3.4% of all epochs was excluded because voltages in at least one channel had exceeded ±100 μV (START: 2.5%; CHANGE: 4.4%). ICA was used for eye artifact correction. In total, 12.2% of all epochs was excluded because of eye-movement artifact removal by ICA.

Electrodes and regions of interest (ROIs) were chosen in line with the literature but generally also confirmed in the present data. The electrodes chosen for N170 analysis were P7 and P8 in line with sites of large eye gaze effects (e.g., Latinus et al., 2015). For each condition and participant, average ERPs were generated for epochs synchronized to face onsets and to gaze changes. First, for detecting the N170 amplitude, the minimum voltage was identified in a broader time window from 150 to 300 ms to stimulus onset and after stimulus gaze change. Two distinct time windows (150–190 and 220–270 ms) were extracted from this broad window to make the N170 amplitude easier to observe and score within individuals. Next, the ERP peak amplitude at its latency was measured.

For the EPN, a region of interest (ROIs) was defined according to the literature (Rellecke et al., 2011; Bublatzky et al., 2017): P8, PO8, O2, Oz, O1, PO7, P7, PO5, PO6, PO3, PO4. The averaged EPN amplitude across these electrodes was quantified as mean amplitude in the time windows 200–250, 250–300, 300–350, and 350–400 ms after stimulus onset, separately for the START and CHANGE intervals.

Statistical Analysis

Statistical analyses of ERP peak amplitudes and topographies were performed with MATLAB R2019a and the R Software for Statistical Computing (Version 3.2.2). Analyses of variance (ANOVA) were performed on ERP amplitudes with repeated measure on factors Gaze direction (averted, direct) and Emotion (neutral, angry), separately for the START and CHANGE intervals. The sphericity assumption was assessed using Mauchly's test and adjustments were made applying Huynh–Feldt correction, if needed. Pairwise comparisons were performed between emotional categories, adapting p-values according to the Bonferroni correction method.

Results

The ERPs to the initial face presentations (START interval) showed a significant effect of emotion on N170 amplitudes during the 220–270 ms interval [$F(1,29) = 22.28$, $p = 0.02$, $\eta^2 = 0.291$], with larger amplitudes to anger (P7: −4.27 and P8: −3.57) than neutral expressions (P7: −3.23 and P8: −1.89) (see **Figure 2**). There was no effect of gaze direction for the N170 component [$F(1,29) = 1.95$, $p = 0.07$], nor was there an interaction between emotion and gaze [$F(1,29) = 0.01$, $p = 0.09$].

For the EPN component, an emotion effect was observed in the 200–250 ms time window [$F(1,29) = 6.17$, $p = 0.01$, $\eta^2 = 0.054$]. Thus, EPN amplitudes in the angry condition were more negative than in the neutral condition (−1.42 vs. −0.87 μV). There was no effect of gaze direction for the EPN, nor was there an interaction between emotion and gaze [$F(1,29) = 0.01$, $p = 0.09$]. There was no correlation between the Autism Diagnostic Observation Schedule (ADOS) score and any ERP parameter during the start interval.

In the following CHANGE interval, there was a main effect of gaze change on N170 amplitudes at the time window of 220–270 ms [$F(1,29) = 5.48$, $p = 0.02$, $\eta^2 = 0.0581$]. The ERP was more negative for averted than for direct gaze (−3.63 vs. −3.18 μV) (see **Figure 3**). No significant effect was found on the N170 amplitudes in time window of 150–190 ms [$F(1,29) = 0.01$, $p = 0.08$]. There was neither main effect of emotion nor interaction.

For the EPN ROI there were no significant main effects or interactions in any of the measurement intervals.

Within the early interval (150–190 ms) of N170 in change interval, there was a significant correlation (Spearman rank-order correlation) of ADOS and the individual gaze change effect for angry faces (ERPs in the direct to averted condition minus the averted to direct condition): $r = 0.35$; $p < 0.05$ (vs. neutral $r = 0.24$; $p > 0.05$) (see **Figure 4**). The positive correlation indicates that participants with low ADOS scores tended to show the commonly observed larger N170 amplitudes to dynamic gaze changes from direct to averted than for averted to direct. As ADOS scores increased, the gaze effect on the N170 diminished, yielding a positive relationship.

Discussion

In Experiment 1 we investigated whether ERPs associated with emotion and gaze processing are related to the degree of autistic trait in children. Results concerning the correlation between ADOS scores and ERPs indicate that gaze effects to angry faces and each sub-score of the ADOS (communication and reciprocal social interaction) and the total score were positively correlated, albeit modestly. This correlation across participants was observed in the absence of a gaze effect on the group mean.

Similar to previous reports (e.g., Batty et al., 2011), children in our study showed a very large right-lateralized P1 to the onset of visual stimuli (in the START interval; see **Figure 2**). Therefore, any experimental effects on the N170 during the START interval were superimposed by the P1, possibly pushing N170 latency toward larger values or just obscuring this component. A gaze effect was only seen in the change interval on the N170 component between 220 and 270 ms at electrodes P7 and P8. This gaze effect followed the typical pattern observed in non-social tasks: gaze aversion (gaze averting to the left or right from direct) elicits a larger negativity than gaze moving from averted to direct.

de Jong et al. (2008) and Akechi et al. (2010) also found differences between ASD and TD groups at P1 and N170. They showed that in ASD individuals, integrating emotional facial expressions and gaze direction is impaired at the level of visual analysis. Nevertheless, we observed a strong early effect of emotion on the N170 in the START interval, which was followed by a typical EPN effect. There were no emotion

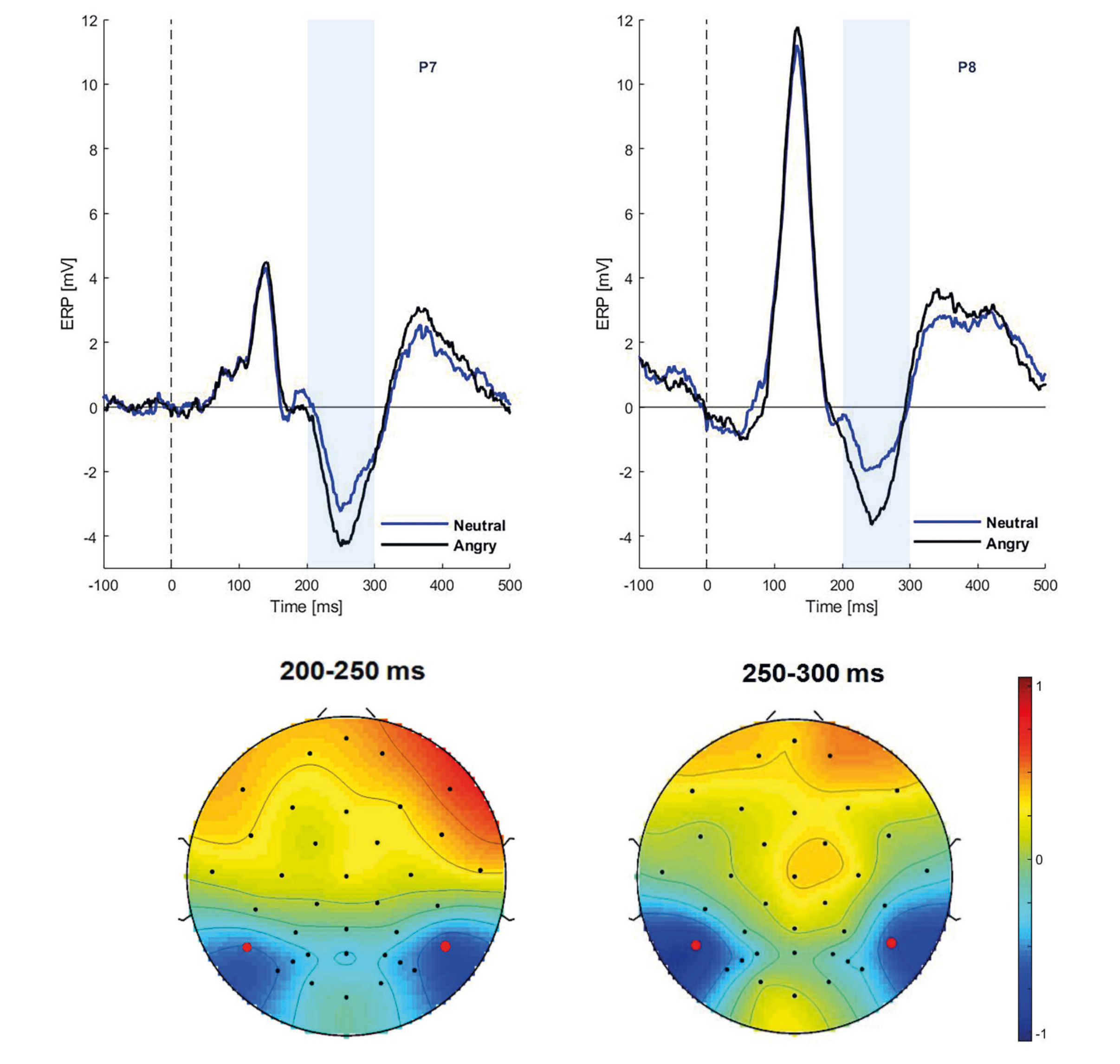

FIGURE 2 | Grand average ERPs in the START interval. *Top*: ERPs at electrodes P7 and P8 for neutral and angry expressions. *Bottom*: Scalp topographies of the emotion effect (angry minus neutral) for the time window of 200–250 and 250–300 ms.

effects in the CHANGE interval, which is not surprising because in this condition only gaze direction but not the facial expression changed.

Early emotion effects have been reported in a number of studies with adults (Faja et al., 2016). Rellecke et al. (2013) suggested that the N170 may be overlapped by early onset EPN signals. Since only one study (Faja et al., 2016) measured N170 and EPN components simultaneously, it is difficult to tell how far the effects of facial expressions found in the N170 component were driven by overlapping EPN effects (Rellecke et al., 2013). In Faja et al. (2016), fearful facial expressions elicited larger N170 amplitudes than neutral expressions, whereas the EPN was larger to neutral as compared to fearful faces in both ASD and TD groups. It was therefore argued that there is a genuine emotion effect on N170 amplitude. Only Vlamings et al. (2010) and Tye et al. (2014) found main effects of emotion on N170 latency in ASD individuals. Of note, most of the studies reported a main effect of emotion and emotion by group interactions for amplitude and latencies during the processing of fearful and neutral facial expressions. Other emotional expressions have been neglected so far. Some studies reported a main effect of facial emotions only for the control groups, but not for the ASD groups

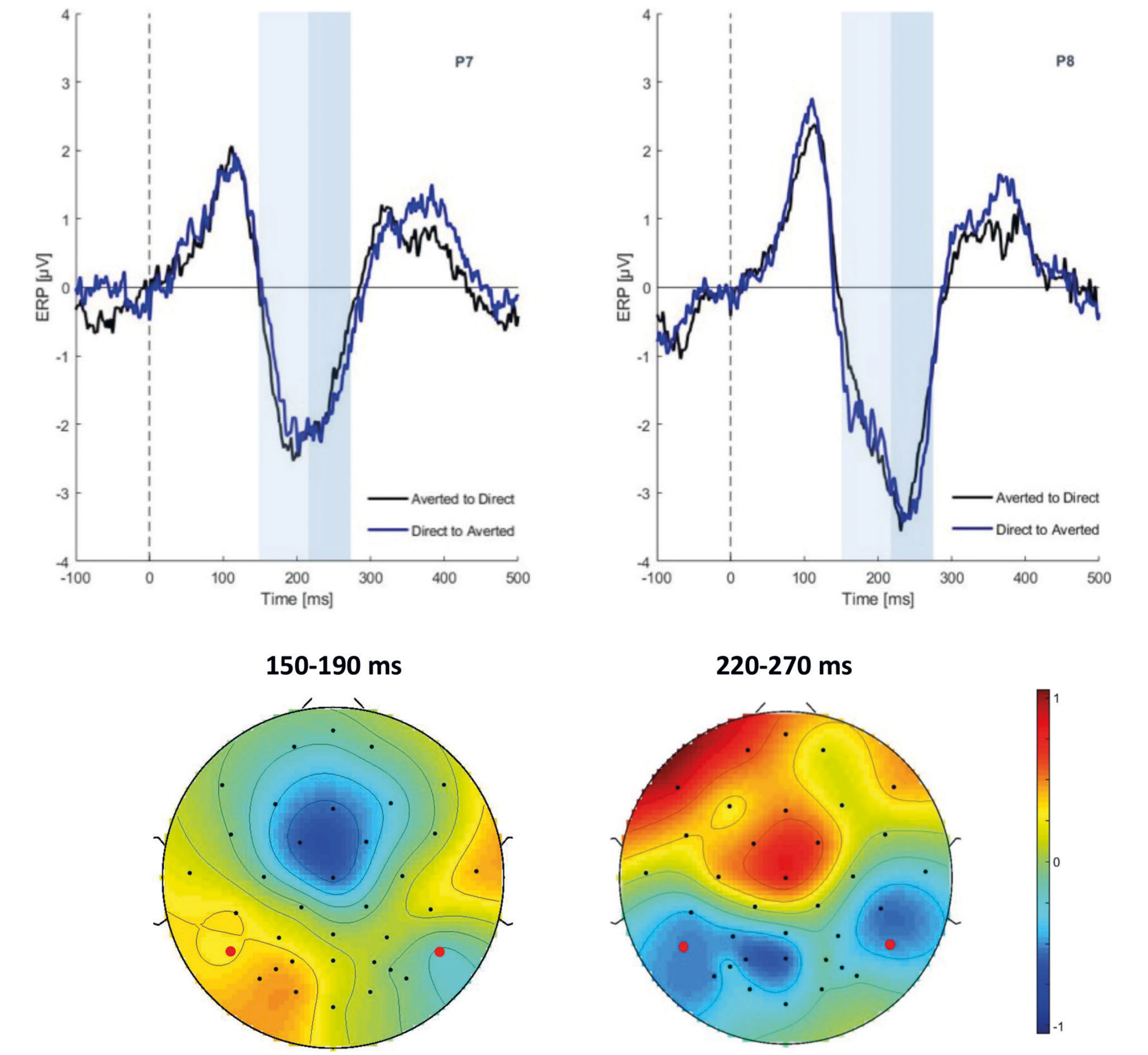

FIGURE 3 | Grand average ERPs in the CHANGE interval. *Top*: ERP waveform of gaze conditions at electrode P7, P8. *Bottom*: Scalp topographies of the gaze effect (ERPs in the direct to averted condition minus the averted to direct condition) in the time segments 150–190 ms (ns) and 220–270 ms.

(see Monteiro et al., 2017 for a review). In summary, studies generally indicate differences between ASD and TD individuals in the discrimination of emotional facial expressions, which may thus be a differential characteristic of ASD.

EXPERIMENT 2

While in Experiment 1 emotional expression was not task-relevant but an implicit variable, Experiment 2 required explicit classification of emotional facial expressions, with gaze direction being implicitly manipulated. Eye movements in two closely matched groups of children diagnosed with ASD and TD children were recorded.

According to numerous reports (Kuusikko et al., 2009; Uljarevic and Hamilton, 2012; Lozier et al., 2014), autistic individuals perform worse in recognizing emotional facial expressions than healthy controls, especially in regard to negative emotions such as fear, sadness (Pelphrey et al., 2005; Ashwin et al., 2006; Wallace et al., 2008; Tell et al., 2014), and anger (Rump et al., 2009; Law Smith et al., 2010; Tanaka et al., 2012; Lozier et al., 2014). However, the pattern of gaze direction of the expressor face in combination with positive or negative facial expressions has not yet been extensively studied. Therefore, the

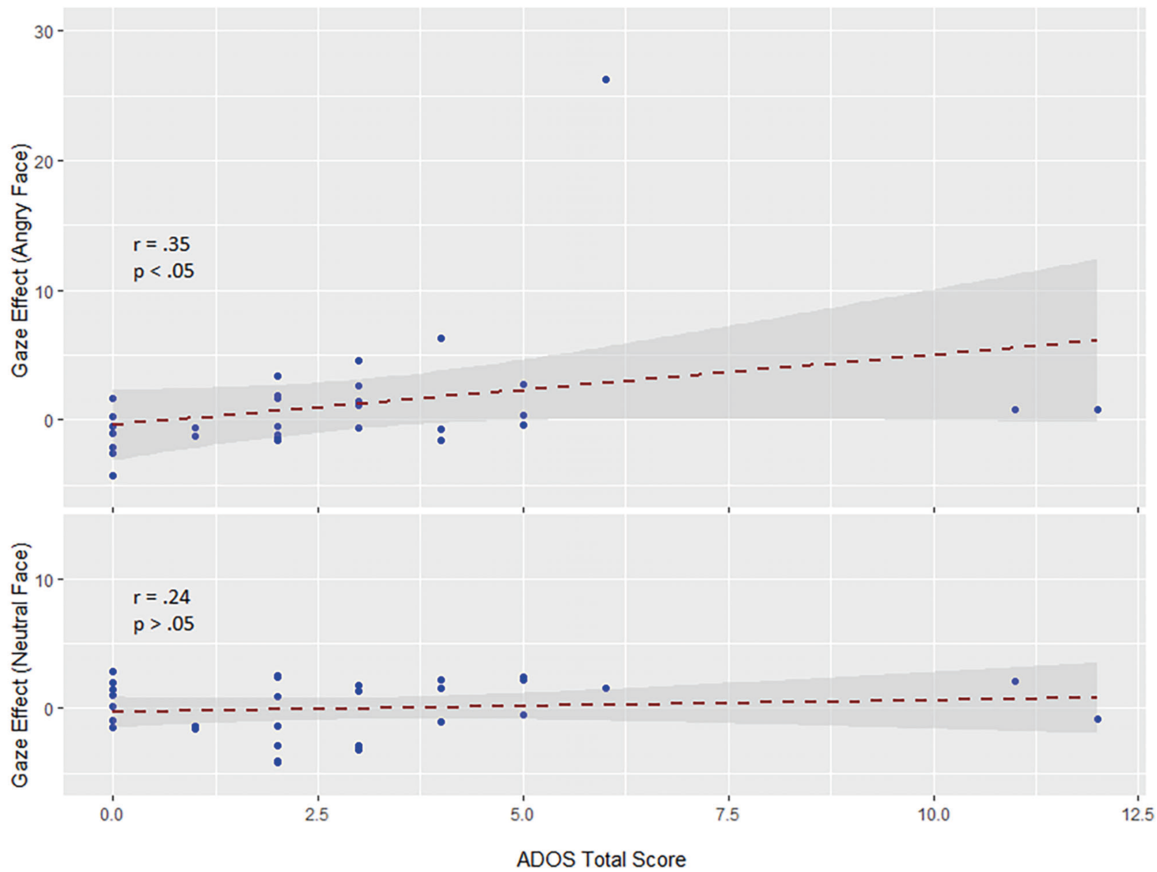

FIGURE 4 | Correlations between the sum sore of the ADOS scale and the gaze effect to angry (top) and neutral faces (bottom) (data are untransformed; correlation is Spearman). Exclusion of extreme values neither changed the positive slope nor the significance of the correlation ($r = 0.32$; $p < 0.05$).

task in Experiment 2 required the classification of facial emotions. In order to avoid ceiling effects, we used composite faces where two different emotions were shown in the top and bottom halves, one of which was to be classified. All faces were presented either with direct or averted gaze. Following the assumptions of the SSH, we expected that classification performance in approach-oriented emotions (e.g., happiness and anger) would be better when gaze was direct and in avoidance-oriented emotions (e.g., disgust and fear) when gaze was averted. This effect was expected to be diminished in autistic individuals.

In addition to measuring classification accuracy, we tracked the eye gaze behavior of the participants. If the relevant face half was at the bottom, we expected eye movements to be reflexively attracted to the eyes. This effect was assumed to be less pronounced in the ASD group. If the top half of the face was relevant, the particular emotion was expressed mostly around the eye region, that is, fixation on the eyes should be helpful for task performance. If individuals with ASD tend to avoid eye contact, we expected them to fixate less on the eyes than normal controls, especially in expressions with direct gaze.

Methods

Participants

By applying propensity score matching (Austin, 2011), 22 German-speaking TD children were matched by age (8–18 years), sex and intelligence with 22 children with a diagnosis of ASD (8 females and 14 males). The clinical diagnosis of ASD (DSM-V) was given or confirmed by an expert adolescent psychiatrist and substantiated by reviewing the medical files of the individuals in addition to the available diagnostic documents. More than half of the ASD sample received extensive clinical training targeting social competencies prior to study participation. In addition, subgroup of (n = 9) autistic children were reported by the clinician to be hitherto poorly trained with respect to social competence. The study was conducted in according to the Declaration of Helsinki and it was approved by the Ethics Committee of the University of Greifswald.

Stimuli

Stimuli were taken from the child affective facial expression (CAFE) database (LoBue, 2014; LoBue and Thrasher, 2015) consisting in 48 images of 8 different identities. Faces of four girls and four boys (between the ages of 4.6 and 6.8 years) displaying expressions of six basic emotions were selected according to the accuracy of the expression. The images were modified and optimized for the experimental design (see **Figure 5**) using Adobe Photoshop CS6 2012 (by Adobe Systems and the Adobe Photoshop development team © 1988–2016, Version 3.0 × 64).

The external features of the faces, such as ears and hairline were removed by overlaying an elliptical mask. Then, the faces were horizontally divided at the middle of the bridge of the nose. Thus, half-faces of each emotional expression and each individual picture were prepared for recombination. Face halves were reassembled within a given identity according to a composite design scheme. Nine different re-combinations per identity were created, yielding a total of 72 composite faces. Upper face halves showed fear, sadness, or anger, emotions that are most easily recognized in the top part of the faces and lower face-halves showed happy, surprise, or disgust, emotions that are best recognizable from the lower face (see **Figure 5**). The separation line between the face halves was always visible. Each composite face was 200 × 300 pixels in size. **Figure 5B** shows examples for composite faces of a female identity. Finally, 36 composite faces were edited to change gaze direction (18 faces each displaying left and right averted gaze) while 36 faces showed direct gaze.

Experimental Design

The emotional composite face task validly and reliably measures the ability to recognize emotion expression (e.g., Wilhelm et al., 2014; Hildebrandt et al., 2015). **Figure 5A** shows an example for one trial. Each trial began with a fixation cross presented for 200 ms in the middle of the screen, followed by a composite face together with six color-framed labels for the six emotions and a prompt ("TOP" or "BOTTOM") placed above the composite face, cueing which face half was to be categorized. Emotion labels and the face remained on the screen until a decision was made about the displayed emotion by clicking one of the emotion labels with the mouse. The task started with nine practice trials, where participants were given feedback about the correctness of their response. In the following experimental trials, no feedback was provided. In total, 72 experimental trials were presented in random order.

Eye Tracking

The gaze behavior of participants was tracked with a remote device [*Eye Tribe Tracker* (from *The Eye Tribe ApS* © 2013–2016)], recording binocular fixation positions in 60 Hz mode using an integrated camera. The eye tracker was placed below the monitor aiming at the eye region of the participant. Prior to the task, the device was calibrated twice by instructing the participants to follow the movements of a sphere across the screen with their eyes. If this calibration process was completed with satisfactory quality (at least three out of five "stars"), the experiment started. If necessary, participants were given feedback about the tracking quality on the screen, allowing to correct their sitting position, direction of view or posture. The distance to the eye tracker was individually adjusted to achieve the best possible measurement quality. During the experiment, participants were not to move their heads, but keep their eyes on the screen. The raw data of the eye tracker were converted into fixation points on the screen surface using a coordinate system. The resolution of the eye tracking system was 17 ms, which is also the lower bound of the fixation times. Worthy to mention, the eye tracking data was analyzed based on all eye gaze position at every time point.

Eye tracking behavior was analyzed in two ways. Firstly, the mean of the median vertical position on the screen was calculated for 10 consecutive intervals of 200 ms for a total of 2 s from stimulus onset. This was done for each combination of emotional expression, gaze direction of the face on display, and participant. Since the vertical position in the picture does not allow to address the question whether the eyes were directly fixated when participants looked at the upper half of the faces, we conducted an additional more fine-grained analysis of the fixation behavior in the upper face half. Three regions were defined in the upper face half, representing each eye and the area in between (see **Figure 5C**). Then, we determined the total fixation duration in each of these regions during four consecutive intervals of 500 ms after stimulus onset. From these fixation durations we calculated an eye avoidance index (EAI), reflecting the relative amount of time spent outside as compared to inside the eye regions

$$\mathrm{EAI} = \left(\mathrm{FD}_{\mathrm{inter-eye}} - \mathrm{FD}_{\mathrm{left\ eye}} + \mathrm{FD}_{\mathrm{right\ eye}}\right) / \mathrm{FD}_{\mathrm{upper\ face}}$$

where FD is the fixation duration, and the indices inter-eye, left eye, right eye, and upper face correspond to the designated face regions (see **Figure 5C**). The larger EAI, the less time is spent on the eye area if fixation is in the upper face half.

Results

Performance accuracy is shown in **Figure 6**. Clearly, fear was extremely difficult to classify and surprise processing was not influenced by gaze direction or group at all. We therefore confined all further analyses to the expressions of happiness, anger, disgust, and sadness, orthogonally combing the display in the top and bottom halves of the composite faces (anger and sadness vs. happiness and disgust) and the tendency to approach and avoid (happiness and anger vs. disgust und sadness). ANOVA with factors group and repeated measures on emotion (four levels) and gaze direction yielded a main effect of group, indicating that individuals with ASD showed lower accuracy than TD participants [$F(1,54) = 4.37$, $p = 0.04$, $\eta^2 = 0.0208$]. In addition, main effects of gaze [$F(1,54) = 7.34$, $p = 0.001$, $\eta^2 = 0.0119$] and emotion [$F(3,162) = 1.39$, $p = 0.001$, $\eta^2 = 0.0901$], and an interaction of emotion and gaze [$F(1,162) = 7.91$, $p = 0.001$, $\eta^2 = 0.0358$] were observed. As illustrated in **Figure 6**, these effects are due to variable performance accuracy across emotions ($M_{\mathrm{anger}} = 0.65$; $M_{\mathrm{disgust}} = 0.55$; $M_{\mathrm{happy}} = 0.56$; $M_{\mathrm{sadness}} = 0.36$), better emotion recognition for expressions with direct than averted gaze ($M = 0.56$ vs. 0.37) and the gaze effect depending on emotion, being largest for happiness, intermediate for anger and sadness, and intermediate for disgust. However, there was no significant interaction of group with emotion, gaze, or both factors (Fs < 1). The ANOVA was repeated for the subgroup of autistic children less trained in social competence. Again, no significant

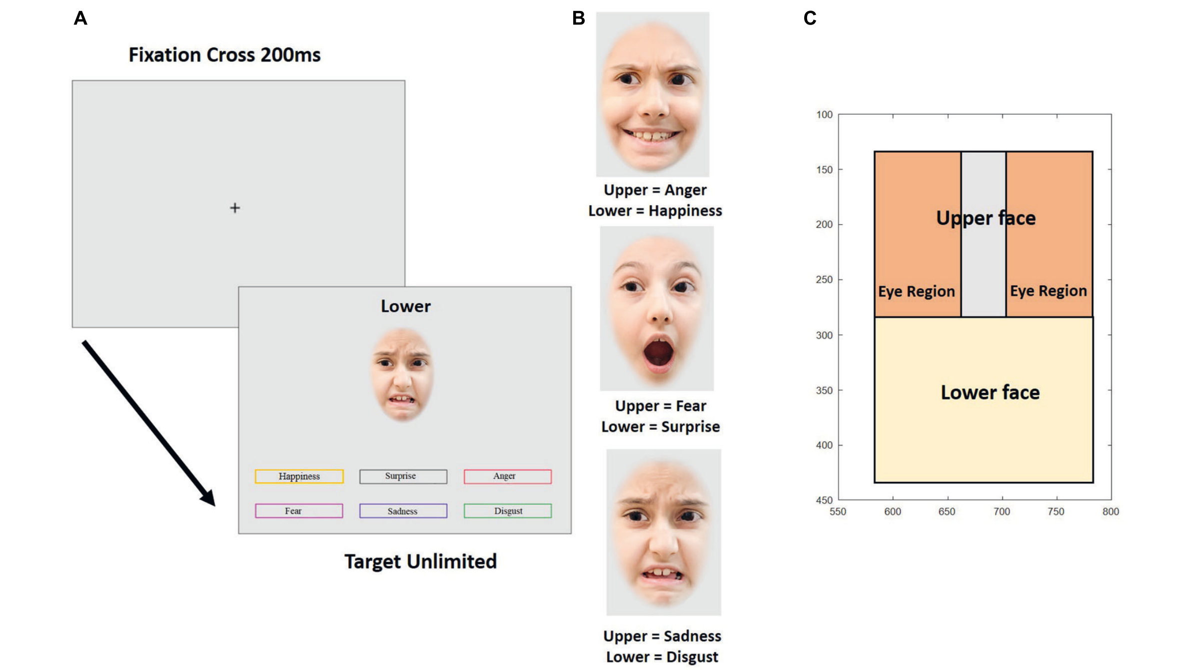

FIGURE 5 | Experiment 2. **(A)** Temporal sequence of a trial in the emotion composite task. Example trial with the target emotion "disgust" at the bottom half of the face. **(B)** Examples of emotional composite faces. **(C)** Parameterization of the variables for gaze behavior. The axes show pixels coordinates on the screen. The pictures are for illustration only and were neither taken from the CAFE database nor used in the experiment.

interaction between emotion and group [$F(1,48) = 0.71$, $p = 0.05$] was obtained. All other results were in line with those in the full sample.

Figure 7 visualizes the gaze behavior within the first 2 s of stimulus presentation. At around 500 ms after stimulus onset, a general tendency to look at the upper half of the faces (into the eye region or at the prompt) can be observed. This is either continued until the end of the recording epoch, or fixation turns toward the lower face half, depending on whether the upper or lower face half was task-relevant (i.e., anger, fear vs. happiness, disgust). In any case, there is no evidence for a differential main effect or interaction of emotion with gaze direction of the stimulus face for the participant groups. This impression was confirmed by ANOVA with factor group, and repeated measures on gaze, for each emotion, which did not show any significant interaction of group and gaze: angry [$F(1,42) = 0.92$, $p = 0.34$], happy [$F(1,42) = 0.37$, $p = 0.54$], disgust [$F(1,42) = 1.53$, $p = 0.22$], and sad [$F(1,42) = 2.55$, $p = 0.11$].

Figure 8 shows the EAI for each emotion and gaze direction of the composite face, superimposed for the two groups. The EAI index indicates that except for disgust, there is mostly an overlap between the groups. For disgust, however, the EAI revealed an interaction of group and gaze direction of the stimulus face, as confirmed by the ANOVA of the EAI with factor group and repeated measures on time [$F(1,42) = 6.99$, $p = 0.01$, $\eta^2 = 0.0256$]. *Post hoc* tests showed an effect of gaze direction for TD children [$F(1,29) = 18.03$, $p = 0.001$] who looked more at the eyes when gaze was direct than when it was averted. In contrast, in the ASD group there was no effect of gaze direction [$F(1,29) = 0.68$, $p = 0.4.09$].

Discussion

In Experiment 2 we investigated the ability to recognize emotions from facial expressions and its modulation by gaze direction in ASD and TD children by means of the emotion composite task. The observed overall lower performance of the ASD group as compared to TD children might reflect a global deficit in categorizing facial expressions as reported in many other studies (Wong et al., 2008; Chronaki, 2016). However, since we had no non-emotional control task, it might also reflect a more general phenomenon in the ASD group, e.g., task compliance related differences between the groups.

Gaze behavior was strongly modulated by the position of the relevant face half. For emotions in the lower half (happiness, disgust) there was a tendency to look at the upper face half after which fixation returned to the lower half. Importantly, this was not modulated by the gaze direction of the picture nor by the participant group. For the emotions displayed in the upper face half, the participants' fixations remained in this part but again, there was no modulation by picture gaze or group. In contrast with Tanaka and Sung (2016), it is noted that none of the present findings support the active avoidance of eyes in ASD individuals, even in direct gaze conditions, which should have been evident in our EAI.

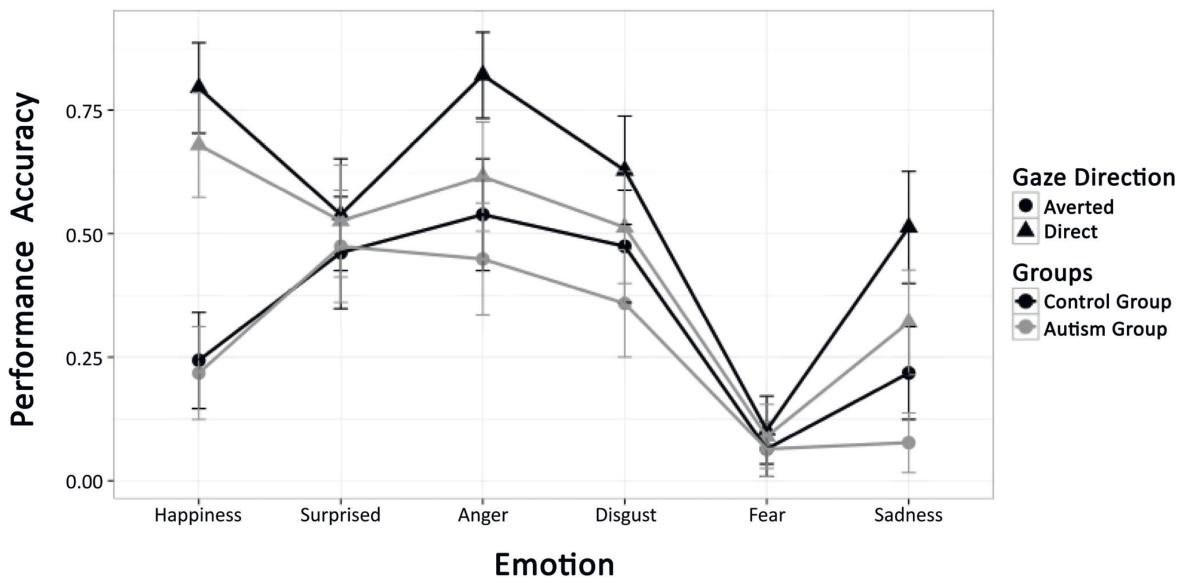

FIGURE 6 | Mean performance accuracy of the ASD and TD groups for all emotion conditions and direct and averted gaze of stimulus faces.

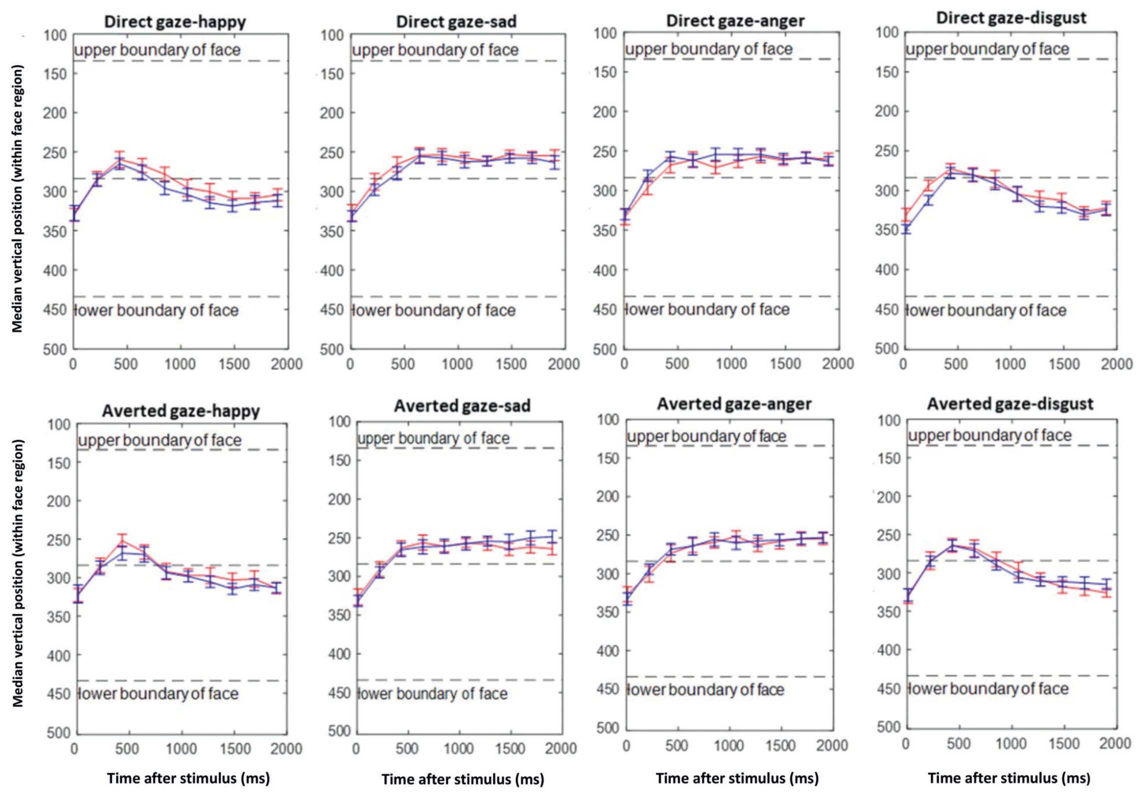

FIGURE 7 | Emotion composite task. Mean of median vertical gaze positions of the ASD (red) and TD (blue) groups during the first 2 s after stimulus presentation in consecutive time bins of 200 ms.

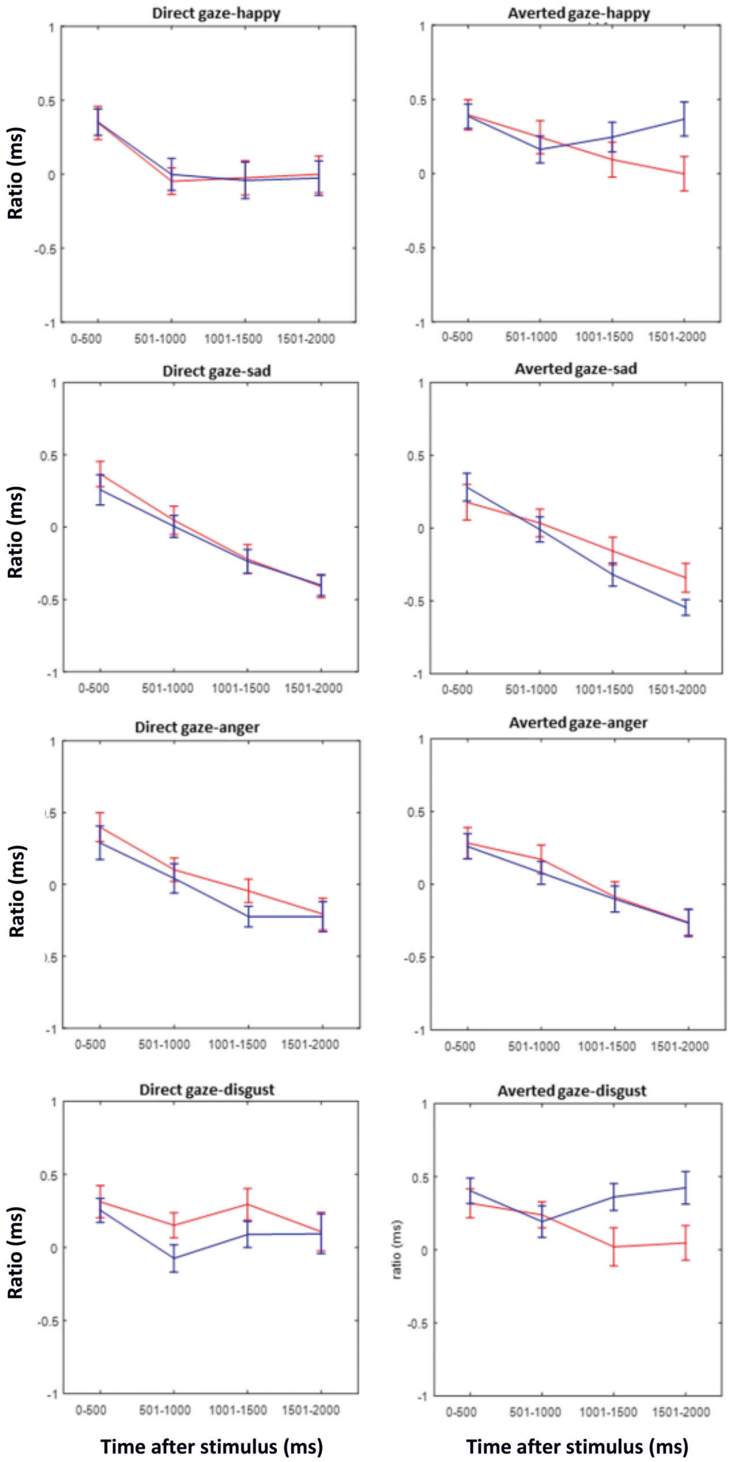

FIGURE 8 | Eye avoidance index (EAI) for the ASD (red) and TD (blue) groups during the first 2 s after stimulus presentation in intervals of 500 ms for all emotions and both gaze directions of the stimulus faces.

Nevertheless, a difference between the groups was present when disgust was the relevant emotion to be classified and when the EAI was considered. According to this index, when the relevant (bottom) face half showed a disgusted expression, TD children looked more at the eyes of the composite face when gaze was direct than when it was averted. Since the prompted face half was in the lower part of the composite face, this effect should be considered implicit, maybe a reflexive eye contact even though it was task-irrelevant. In stark contrast, no such effect was present in children diagnosed with ASD. These findings point toward an insensitivity for gaze direction in the ASD group in an emotion, where normal children are highly sensitive to gaze direction. It is of interest that disgust was the only emotion condition, where TD children showed such a gaze sensitivity. Therefore, the present results may not support an emotion specificity of this effect; the effect might well general to other emotions if the tasks were more sensitive.

GENERAL DISCUSSION

To our knowledge, this is the first study reporting on the interaction between facial emotion processing and gaze direction in children with different levels of autistic traits. Our starting point was that according to the SSH, approach-related emotions, for example, happiness and anger, are more easily recognized when the observer is directly looked at. In contrast, avoidance-related emotions, such as sadness and disgust, are better recognized with averted gaze. We expected that these benefits would be less pronounced or even absent in children with ASD as compared to TD children.

The present data provided some limited support of the SSH in its original form. In Experiment 1, the facial emotion expression was implicit and the gaze direction was incidental to the task. Yet, we did not find an interaction between emotion and gaze in the ERPs. In Experiment 2, when participants were required to explicitly categorize emotion expressions, performance was indeed best when gaze was direct. This effect was most pronounced for smiles and anger, which are both considered approach-related emotions. However, the avoidance-related emotion, sadness, revealed a similar effect as anger, and disgust recognition was facilitated by direct as compared to averted gaze, albeit with a relatively small effect.

Although the SSH cannot only partially account for the full pattern of associations revealed by the present data in TD children, we found some evidence that autistic trait is related to diminished sensitivity to gaze in the context of processing facial emotions. Although there was no interaction of gaze direction and emotion at the group level in Experiment 1, the gaze effect in the N170 amplitude elicited by angry faces correlated positively with the ADOS score. This correlation is broadly in line with the SSH, which assumes an interaction between eye gaze and emotion. Thus, when gaze direction (from direct to averted in our experiment) was combined with the intent communicated by a specific expression (anger in our study), the perceptual analysis of that emotion was enhanced. Therefore, the observed correlation between the N170 gaze effect in angry faces and its attenuation with increasing ADOS seems to fit the hypothesis: avoiding/averting gaze is a signal shared with the non-affiliative emotion of anger in neurotypical (low ADOS) individuals. And the loosening or reversal of this association at higher ADOS scores is in line with what one might expect for higher autistic trait expression. Hence, these data are consistent with the observation that in a naturalistic setup, in which dynamic emotional gaze cues require the integration of emotional information and gaze information, individuals with ASD differ from TD individuals in their responses to eye gaze in emotional faces.

Although in Experiment 2 only a global deficit in emotion recognition, independent of the particular emotion and gaze direction was found between in the ASD relative to the TD group, eye tracking data revealed that TD children fixated longer on the eyes when the facial emotion expression was disgust, while the ASD group did not demonstrate such pattern. Again, this would indicate a lack of sensitivity for gaze direction in the ASD group in the context of a specific emotion. Hence, together, our results indicate a partially diminished sensitivity in processing gaze direction in emotional faces among children with ASD or high in autism trait. The relative indifference to gaze direction may be an important problem in understanding emotional expressions where gaze is an important constituent. Therefore, the present findings show that indirect multimodal measures of emotion/gaze processing may be able to uncover subtle deficits of ASD-related traits, where performance is not sensitive enough to indicate such problems. The present findings indicate that it would be promising to increase the spectrum of emotions investigated while combining eye tracking in unrestrained viewing conditions in stimuli with varying gaze behavior. Recent methodological advances, such as the co-registration of EEG and eye movements (Dimigen et al., 2011) and the employment of dynamic stimuli in gaze-contingent display situations (Stephani et al., 2020) already make such an approach feasible.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by review board of the Hong Kong Baptist University and Ethics Committee of the University of Greifswald. Written informed consent to participate in this study was provided by the participants' legal guardian/next of kin. Written informed consent was obtained from the individual(s) for the publication of any identifiable images or data included in this article.

AUTHOR CONTRIBUTIONS

SB-A: conceptualization, methodology, investigation, formal analysis, and writing – original draft. GL: investigation and writing – review and editing. GO: formal analysis and writing – review and editing. CZ: writing – review and editing. AH: resources, conceptualization, methodology, and writing – review and editing. WS: conceptualization, methodology, writing – original draft, and supervision. ML: conceptualization, methodology, writing – original draft, and resources. All authors contributed to the article and approved the submitted version.

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Motherhood alters the Neural Correlates of Processing Infant Faces, their Emotional Expressions and Gaze Direction: An ERP Study

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Abstract

As a social species, humans use their face to transmit interpersonal signals. The emotional expression of a face and the direction of eye gaze are both highly relevant cues for social interaction. The postpartum period in mothers has been suggested to be special in terms of facial expression decoding and eye contact behavior. However, the neural correlates of this altered processing of faces during motherhood are still poorly understood. In the present study, we recorded event-related brain potentials (ERPs) from 59 mothers of infants and 55 age-matched nulliparous women (never having born offspring). To both groups, we presented pictures of adult and infant faces with neutral, happy, or angry expressions. At initial presentation, each face showed either a direct or averted gaze; after one second the direction of eye gaze changed in most trials but in some did not, while the expression remained the same. Participants detected the gaze changes. We replicated previously reported electrophysiological effects of gaze direction and emotion. Compared to adult faces, infant faces elicited a larger N170 component and a larger early posterior negativity (EPN), especially when they displayed an angry facial expression. Both effects were more pronounced in mothers than in nulliparae, and particularly so, when an angry infant face dynamically directed its gaze towards the mother. Altogether, the present results suggest that mothers show (1) an enhanced structural encoding of infant faces and (2) stronger reflexive emotion effects in response to infant faces that display emotional expressions together with dynamic gaze movements. Hence, mothers can be characterized by greater sensitivity to emotional children faces at the level of structural face encoding and reflexive attention.

Keywords: gaze direction, facial expressions, motherhood, infant faces, N170, EPN

1. Introduction

For the well-being and social-emotional development of infants it is import that caregivers accurately and promptly respond to their needs. Facial expressions represent a main modality of infant communication (Ferrey et al., 2016; Leyh et al., 2016). Therefore, caregivers need to understand this information and respond appropriately. In preparation for maternal behavior, the brains of mothers undergo multiple structural and functional adaptations under the influence of hormones (Hoekzema et al., 2017; Kim et al., 2010). It is commonly believed that these neurohormonal changes also facilitate mothers' sensitive caregiving and responsiveness to the infants' facial signals (see Deans, 2020, for a review). Essentially, hormones modulate brain activity in areas associated with social cognition and thus appear to be central neuromodulators for interpersonal perception and communication (Febo et al., 2005). Previous research indicates that higher levels of maternal hormones such as oxytocin facilitate the decoding of facially expressed emotions, enhance facial processing by increasing the focus on the eye region and increase the orienting of attention according to gaze cues (Guastella et al., 2008; Kanat et al., 2015; Theodoridou et al., 2009). Conversely, evidence has shown the direct gaze of mothers enhances facial recognition and processing by infants and increases engagement in nteraction with her (Farroni et al., 2007; Rigato et al., 2010).

Infant faces have distinct features that tend to draw the observer's attention, such as a large head and eyes, chubby cheeks and small nose (DeBruine et al., 2016; Glocker et al., 2009; Luo et al., 2015; Thompson-Booth et al., 2014). Mother-infant interaction including mutual gaze is positively associated with the development of the infant's attentional control (Niedźwiecka et al., 2018), language learning (Topping et al., 2013; Wu et al., 2014) and socio-emotional skills (Abraham et al., 2016; Cerezo et al., 2008; MacLean et al., 2014). Consequently, an infant's facial cues and eye gaze seem to be important elicitors of caregiver responses, prompting mothers to employ a range of playful or soothing behaviors for the infants.

A deeper understanding of face processing by mothers (and fathers) can be achieved by considering the time course of the neurocognitive processing of infant face cues. To this end, a number of studies have employed electroencephalography (EEG) and measured event-related potentials (ERPs), benefiting from the millisecond temporal resolution of these measures. Some studies have reported neural responses to infant stimuli (see Maupin et al., 2015 and Vuoriainen et al., 2022 for reviews) and variously tested whether becoming a parent and the experience of parenting, modulates the brain-electric responses to a child's face (as compared to adult's faces). Noll et al. (2012) and Peltola et al. (2014) found no difference in the processing of infant faces between mothers and nulliparous women (never having born offspring). Other studies investigated whether parental ERPs are augmented in response to images of one's own versus other's children and found that parents typically respond stronger to the face of their own child (Bernard et al., 2018; Grasso et al., 2009; Kuzava & Bernard, 2018; Weisman et al., 2012). Others addressed whether variations in mothers' ERP responses to their own child's face are associated with parenting quality. Thus, Bernard et al. (2015) reported that larger responses to emotional infant faces were associated with greater parental sensitivity. Groh and Haydone (2018) and Leyh et al. (2016) found that an insecure attachment style of mothers was associated with larger ERP responses specifically to pictures of distressed infant faces (negative stimuli), whereas in securely attached mothers, responses to positive and negative infant stimuli were hard to distinguish.

Altogether, these findings indicate that there are pervasive – albeit not entirely consistent – associations of motherhood and the neural correlates of processing emotional facial expressions and eye gaze. In order to understand the degree to which motherhood is associated with socio-emotional abilities, it is helpful to identify the level or stage at which the eye gaze and facial emotion processing in mothers differs from nulliparae by means of ERP recording. Comparing responses to facial expressions of infants and adults will also advance our understanding how mothers perceive these expressions. In perspective, these findings would provide a basis for elucidating how mothers regulate their emotional expressions during non-verbal mother-infant interactions.

1.1 Neural correlates of emotional facial expression and eye gaze processing in motherhood

ERPs allow to study the different stages of information processing in response to short-lived and dynamic events such as eye gaze and emotional expressions. In particular, the excellent temporal resolution of ERPs can reveal whether motherhood influences the early structural processing of faces or later stages of face processing, which involve the allocation of attention and the assignment of significance to a face. For present purposes, the most important components of the ERPs are the N170 and the early posterior negativity (EPN). The N170 is an occipito-temporal negativity that peaks around 170 ms after stimulus onset. It is greatly enhanced for face stimuli as compared to most other objects and typically lateralized to the right hemisphere (Eimer, 2011). The neural generators of the N170 have been traced to visual face-sensitive areas, such as the fusiform gyrus (Deffke et al. 2007 Eimer & Holmes, 2002; Gao et al., 2019), the occipital face area (Rossion et al. 2000) or superior temporal gyrus (Itier & Taylor, 2004; Nguyen & Cunnington, 2014). The N170 is interpreted as indicator of structural encoding of facial features (Bentin et al., 1996; Carmel et al., 2002; Eimer, 2011) and can also be modulated by emotional expressions (Bagherzadeh-Azbari et al., 2022; Hinojosa et al., 2015; Rellecke et al., 2011, Stephani et al., 2020). However, some of the reported emotion effects on the N170 might be due to differences in low-level facial features, for example, visible teeth (DaSilva et al., 2016) or temporal overlap with the early onset of the subsequent EPN component rather than to modulations of the N170 itself (Rellecke et al., 2013).

During pregnancy, women show increased N170 amplitudes when looking at faces, indicating that their ability to structurally analyze faces is enhanced (Raz, 2014). After pregnancy, mothers show larger N170 responses to their own infant's face as opposed to another's infant face (Weisman et al., 2012), indicating heightened perceptual processing of their own infant faces.

Consistent with the generally enhanced sensitivity to faces, the processing of emotional facial expressions also appears to differ as a function of motherhood. Larger N170 amplitudes were observed in pregnant women looking at angry faces as compared to neutral faces (Raz, 2014) and in mothers looking at happy as compared to neutral infant faces (Rutherford et al., 2017). Complementary results also indicate an increased sensitivity of the N170 component to emotional facial expressions in non-neglectful as compared to neglectful mothers. The former showed significantly larger N170 amplitudes to crying infant faces than to neutral or laughing faces, whereas neglectful mothers showed small N170 amplitudes for all emotional expressions (Rodrigo et al., 2011). These findings indicate a special role of the interaction between mothers and infants in terms of early face processing.

The N170 is particularly sensitive for isolated eyes, which can elicit even larger brain responses than complete faces (Bentin et al., 1996; Parkington, & Itier, 2018). Given that the N170 is associated with the structural encoding of faces, the eye sensitivity of the N170 underlines that eyes play an outstanding role among the facial features (Parkington & Itier, 2018). Studies addressing the role of the N170 in processing gaze direction have shown differences in N170 amplitude between direct and averted gaze. In brief, larger amplitudes for N170 have been found in response to faces with averted gaze (when the eyes look away from the participant/observer) as compared to direct gaze (when the eyes appear to look directly at the participant/observer; Bagherzadeh-Azbari et al., 2022; Latinus et al., 2015; Stephani et al., 2020). In a previous study, Bagherzadeh-Azbari et al. (2022) observed larger N170 amplitudes in response to averted than direct gaze during the initial presentation of a face. A subsequent gaze shift in the face stimulus face, elicited an N170 that was larger when the gaze moved from direct (at the observer) to averted as compared to averted to direct.

Structural encoding of the eyes and their importance is also reflected in mothers' more frequent and longer eye fixations toward their infant's eyes (De Pascalis et al., 2017). Doi and Shinohara (2012) extended this work by evaluating maternal sensitivity to child gaze direction as a basis for the dyadic relationship between mothers and infants. In their study, mothers showed larger N170 amplitudes when viewing their own child's face with direct rather than averted gaze, which was not the case for unfamiliar children. The authors suggested that gaze information from a mother's own child with direct gaze induces differential neural responses already at early perceptual stages of face processing, thereby producing a significant interaction between facial familiarity/identity and gaze direction (Doi & Shinohara., 2012).

The ERP components following the N170 are associated with more elaborated processing (Recio et al., 2014; Schacht & Sommer, 2009). Of particular interest here is the early posterior negativity (EPN) that can be regarded as indicator of the attention directed at emotional stimuli, among others of faces with emotional expressions. The EPN is observed at occipito-parietal sites and emerges as early as around 150 ms after face onset (Rellecke et al., 2011). While this onset latency is similar to that of the N170, the EPN lasts much longer, sometimes until about 600 ms, and typically reaches a maximum around 260 - 280 ms after face onset (Bagherzadeh-Azbari et al., 2022; Schacht & Sommer, 2009; Schupp et al., 2006). The EPN is generally seen as a component that indexes the reflexive allocation of visual attention towards a stimulus (Schupp et al., 2006). Its amplitude is affected by the emotional arousal-value of the stimulus, and therefore larger for emotional as compared to neutral stimuli. However, the EPN amplitude frequently does not differ between positive versus negative emotional valence (Recio et al., 2014). It should be noted that differences in EPN amplitude have also been observed for non-emotional facial movements, such as for (relatively large) jaw movements as compared to (relatively small) eye blinks by the stimulus face (Recio et al., 2014).

There is some evidence that in comparison to nulliparae, mothers show greater attentional bias with emotional facial expressions and infant faces, which is thought to be biologically salient to the mother and incentivize caregiving behavior (e.g., Ferrey et al., 2016; Thompson-Booth et al., 2014) This maternal bias towards infant emotion has also been found in functional magnetic resonance imaging (fMRI) with stronger activation to crying as compared to laughing infants (Seifritz et al., 2003). In EEG, Peltola et al. (2014) found larger EPN amplitudes in mothers who viewed distressed rather than happy infant faces when the task required focusing attention on these faces; this difference was not found in non-mothers.

Other commonly reported ERP components in studies measuring brain responses to infant or children faces are the late positive potential (LPP) and the P300 (Doi & Shinohara, 2012; Endendijk et al., 2018; Kuzava & Bernard., 2018; Kuzava et al., 2019; Peltola et al., 2014). As an example, Doi and Shinohara (2012) showed that mothers' P300 amplitudes were significantly larger in response to an unfamiliar child's gaze as compared to their own child's gaze, specifically in a direct gaze condition. Their finding suggests that eye-gaze may also modulate later stages of face processing, specifically regarding the attentional bias with infant stimuli in maternal samples (Doi & Shinohara., 2012).

In the present work, we will focus on the two components reflecting structural face encoding (N170) and reflexive attentional processing (EPN). In our previous study (Bagherzadeh-Azbari et al., 2022), the perception of gaze and emotional facial expressions interacted, as indicated by the dependence of the emotion effect on gaze change direction. During later stages of gaze processing (200-400ms), the EPN to happy facial expressions was stronger for faces with direct than for faces with averted gaze. From this finding, we concluded that happy faces reflexively attract attention when they look at the observer rather than away (Bagherzadeh-Azbari et al., 2022).

1.2 Motherhood sensitivity to infant signals

Our attention is easily drawn towards infant faces. Using a reaction time task, Thompson-Booth et al. (2014) reported that although infant faces captured attention more strongly than adult faces in both mothers and nulliparae, the attentional bias towards infant faces was more pronounced in mothers. There are not many ERP studies investigating the effect of motherhood on child face processing at either earlier structural encoding stages (N170) or at later, more elaborate processing stages (EPN). Larger N170 and EPN responses to child's faces in parents as compared to adults without children could indicate increased perceptual processing and sustained attention to parenting-relevant cues, potentially due to neural and hormonal changes associated with the transition to motherhood or greater experience with infant faces. As mentioned above, there is some evidence that parental status modulates N170 and EPN (and some later ERP components like LPP) in response to children's faces, but the initial findings have been inconsistent (Noll et al., 2012; Peltola et al., 2014; Proverbio et al., 2006; Weisman et al., 2012). Thus, regarding N170, Weisman et al. (2012) found a larger N170 response to children's faces in parents compared to single non-parents, whereas other studies found no difference between mothers and nulliparous women (Noll et al., 2012; Peltola et al., 2014). Proverbio et al. (2006) found smaller N170 (their N160) amplitudes in mothers compared to fathers, while there was no difference between male and female non-parents. Regarding the EPN, it appears that only Peltola et al. (2014) investigated it in parents. They observed larger EPN responses to child's faces in parents compared to non-parents. Furthermore, Weisman et al. (2012) found smaller LPP amplitudes to (unfamiliar) infant faces in parents as compared to non-parents.

1.3 Aims and Hypotheses

In the present study we investigated the influence of motherhood on the effects of emotional expressions, eye gaze, and their interactions in a similar paradigm as used by Bagherzadeh-Azbari et al. (2022). Motherhood was investigated by comparing a large group of mothers with infants below 6 months of age and nulliparae. Specifically, we asked whether there are any processing differences due to motherhood and if so, can they be functionally localized at the early stage of structural face encoding, as indicated by the N170 component or at a later stage, as indicated by the EPN. In other words, the modulation of N170 and EPN components by emotion, stimuli age, direction of the gaze and motherhood and their interaction in early and late ERP stages could elucidate how information is being differentially integrated into the assessment of face stimuli in mothers as compared with nulliparae. Based on our previous findings we argue that both gaze and emotion are properties that can provoke attention (Dolcos et al., 2020), giving rise to interactions at the EPN stage of processing (Bagherzadeh-Azbari et al., 2022). However, if motherhood is associated with gaze and emotion processes, the interaction should be replicated for adult faces but enhanced for infant faces.

More specifically, we addressed the following questions. Firstly, we aimed to replicate the N170 and EPN findings about emotion and gaze direction in a nonsocial (gaze change detection) task and their interaction. Second, we aimed to study the association of motherhood with gaze and emotion processing and their interplay and investigate whether this depends on stimulus age (adult versus infant stimuli). Finally, we explored whether the associations above differ between static versus dynamic gaze. In order to address these questions, we presented infant and adult faces that displayed a happy, angry, or neutral expression in combination with direct or averted gaze directions (see Fig. 1). After one second, in 80% of the trials, the gaze direction changed, while the emotional expression remained the same. This design allows to analyze ERPs both, relative to the initial presentation of the face (in the following termed *initial gaze phase*) as well as, relative to the subsequent gaze change (*gaze change phase*). Importantly, we used a "non-social" task (Latinus et al., 2015) in which participants merely had to detect whether the gaze had changed direction during the trial or not. We chose this task because Latinus et al. (2015) had shown that gaze direction effects on the N170 are predominantly seen in such non-social tasks but not in "social" tasks, where participants decide, for example, whether the stimulus face is looking at them.

For the N170, we expected to replicate our previous findings (Bagherzadeh-Azbari et al., 2022, Stephani et al., 2020) of larger amplitudes for averted relative to direct gaze in the initial gaze phase and larger amplitudes for direct-to-averted as compared to averted-to-direct gaze changes in the gaze change phase. These predictions are also in line with Itier et al. (2007) who observed larger N170 amplitudes for averted gaze in static images and Latinus et al. (2015) and Puce et al. (2000) who found corresponding effects in dynamic gaze changes. Based on Rutherford et al (2017) and Raz (2014) who showed larger N170 amplitudes in mothers when looking at faces compared to nullipara, we also expected larger amplitudes for gaze aversions in mothers compared to nullipara.

The N170 is sensitive to both structural properties of faces (Eimer, 2011) and, at least in some studies, to emotional expressions (Bagherzadeh-Azbari et al., 2022; Rellecke et al., 2013; Stephani et al., 2020). Based on the findings of Rodrigo et al. (2011) that the sensitivity of the N170 to emotional facial expressions is increased in mothers, especially for crying infant faces, we anticipated larger N170 amplitudes for emotional faces in mothers, specially to anger relative to neutral expressions in infants.

Since the N170 to facial expression reflects sensitivity to structural face properties, we expect larger N170 amplitudes for infant faces with their distinct facial features as compared to adult faces, as reported by (DeBruine et al., 2016; Glocker et al., 2009; Luo et al., 2015; Thompson-Booth et al., 2014; Weisman et al., 2012).

In the time window following the N170, after 200 ms, we expected the classic EPN finding during the initial gaze phase, that is, more negative amplitudes for happy and angry faces relative to neutral expressions (e.g., Schacht & Sommer, 2009) for both mothers and nullipara. Based on Peltola et al. (2014) who reported larger EPN amplitudes in mothers to distressed infant faces compared to infant faces displaying pleasure, we expected larger EPN amplitudes to infants showing angry emotions in mothers as compared to non-mothers.

2. Materials and Methods

2.1 Participants

The women participating in the present study were recruited through flyers, a German website for small ads ("eBay Kleinanzeigen"), advertisements on Facebook, in news magazines, a maternity ward photographer, gynecologists and obstetricians. Participants were required to be either nulliparous (non-mothers) or the mother of a child of two to six months of age; additionally, they should be between 18 to 50 years old, currently living in a heterosexual partnership, highly proficient in German, without a history of psychological or neurological disorders or the intake of psychoactive medication or recreative drugs and report normal or corrected-to-normal visual acuity. Overall, 120 women were enrolled. Six had to be excluded because of excessive loss of EEG data during preprocessing, resulting in a final sample of 58 mothers and 56 nulliparae. Of the mothers, 49 were exclusively breast-feeding their infant at the time of the experiment, whereas nine were exclusively bottle-feeding. The mothers' mean age was 30.4 years (SD = 5.01, range 19-44) and the mean age of their infants was 4 months (SD = 1.1, range = 1.9-6.2 months). The mean age of the nulliparae was 24.8 years (SD = 4.4, range 18-34). All participants, but one, were right-handed (M = + 91.40, SD = 24.57), as assessed by the German version of the Edinburgh Handedness Inventory (Oldfield, 1971). Moreover, educational backgrounds were heterogeneous; 67.3% of mothers had a secondary school degree and 32.7% had an early or middle school degree; 75.5% of the nulliparae had a secondary school degree and 24.5% had an early or middle school degree. Participants provided written informed consent as approved by the institutional ethics review board of the Department of Psychology of the Humboldt-University at Berlin and received a compensation of 10, - Euros per hour.

With regard to our sample size 114 participants, we conducted a post-hoc power analysis with G*Power for a mixed-measures analysis of variance (ANOVA) with 2 groups and 4 measures aimed at detecting a small effect size of $f = 0.25$ (Cohen, 1988) with a power of 0.8 (Erdfelder et al., 1996). The correlation between measures was assumed to be 0.5. Power analyses showed a minimal sample size of $N = 24$ to detect a small within-subject effect, $N = 108$ for a small between-subjects effect, and $N = 176$, for the within-between interaction. Thus, with regard to small effects, the interaction analyses are underpowered and will be interpreted with caution.

2.2 Materials

Face stimuli were taken from the Radboud Database (Langner et al., 2010) and edited with Adobe Photoshop (version CC 2015, Adobe Systems, San Jose, CA). A total of 36 face identities (18 female, 18 male) with frontal views were selected. Each identity displayed three different expressions (neutral, angry, and happy), and a direct, left- and right-averted gaze. In addition, images of 40 Caucasian infants (20 male and 20 female identities) were taken from online media sources. Infants showed neutral expressions, happiness or anger (see Fig. 1 for examples). It was not possible to find identities of infants depicted with all three emotions required here; therefore, each identity showed only one of these expressions.

Images of adult and infant faces were edited such that the eyes were always located at the same horizontal and vertical positions within the picture (for details, see also Bagherzdeh-Azbari et al., 2022). Furthermore, all external features of the face (e.g., hair, neck, or visible clothing) were removed. Because gaze motion was created from static images by presenting two images with different gaze direction sequentially (see Fig. 1), we had to ensure that only eye gaze, but no other facial features, would change between the subsequently and seamlessly presented pictures with different gaze directions. Therefore, we edited the stimuli as follows: For each depicted individual and emotional expression of this individual, the eye region of the picture with a left- or right-averted gaze was copied and carefully pasted into the eye region of the corresponding picture with direct gaze using Photoshop (see Fig. 1 for an example). Thus, for each identity and emotion, we created three images showing an averted gaze to the left and to the right, and a direct gaze at the observer, everything else being exactly the same for a given identity and emotion.

2.3 Procedure

Stimuli were presented on a 22-inch CRT monitor (IIyama Vision Master Pro 512, vertical refresh: 160 Hz, resolution: 1024 × 768 pixel). The face images subtended 7.07 (vertically) × 9.41° (horizontally) of visual angle (or 280 × 210 pixel) and were presented in the center of the screen (using *Presentation* Software (Neurobehavioral Systems, Berkely, USA).

The experiment was implemented using *Presentation* software (version 18.10, Neurobehavioral Systems Inc, Albany, CA). Before the experiment proper, we collected prototypical eye-movement and blink artifacts to be used later for ocular artifact correction. Then, 12 practice trials were administered.

The experiment proper consisted of a total of 864 trials, which were presented in random order, with a short break after every 108 trials. As shown in Figure 1, each trial began with a fixation cross shown for 800 ms on a white screen. Then, the first image of a face appeared for 1000 ms, displaying one of three emotional expressions with either a direct, left-averted or right-averted gaze. The presentation of the first image was then seamlessly followed by the second image for another 1000 ms. In 20% of the trials, the second image was identical to the first one (no change trials). In the other 80% of trials, the second image showed the same emotional expression but a different gaze direction (gaze change trials). In other words, in these trials, the person's gaze direction changed. The second face image was shown for 1000 ms and followed by a blank screen, during which participants were asked to indicate by a button press with their left or right index finger whether or not a gaze change had occurred during the trial. Participants were told to focus on response accuracy. In case of a premature or incorrect response, feedback was given via a written statement in red ("Fehler", *error*) for 500 ms. After the button press, the next trial started. Participants were instructed to sit calmly, to look at the fixation cross while visible, and to avoid blinking during the presentation of the faces. They were encouraged to blink at the end of the trial, after the offset of the second image.

In the following, we will distinguish between the *initial gaze phase,* beginning at the onset of the initial face presentation, and the *gaze change phase*, beginning at the gaze change and lasting until the end of the trial. In the initial gaze phase, happy, neutral, and angry expressions appeared equally often and were orthogonally balanced with a direct, left-averted, and right-averted gaze direction. At the onset of the gaze change phase, in the 80% of trials in which a gaze change occurred, the gaze either change from a direct gaze to an averted gaze (in 50% of those gaze-change trials; with an equal probability of changing to left-averaged and right-averted), or it changed from an averted gaze (left- or right-averted) to a direct gaze in the other 50% of those gaze-change trials. There were no changes from an averted position to another averted position.

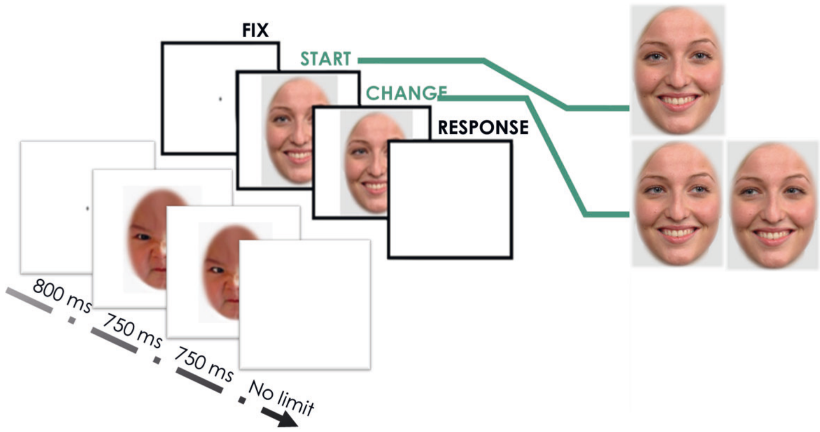


Figure 1. Trial structure, illustrated with two examples. A fixation cross (fix) was presented for 800 ms, followed by a first face image for 1000 ms (initial gaze phase), and a second image for another 1000 ms (gaze change phase). The second image involved a gaze change in 80% of the trials (as shown here). The second image was followed by a blank screen interval during which the participants indicated by a button press whether or not a change had occurred (response). The upper example shows a trial with an adult face, the lower example shows a trial with an infant face.

2.4 Data Acquisition

Participants were seated in an electrically and acoustically shielded recording chamber. The EEG was recorded from 47 Ag/AgCl electrodes using a BrainAmp DC amplifier (BrainProducts GmbH, Gilching, Germany). Most electrodes were placed inside an elastic electrode cap (Easycap, Herrsching, Germany) at standard positions of the International 10 - 10 System. Four electrodes were placed at the outer canthus and infraorbital ridge of each eye to record the electrooculogram. An additional electrode placed at FCz was used as ground. Electrode impedances were kept below 10 kΩ. During recording the EEG was referenced to the left mastoid, band-pass filtered at 0.1 to 250 Hz and digitized at a sampling rate of 1000 Hz with a 0.1 μV amplitude resolution.

2.5 Data Analysis

Response accuracy. Behavioral response data, collected by the *Presentation* software, was exported for analysis into the R Software for Statistical Computing (Version 3.2.2). Mean accuracy was calculated for each participant and condition and analyzed descriptively. Because the task was not speeded, response times were not analyzed.

EEG Data Preprocessing. EEG data preprocessing was performed in MATLAB R2019a (The MathWorks Inc., Natick, MA) and EEGLAB v14.1.1b (Delorme & Makeig, 2004). In a first step, the continuous EEG was first low-pass filtered at 30 Hz and then high-pass filtered at 0.03 Hz (passband edges) using EEGLAB's windowed sinc FIR filter (pop_eegfiltnew.m) with default transition bandwidth settings. Then, the EEG was re-calculated to an average reference.

Eye movement and blink artifacts were corrected using the surrogate variant of the Multiple Source Eye Correction procedure (MSEC; Berg & Scherg, 1994; Ille et al., 2002) as implemented in the BESA software (version 6.0, BESA GmbH, Gräfeling, Germany). The procedure of the MSEC correction followed the steps outlined in the Supplementary Materials of Dimigen (2020). Following the ocular artifact correction, the continuous EEG was segmented into 1.4 second epochs (lasting from -0.2 s to 1.2 s relative to the time-locking events).

For the initial gaze phase, the time-locking event was the onset of the face stimulus. A total of 864 epochs per participant resulted from 48 epochs per combination of gaze direction (averted, direct), stimulus age (infant, adult) and emotion (happy, angry, neutral). For the gaze change phase, the time-locking event was the gaze change (taking place in 80% of all trials), yielding a total of 691 epochs per participant, or 115 epochs for each of the twelve combinations of gaze change direction (averted to direct, direct to averted), stimulus age and emotion.

All epochs were baseline-corrected using a 100 ms pre-stimulus interval. To exclude epochs with residual artifacts (e.g. drifts or EMG bursts), we automatically scanned for voltages exceeding > ±80 µV in any of the channels and excluded those epochs. Following this procedure, 84.5% of all epochs remained for analysis.

As a last step, average ERPs were calculated for each participant and for both the initial eye gaze phase (aligned to face-stimulus onsets) as well as for the gaze change phase (aligned to the onset of gaze changes). In each phase, ERPs were averaged according to the factors emotion (happy, neutral, angry) and gaze direction. For the initial gaze phase, the latter factor distinguished direct gaze and averted gaze (averaging across left- and right-averted conditions) and for the gaze change phase it distinguished between eyes moving from *averted to direct* positions (i.e., averaged over both changes from left- or right-averted to direct) and eyes moving from *direct to averted* positions (i.e., averaged over both changes from direct to left- or right-averted); as mentioned above, there were no transitions from left-averted to right-averted or vice versa.

ERP parametrization. The N170 component was quantified using an occipito-temporal cluster of four electrodes consisting of the two bilateral pairs P7/P8 and PO7/PO8. To estimate the peak of the N170 component, we searched for the minimum voltage in each channel in a time window from 150 to 200 ms after stimulus onset (face onset or gaze change onset). The minimal (most negative) amplitude in this time range was taken as the N170 peak amplitude. The N170 latencies were not included in the scope of the present analysis.

For the EPN, the region of interest (ROIs) comprised the following ten electrodes: P7 / P8, PO9 / PO10, PO7 / PO8, O1 / O2, Oz, and Iz, following Rellecke et al. (2011) and Bublatzky et al. (2017). The EPN amplitude, averaged across all electrodes in the ROI, was quantified as the average voltages across four consecutive time windows: 200 – 250, 250 – 300, 300 – 350, and 350 – 400 ms, within both the initial gaze and the gaze change phases.

2.6 Statistical Analysis

Statistical analyses of ERP amplitudes were performed in R using the "ez" package (version 4.4-0, Lawrence, 2016) by means of analyses of variance (ANOVA) including the group factor motherhood (nulliparae, mothers). For the ERP amplitudes as dependent variable, repeated measures were added on the factors *Emotion*, *Stimulus age* and *Gaze direction*. For the initial gaze phase, gaze direction involved the levels *direct* versus *averted* gaze and for the gaze change phases the levels were *direct-to-averted* versus *averted-to-direct*. For the N170 component, *hemisphere* was included as an additional two-level repeated measures factor. The sphericity assumption was assessed using Mauchly's test and adjustments were made applying Huynh-Feldt correction, if needed. Multiple comparisons were performed between emotional categories, and *p*-values were corrected using the Tukey Honestly Significant Differences (HSD) method.

3. Results

In the following, we will first report the results for initial gaze phase (ERPs locked to stimulus onsets) and then for gaze change phase (ERPs locked to gaze changes). Within each phase, we first report results regarding the N170 and then the EPN component.

4.1 Behavioral results

Overall response accuracy in the change detection task was high with a mean accuracy of 98.21% (*SD* = 0.02). No participant provided less than 91.42% correct responses.

4.2 Initial gaze phase

N170. Figure 2 shows the ERPs in the N170 ROI for the initial gaze phase. ANOVA revealed a significant main effect of stimulus age, $F(1, 112) = 183.23$, $p < .001$, $\eta^2 = .045$, with infant faces (*M* = -2.77 μV, *SD* = 4.38) eliciting much larger N170 amplitudes than adult faces (*M* = -1.06 μV, *SD* = 4.27). In addition, there was a significant main effect of emotion, $F(1, 112) = 69.98$, $p < .001$, $\eta^2 = .012$. Paired *t*-tests indicated that, as compared to neutral faces (*M* = -1.60 μV, *SD* = 4.32), both angry faces (*M* = -2.26 μV, *SD* = 4.42) and happy faces (*M* = -1.89 μV, *SD* = 4.46) showed larger N170 amplitudes ($p < .001$). Moreover, the contrasts between angry versus neutral faces ($p = .019$, $d = 0.06$) and angry versus happy faces indicated significant differences ($p = .019$, $d = 0.06$). However, no significant difference was observed between happy and neutral faces; please see Table 1 for full statistical details and effect sizes for the post-hoc comparisons. There was also a significant main effect of hemisphere, $F(1, 112) = 12.27$, $p < .001$, $\eta^2 = .021$, with larger amplitudes over the right (*M* = -2.49 μV, *SD* = 4.52) than over the left hemisphere (*M* = -

1.34 μV, *SD* = 4.24). Importantly, gaze did not yield a main effect ($F < 1$) nor was there an interaction between gaze direction and emotion ($p > .05$). Interestingly, a significant interactions of Emotion and Group was obtained, $F(2, 224) = 3.36$, $p = .03$, $\eta^2 = .001$. Tukey HSD pairwise comparison showed that in mothers (but not in nulliparae) angry faces elicited larger N170 amplitudes than neutral faces (Fig. 3, Table 1 for further details). Furthermore, there was a significant interaction of Emotion and Stimulus age, $F(2, 224) = 18.02$, $p < .001$, $\eta^2 = .001$. Tukey HSD pairwise comparison indicated that in all emotion conditions, the infant faces elicited larger N170 amplitudes than adult faces. However, N170 to angry infant faces was larger than for both neutral and happy infant faces (see Fig. 4 and Table 1 for details).

Table 1. Test statistics of post-hoc pairwise comparisons (Tukey HSD) of emotion effects on the N170 amplitude in the initial gaze phase.

Contrasts	**Effect Magnitude (μV)**	***95% CI***	***t*-statistic (*df* = 113)**	***p***	***Cohen's d***
		Emotion			
Angry - Neutral	-0.66	[-1.01, -0.31]	11.12*	< 0.001	0.15
Happy - Neutral	-0.28	[-0.63, -0.05]	5.70	0.11	0.06
Angry - Happy	-0.37	[-0.71 -0.03]	6.21*	0.02	0.08
		Emotion x Group			
Angry - Neutral (mothers)	-0.74	[-1.32, -0.16]	19.11*	0.003	0.11
Angry - Neutral (nulliparae)	-0.58	[-1.17, 0.02]	21.07	0.07	0.07
		Emotion x Stimulus age			
Angry - Neutral (infant)	-1.02	[-1.59, -0.44]	27.62*	< 0.001	0.22
Happy - Neutral (infant)	-0.42	[-0.99, 0.15]	9.95	0.29	0.00
Angry - Neutral (adult)	-0.31	[-0.88, 0.27]	13.64	0.65	0.16
Happy - Neutral (adult)	-0.15	[-0.73, 0.42]	5.47	0.97	0.14

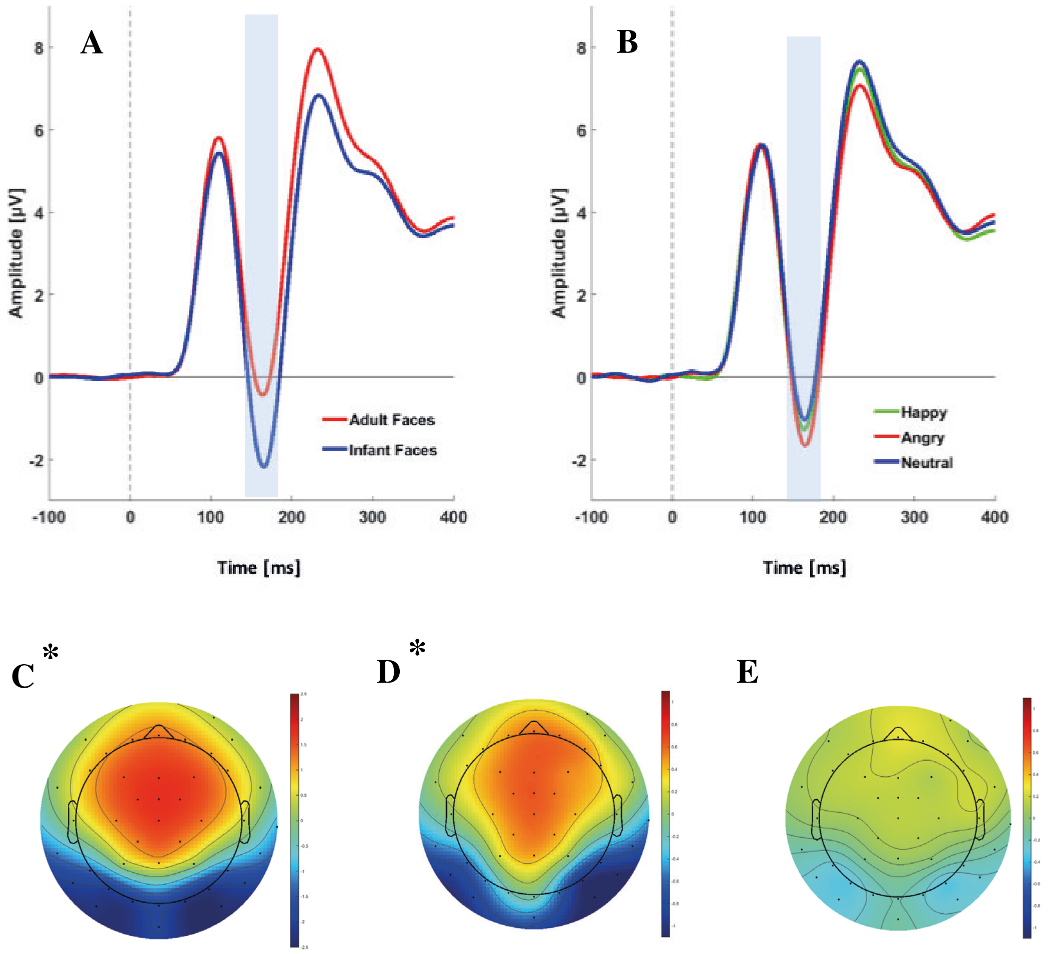


Figure 2. N170, initial gaze phase: Effects of stimulus age and emotion. Top: Grand mean ERPs for the N170 ROI (average of electrodes P7/P8 and PO7/PO8); the N170 time window is shaded. A and B: main effects of stimulus age and emotion, respectively. Bottom: topographies of the N170 effects. C: Stimulus effect (infant minus adult faces). D and E: Emotion effect; angry minus neutral and happy minus neutral, respectively.

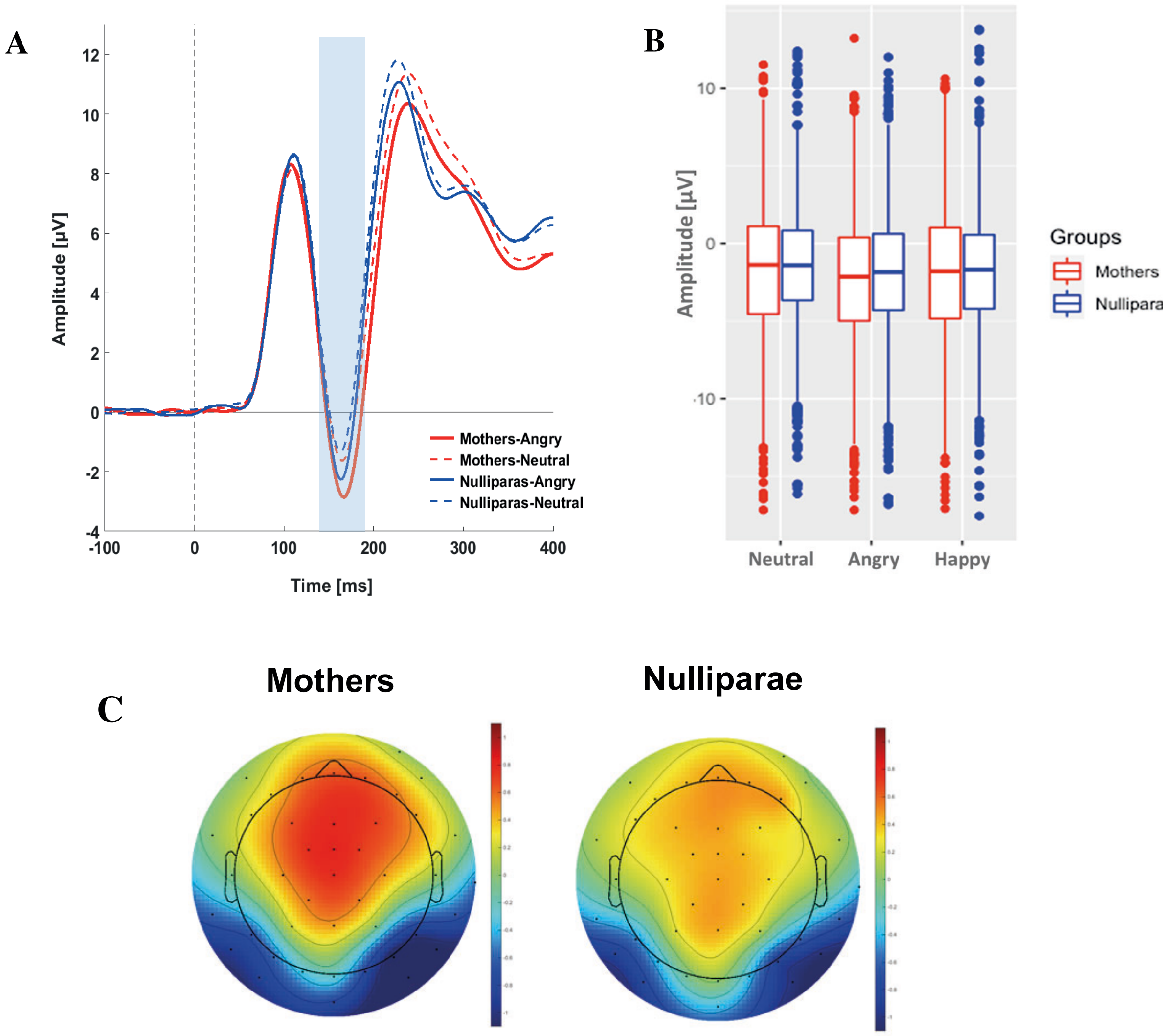


Figure 3. N170, initial gaze phase: interaction of emotional expression and motherhood. A: Grand mean ERPs for anger and neutral expressions in the N170 ROI (average of P7/P8 and PO7/PO8); the N170 time window is shaded. B: N170 amplitudes for the combinations of emotional expressions and group. C: Topographies of the differences anger minus neutral expression in the N170 time window for mothers and nulliparae.

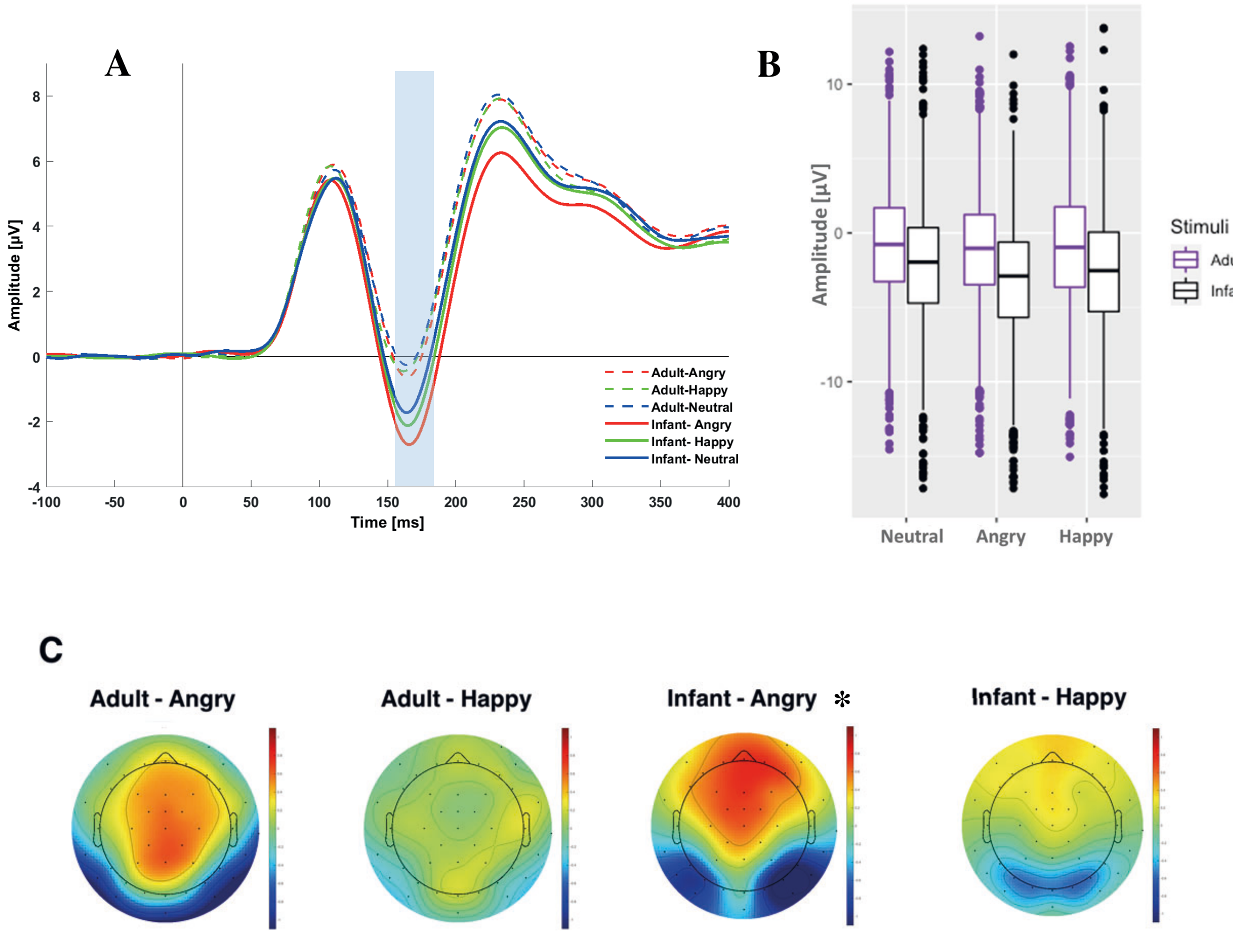


Figure 4. N170, initial gaze phase: interaction of emotional expression and stimulus age. A: Grand mean ERPs for the N170 ROI (average of electrodes P7/P8 and PO7/PO8); N170 time window is shaded. B: N170 amplitude for the combinations of emotional expressions and stimulus age. C: Topographies of the emotion effects (angry minus neutral and happy minus neutral) for each stimulus age.

EPN. ANOVAs of EPN amplitudes in the initial gaze phase revealed main effects of emotion in all four time windows analyzed, $Fs > 14.52$, $ps < .001$, $\eta^2 > .001$, waveshapes of the EPN component are provided in Supplementary Figure S1. Pairwise post-hoc tests for this effect (Table 2) show that the EPN to angry faces was significantly more negative (less positive) than to neutral faces in all 50-ms time windows (M = 5.53 μV, SD = 4.71 vs. M = 6.09 μV, SD = 4.61), (M = 4.98 μV, SD = 4.59 vs. M = 5.12 μV, SD = 4.56), (M = 4.75 μV, SD = 4.46 vs. M = 3.98 μV, SD = 4.27) (M = 4.89 μV, SD = 4.52 vs. M = 5.98 μV, SD = 4.37). The EPN to happy faces was significantly more negative than for neutral faces in the three 50-ms time windows from 250 ms onward (M = 5.12 μV, SD = 4.56 vs. M = 5.08 μV, SD = 4.32), (M = 4.28 μV, SD = 4.28 vs. M = 3.98 μV, SD = 4.27), and (M = 2.85 μV, SD = 3.97 vs. M = 2.52 μV, SD = 3.92). In the first EPN time window (200-250 ms) also the contrast between happy faces (M = 5.87 μV, SD = 4.62) and angry faces (M = 5.53 μV, SD = 4.71) was significant.

An interaction of Emotion and Stimulus age was present in all four time windows, $Fs > 3.98$, $Ps < .05$, $\eta^2 > .001$ (see Fig. 5 and Table 2 for details). Post-hoc tests for the unified time segment (200-400ms) indicated an outstandingly large effect for the expressions angry vs. neutral in infants.

Of special interest in the present context are the effects of motherhood (group). Firstly, in all four 50-ms time windows significant interactions were observed for Emotion and Group $Fs > 3.41$, $Ps < .05$, $\eta^2 > .001$; these results are shown in Figure 6. Because the results were very similar in all four time segments, we averaged them before conducting post-hoc analyses. These analyses revealed that the interaction was due to a significant group effect specifically for angry vs. neutral faces (Table 2), where mothers showed a larger EPN than Nulliparae.

A significant interaction of Stimulus age and Group was observed between 200 and 250 ms, $F(1, 112) = 8.94$, $p < .001$, $\eta^2 = .001$, and between 250 and 300 ms, $F(1, 112) = 6.20$, $p = .01$, $\eta^2 = .001$. In the latter segment this 2-way interaction was qualified by a 3-interaction of Stimulus age, Emotion, and Group $F(2, 224) = 3.11$, $p = .04$, $\eta^2 = .001$ (Fig. 7, Table 2 for details). HSD post-hoc tests (Table 2) indicate that this interaction is driven a stronger emotion effect in mothers angry versus neutral infant faces, where the EPN stands out (Fig. 7C).

Summarizing the result of the EPN component in the initial gaze phase. Here, no effects of gaze or interactions with the other factors were found, However, the expected EPN to happy and angry faces was enhanced for angry infant faces; mothers showed stronger EPN responses to all angry faces but especially for angry infant faces.

In addition, a significant interaction of Stimulus age × Group was observed $F(1, 112) = 8.94$, $p < .001$, $\eta^2 = .001$. Importantly, significant interactions were observed for factors Stimulus age × Group $F(1, 112) = 6.20$, $p = .01$, $\eta^2 = .001$ and Stimulus age × Emotion x Group $F(2, 224) = 3.11$, $p = .04$, $\eta^2 = .001$ (Fig. 7, Table 2 for details). HSD post-hoc tests (Table 2) indicate that the only significant emotion effect at this level was for angry versus neutral for infant faces in mothers. In addition, a significant interaction of Stimulus age × Group was observed $F(1, 112) = 4.08$, $p = .04$, $\eta^2 = .001$. As in the preceding time window, the contrast between neutral and angry faces did not reach significance.

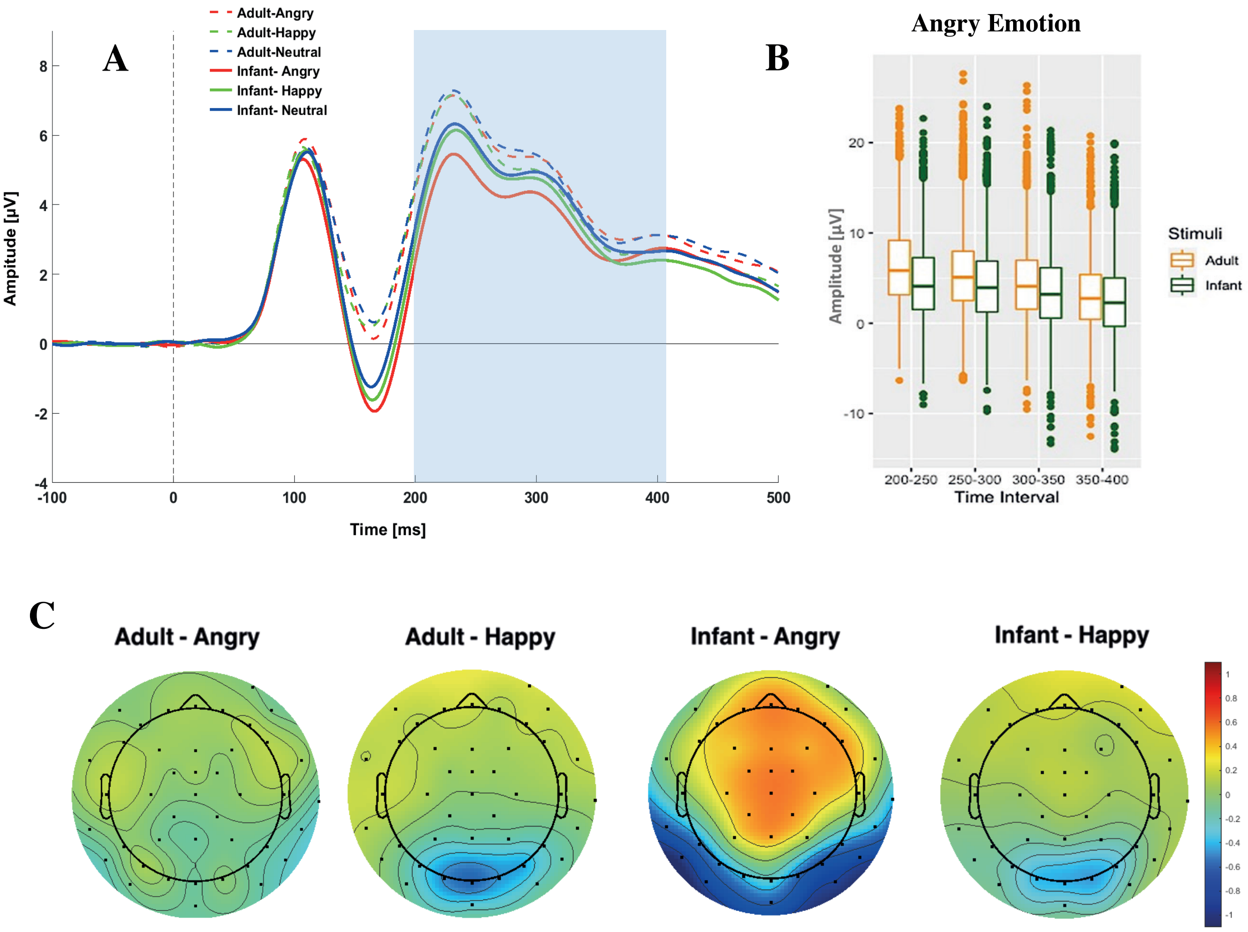


Figure 5. EPN, initial gaze phase: interaction of emotional expression and stimulus. A: Grand mean ERPs for the EPN ROI (average of electrodes P7 / P8, PO9 / PO10, PO7 / PO8, O1 / O2, Oz, and Iz); 200-400 ms time window is shaded. B: EPN amplitude for four 50-ms segments of EPN intervals and stimulus age for angry emotion. C: Topographies of the Emotion x Stimulus age interaction (angry minus neutral and happy minus neutral in infant and adult stimuli) in the 200-400 ms interval.

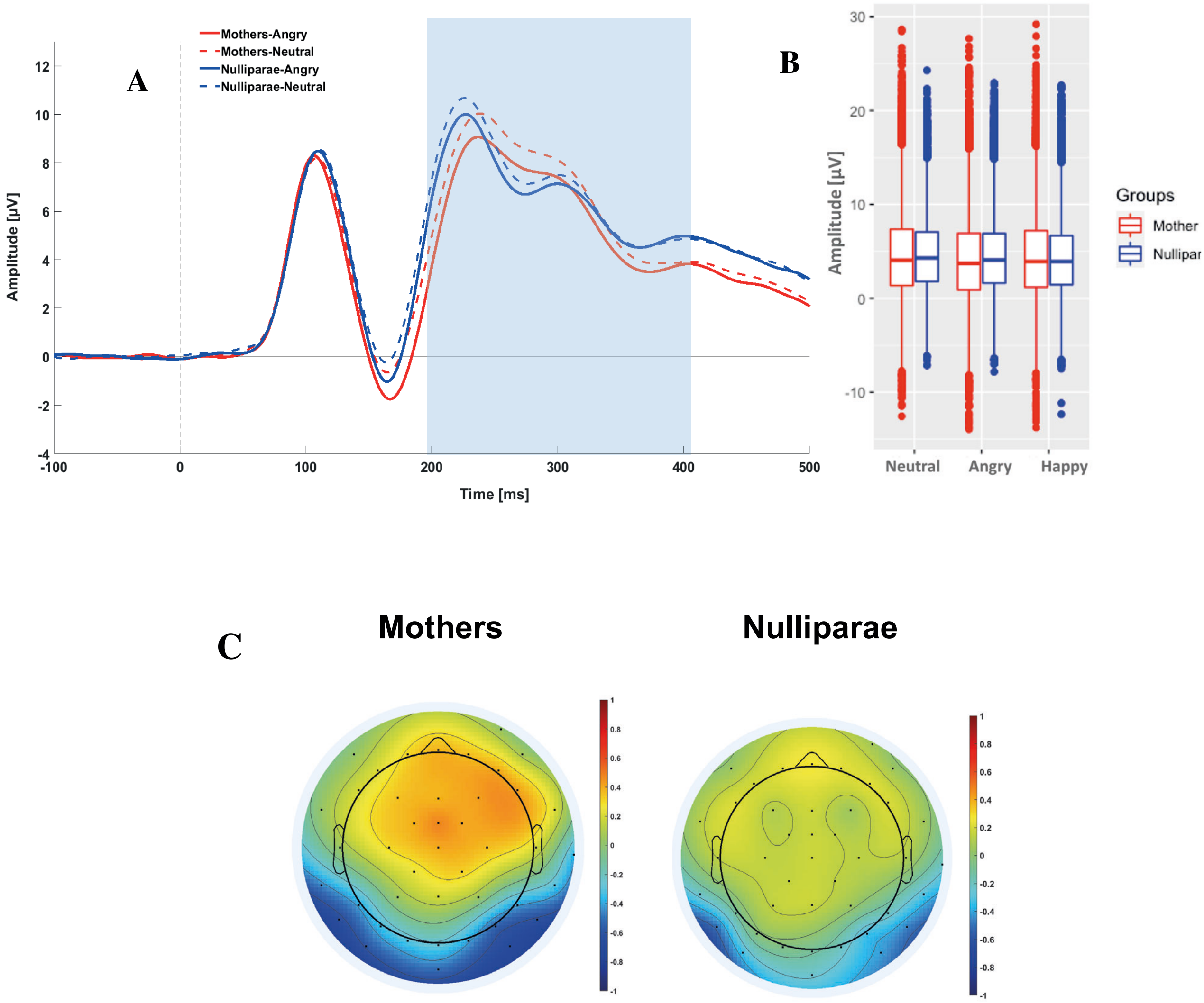
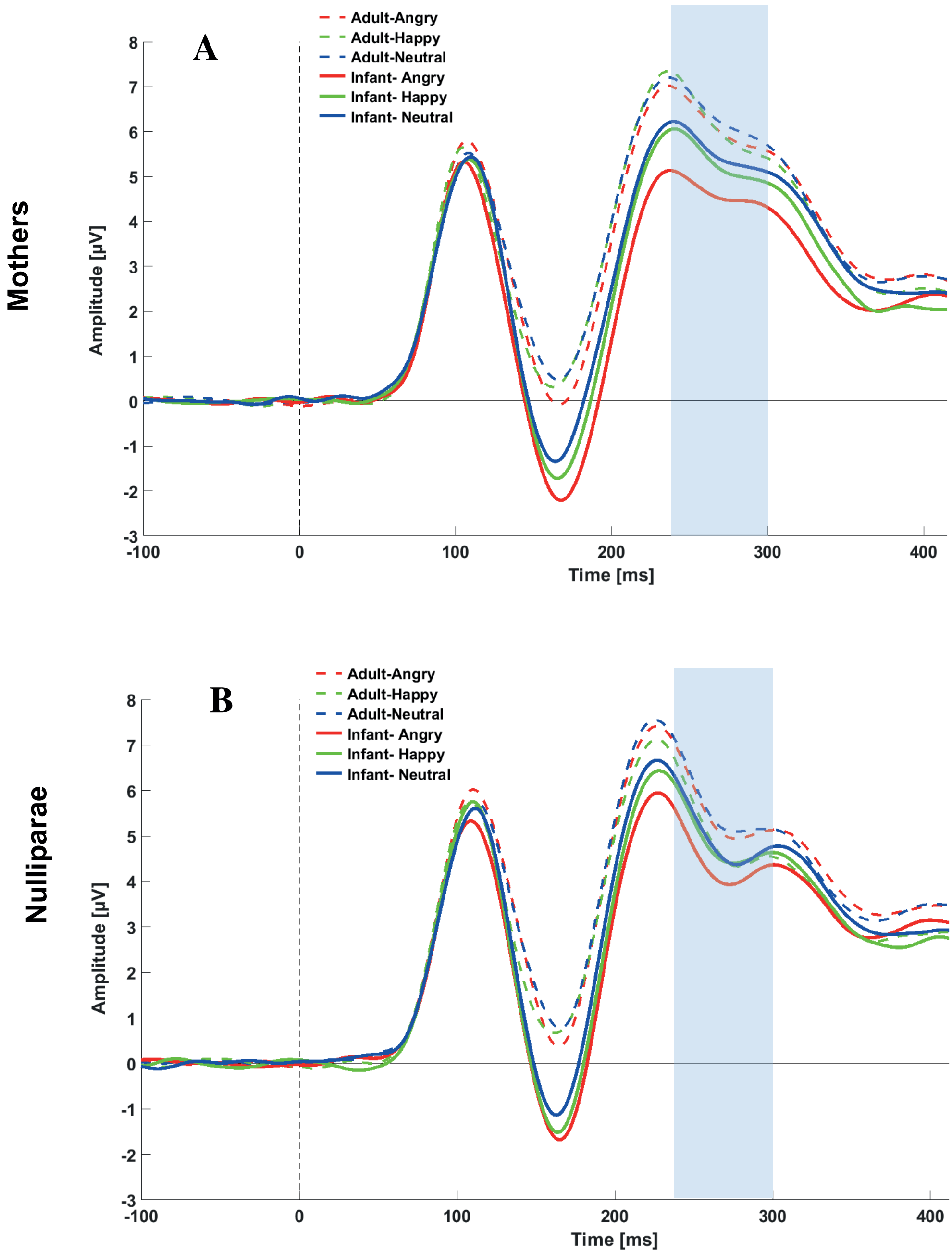


Figure 6. EPN, initial gaze phase: interaction of emotional expression and group. A: Grand mean ERPs for anger and neutral expressions in the EPN ROI (average of electrodes P7 / P8, PO9 / PO10, PO7 / PO8, O1 / O2, Oz, and Iz); 200-400 ms time window is shaded. B: EPN amplitudes for the combinations of emotional expressions and group. C: Topographies of the differences anger minus neutral expression in the EPN (200 – 400 ms) for mothers and nulliparae.


A
Mothers
Adult-Angry
Adult-Happy
Adult-Neutral
Infant- Angry
Infant- Happy
Infant- Neutral
Amplitude [μV]
Time [ms]
B
Nulliparae
Adult-Angry
Adult-Happy
Adult-Neutral
Infant- Angry
Infant- Happy
Infant- Neutral
Amplitude [μV]
Time [ms]

C

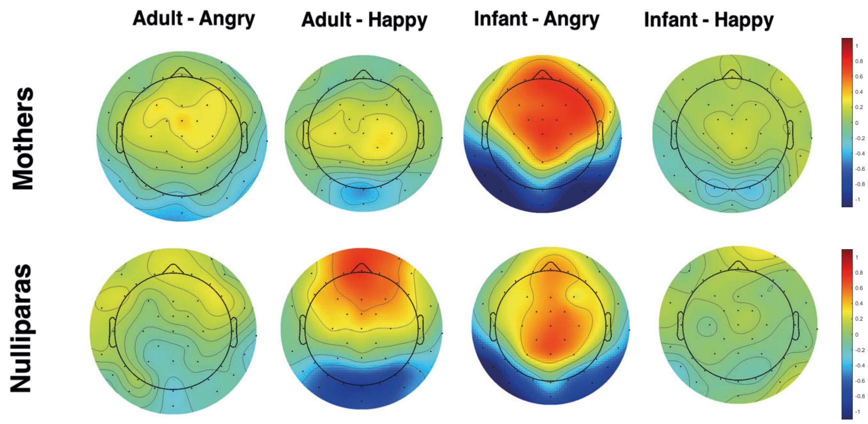


Figure 7. EPN, initial gaze phase: interaction of emotional expression and stimulus age in mothers and nulliparae. A and B: Grand mean ERPs for the EPN ROI (average of electrodes P7 / P8, PO9 / PO10, PO7 / PO8, O1 / O2, Oz, and Iz) in mothers and nulliparae, respectively; 250-300 ms time window is shaded. C: Topographies of the Emotion x Stimulus age x Group interaction (angry minus neutral and happy minus neutral in infant and adult stimuli).

Table 2. Test statistics of post-hoc pairwise comparisons of emotion effects on the EPN component in the initial gaze phase.

	Contrast	Effect Magnitude (μV)	*95% CI*	*t*-statistic (*df = 113)*	*p*	*Cohen's d*
	Emotion					
200-250 ms	**Angry - Neutral**	-0.56	[-0.78, -0.32]	10.35*	< 0.001	0.05
	Happy - Neutral	-0.21	[-0.44, 0.01]	4.53	0.06	0.21
	Happy - Angry	-0.33	[-0.56, -0.11]	6.08*	< 0.001	0.16
250-300 ms	**Angry - Neutral**	-0.42	[-0.65, -0.21]	3.59*	< 0.001	0.22
	Happy - Neutral	-0.28	[-0.51, -0.06]	4.95*	0.01	0.15
	Happy - Angry	-0.14	[-0.36, 0.08]	0.76	0.31	0.09
300-350 ms	**Angry - Neutral**	-0.27	[-0.48, -0.05]	4.01*	0.01	0.01
	Happy - Neutral	-0.29	[-0.51, -0.09]	5.49*	0.01	0.22
	Happy - Angry	-0.02	[-0.19, 0.23]	0.32	0.97	0.13
350-400 ms	**Angry - Neutral**	-0.16	[-0.25, 0.13]	1.93*	0.01	0.09
	Happy - Neutral	-0.54	[-0.53, -0.13]	6.06*	< 0.001	0.07
	Happy - Angry	-0.27	[-0.47, -0.77]	4.81	0.74	0.13
	Emotion x Group[a]					
200-400 ms	**Angry - Neutral (mothers)**	-0.44	[-0.63, -0.25]	30.54*	< 0.001	0.05
	Happy - Neutral (mothers)	-0.21	[-0.41, -0.02]	35.32*	0.01	0.32
	Angry - Neutral (nulliparae)	-0.21	[-0.41, -0.01]	42.01*	0.03	0.11
	Happy- Neutral (nulliparae)	-0.36	[-0.55, -0.16]	33.11*	< 0.001	0.11
	Mother-Nulliparae (Angry)	0.31	[0.11 0.49]	28.02*	< 0.001	0.08
	Emotion x Stimulus age					
200-400 ms	**Angry - Neutral (infant)**	-0.61	[-0.81, -0.42]	50.11*	< 0.001	0.23
	Happy – Neutral (infant)	-0.25	[-0.44, -0.05]	34.33*	0.01	0.09
	Angry - Neutral (adult)	-0.04	[-0.23, 0.01]	23.01	0.98	0.12
	Happy – Neutral (adult)	-0.31	[-0.51, -0.12]	34.54*	< 0.001	0.15

	Stimulus age x Group					
200-250 ms	**Infant – Adult (mothers)**	-1.54	[-1.82, -1.26]	61.13*	< 0.001	0.32
	Infant – Adult (nulliparae)	-1.05	[-1.34, -0.76]	65.02*	< 0.001	0.21
250-300 ms	**Infant – Adult (mothers)**	-0.98	[-1.25, 0.71]	37.52*	< 0.001	0.16
	Infant – Adult (nulliparae)	-0.56	[-0.85, -0.27]	35.11*	< 0.001	0.18
300-350 ms	**Infant – Adult (mothers)**	-0.64	[-0.91, -0.38]	21.74*	< 0.001	0.15
	Infant – Adult (nulliparae)	-0.27	[-0.55, -0.01]	19.26*	0.04	0.03
	Group x Stimulus age x Emotion					
250-300 ms	**Infant: Angry –Neutral (mothers)**	-0.87	[-1.4, -0.26]	-21.31*	< 0.001	0.07
	Infant: Happy – Neutral (mothers)	-0.21	[-0.83, -0.38]	-9.59	0.99	0.02
	Adult: Angry –Neutral (mothers)	-0.21	[-0.82, 0.39]	16.92	0.99	0.6
	Adult: Happy – Neutral (mothers)	-0.24	[-0.85, 0.36]	15.52	0.97	0.02
250-300 ms	**Infant: Angry –Neutral (nulliparae)**	-0.49	[-1.13, 0.13]	18.31	0.29	0.04
	Infant: Happy – Neutral (nulliparae)	-0.07	[-0.69, 0.56]	12.87	0.99	0.07
	Adult: Angry –Neutral (nulliparae)	-0.11	[-0.74, 0.51]	12.11	0.98	0.03
	Adult: Happy – Neutral (nulliparae)	-0.62	[-1.26, 0.01]	13.32	0.05	0.02

*$p < 0.05$
Notes: [a]only significant contrasts are shown

4.3 Gaze change phase

N170. **T**he grand average ERPs for the N170 ROI during the gaze change phase are depicted in Figure 8. ANOVA of the N170 amplitude revealed a significant main effect of hemisphere, $F(1, 112) = 25.54$, $p < .001$, $\eta^2 = .05$, with larger N170 amplitudes over the right (Fig. 7; $M = -5.06$ μV, $SD = 2.63$) than over the left hemisphere ($M = -3.94$ μV, $SD = 2.38$). There was a significant main effect of gaze change direction, $F(1, 112) = 64.11$, $p < .001$, $\eta^2 = .001$, with larger amplitudes for direct-to-averted ($M = -4.72$ μV, $SD = 2.76$) than for averted-to-direct changes ($M = -4.27$ μV, $SD = 2.38$). The effect of Gaze change direction was modulated by Hemisphere, $F(1, 112) = 11.17$, $p < .001$, $\eta^2 = .001$, being larger in the right hemisphere (see Fig. 8C and Table 3 for details). Factor Emotion also yielded a main effect $F(1, 224) = 10.49$, $p < .001$, $\eta^2 = .002$. Pairwise comparisons indicated that, as compared to neutral faces, ($M = -4.37$ μV, $SD = 2.57$), both angry faces ($M = -4.63$ μV, $SD = 2.62$) and happy faces ($M = -4.51$ μV, $SD = 2.58$) showed larger N170 amplitudes (see Fig 8 and Table 3 for details). No significant differences were observed between happy faces as compared to neutral or angry faces. No interaction between emotion and gaze direction were obtained ($p > .05$).

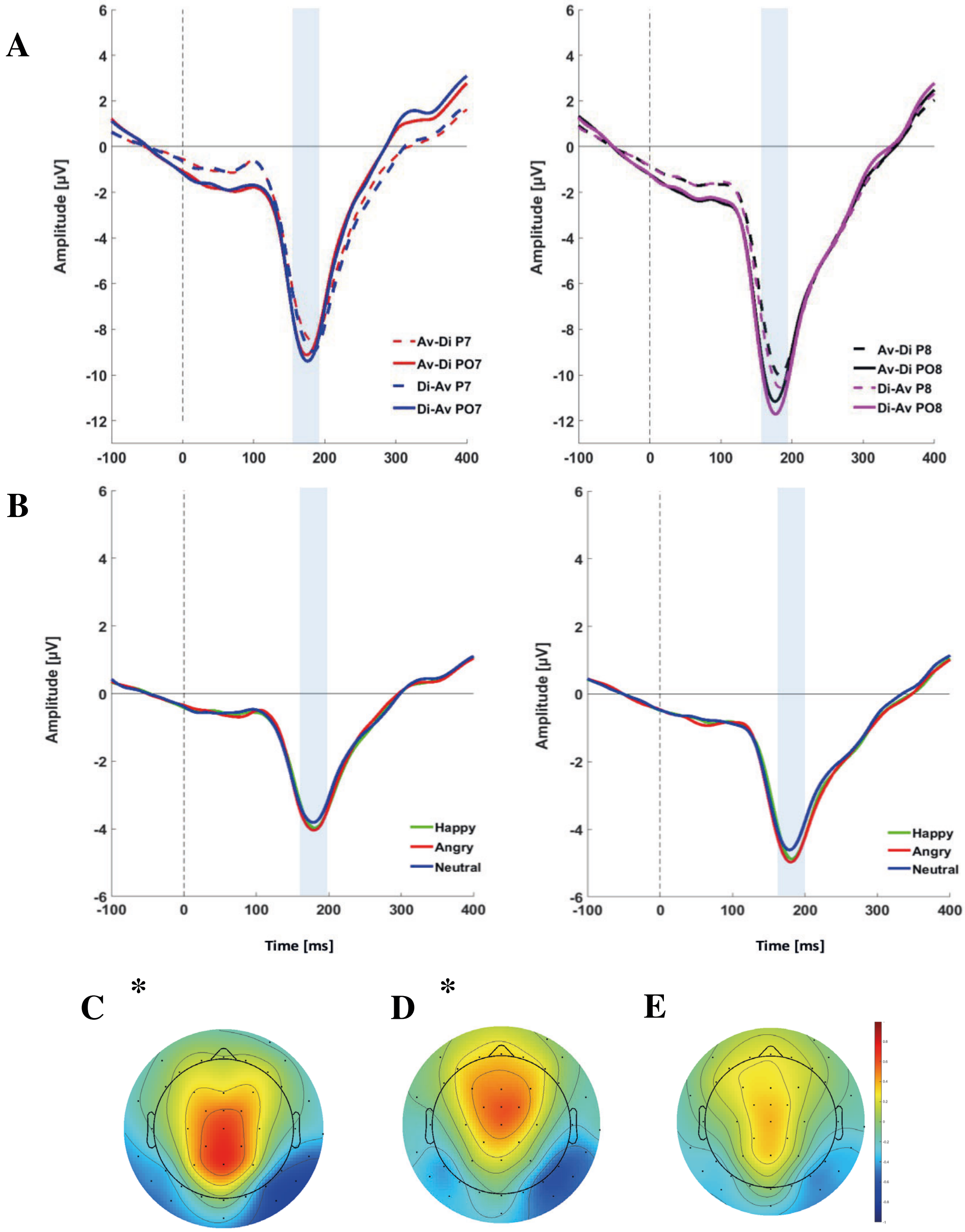

A
Amplitude [μV]
Av-Di P7
Av-Di PO7
Di-Av P7
Di-Av PO7
Av-Di P8
Av-Di PO8
Di-Av P8
Di-Av PO8
B
Amplitude [μV]
Happy
Angry
Neutral
Time [ms]
C *
D *
E

Figure 8. Gaze Change phase: Effects of gaze change direction and emotion on the N170 component. Top: Grand mean ERPs for the N170 ROI (electrodes P7/P8 and PO7/PO8); the time window for the N170 analysis is shaded. A: Effect of gaze change direction. B: Effect of emotion. Bottom: Difference topographies for the N170 time window highlighted above. C: Gaze change effect (direct to averted minus averted to direct gaze). D: Emotion effect (angry minus neutral). E: Emotion effect (happy minus neutral).

Table 3. Post-hoc pairwise comparisons of experimental effects on the N170 component in the gaze change phase.

Contrasts	**Effect Magnitude (μV)**	***95% CI***	***t*-statistic *(df = 113)***	***p***	***Cohen's d***
		Emotion			
Angry - Neutral	-0.26	[-0.46, -0.62]	4.79*	0.01	0.05
Happy - Neutral	-0.28	[-0.33, -0.07]	2.49	0.28	0.21
Angry - Happy	-0.13	[-0.33, -0.06]	2.07	0.27	0.07
		Gaze x Hemisphere			
Direct → Averted – Averted → Direct (Left Hemisphere)	-0.31	[-0.56, -0.06]	11.31*	< 0.01	0.07
Direct → Averted – Averted → Direct (Right Hemisphere)	-0.58	[-0.83, -0.33]	21.42*	< 0.001	0.05

EPN. Figure 10 shows the ERP waveshapes and Figure 9 illustrates the topographies of the EPN in the gaze change phase. ANOVAs of EPN amplitude revealed main effects of stimulus age in all four 50-ms time windows between 200 and 400 ms: *Fs* (2, 224) = 18.31, 11.42, 9.87, 6.47, respectively; *ps* < .01; η^2 = .02, .00, .00, .00, respectively. As illustrated in Figure 9, the mean amplitude in the EPN in a 200-400 ms window was more negative for infant faces (*M* = -1.19 μV, *SD* = 2.61) than for adult faces (*M* = -0.98 μV, *SD* = 2.45). In the interval between 200 and 250 the stimulus age effect was modulated by gaze direction $F(2, 224) = 5.29$, $p = .02$, $\eta^2 = .00$ (see Fig. 10). As compared to adult faces, for infant faces we found larger gaze change effects (direct-to-averted minus averted-to-direct) (see Table 4 for details).

More interestingly, although emotions in this phase were the same as in the initial phase, there were main effects of emotion in all four 50-ms time windows between 200 and 400 ms: *Fs* (2, 224) > 5.71; *ps* < .01, $\eta^2 s$ = .00 (see Fig. 9 and Table 4 for details). Post-hoc pairwise comparisons (see Table 4) between emotion levels revealed significantly more negative amplitudes for angry as compared to neutral faces and for happy than for neutral faces in each window, whereas happy and angry faces did not differ in any time window.

Between 300 and 400 ms, the emotion effect was modulated by stimulus age, *Fs* (2, 224) > 4.73; *p* < .001, $\eta^2 s$ = .001 (see Fig. 11), with more negative EPN amplitudes for angry emotion in infant than adult faces (*M* = 3.61 vs. 3.09 *u*V), and by stimulus age and gaze change direction, $F(2, 224) > 3.45$, $p < .05$, $\eta^2 s$ = .001 (see Fig. 12 and Table 4).

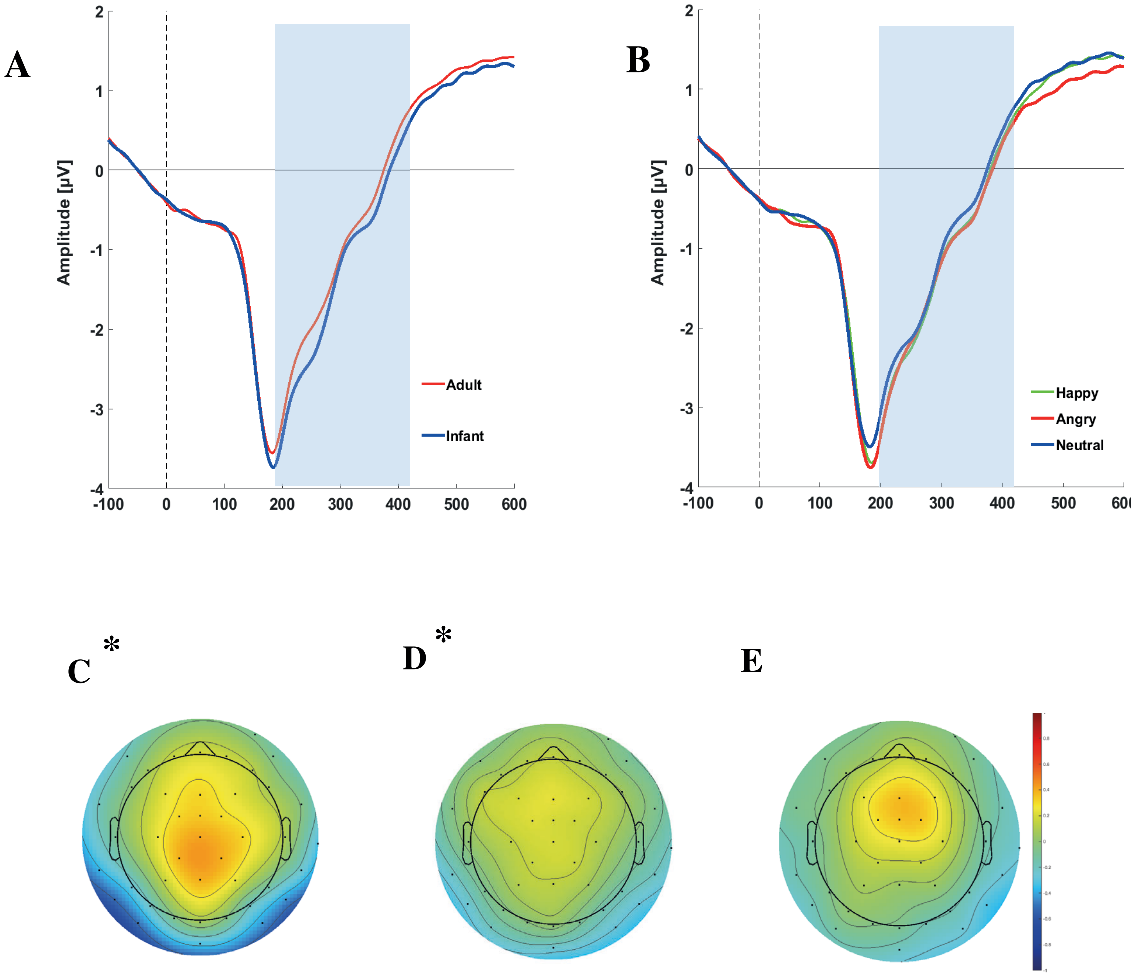


Figure 9. EPN, Gaze change phase: Effects of stimulus age and emotion on the EPN (200-400 ms). Top: Grand mean ERPs for the EPN region (average of electrodes P7 / P8, PO9 / PO10, PO7 / PO8, O1 / O2, Oz, and Iz); the time window of EPN analysis is shaded. A and B: main effects of stimulus age and emotion, respectively. Bottom: topographies for the EPN effects. C: Stimulus age effect (infant minus adult faces). D and E: Emotion effect; angry minus neutral and happy minus neutral, respectively.

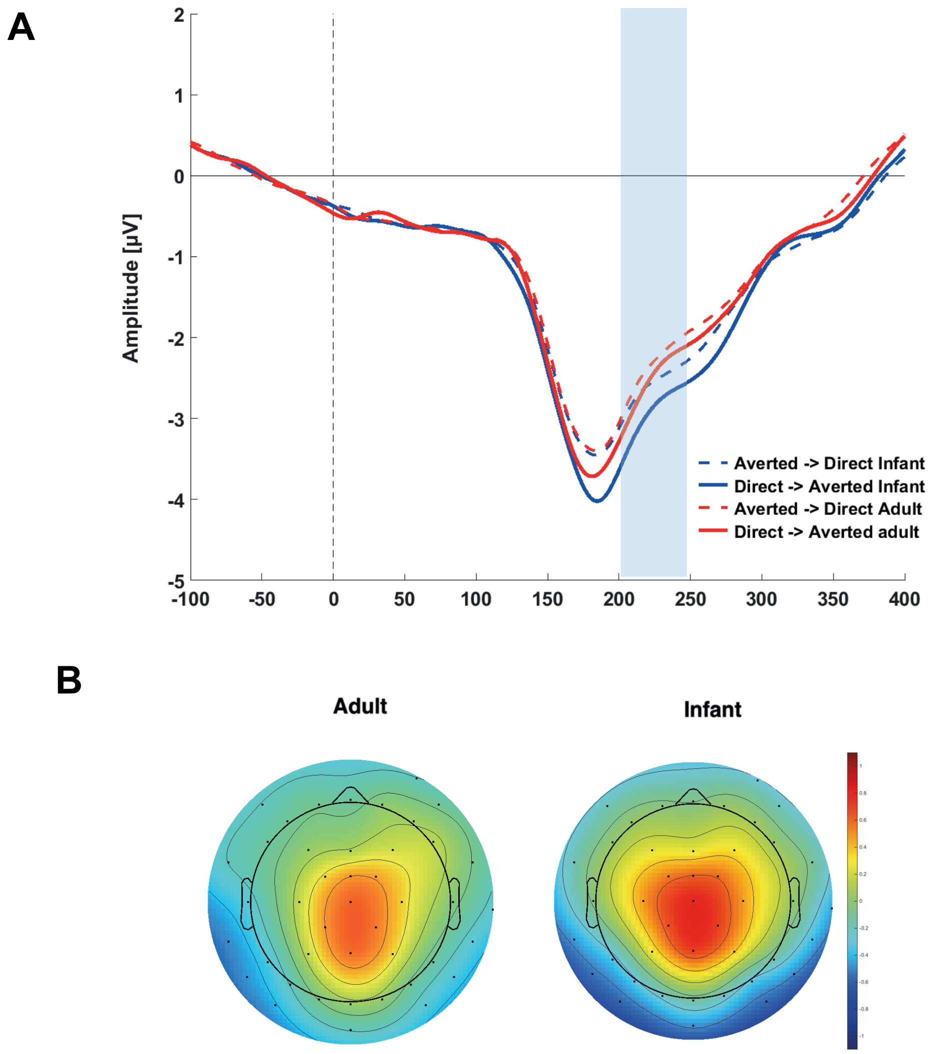


Figure 10. Gaze change phase: Interaction of gaze change direction and stimulus age in the EPN (time window 250-300 ms). A: Grand mean ERPs of gaze and stimulus age interaction for the EPN ROI (average of electrodes P7 / P8, PO9 / PO10, PO7 / PO8, O1 / O2, Oz, and Iz); 200-250 ms time window is shaded. C: Topographies of the gaze effect for infant and adult faces.

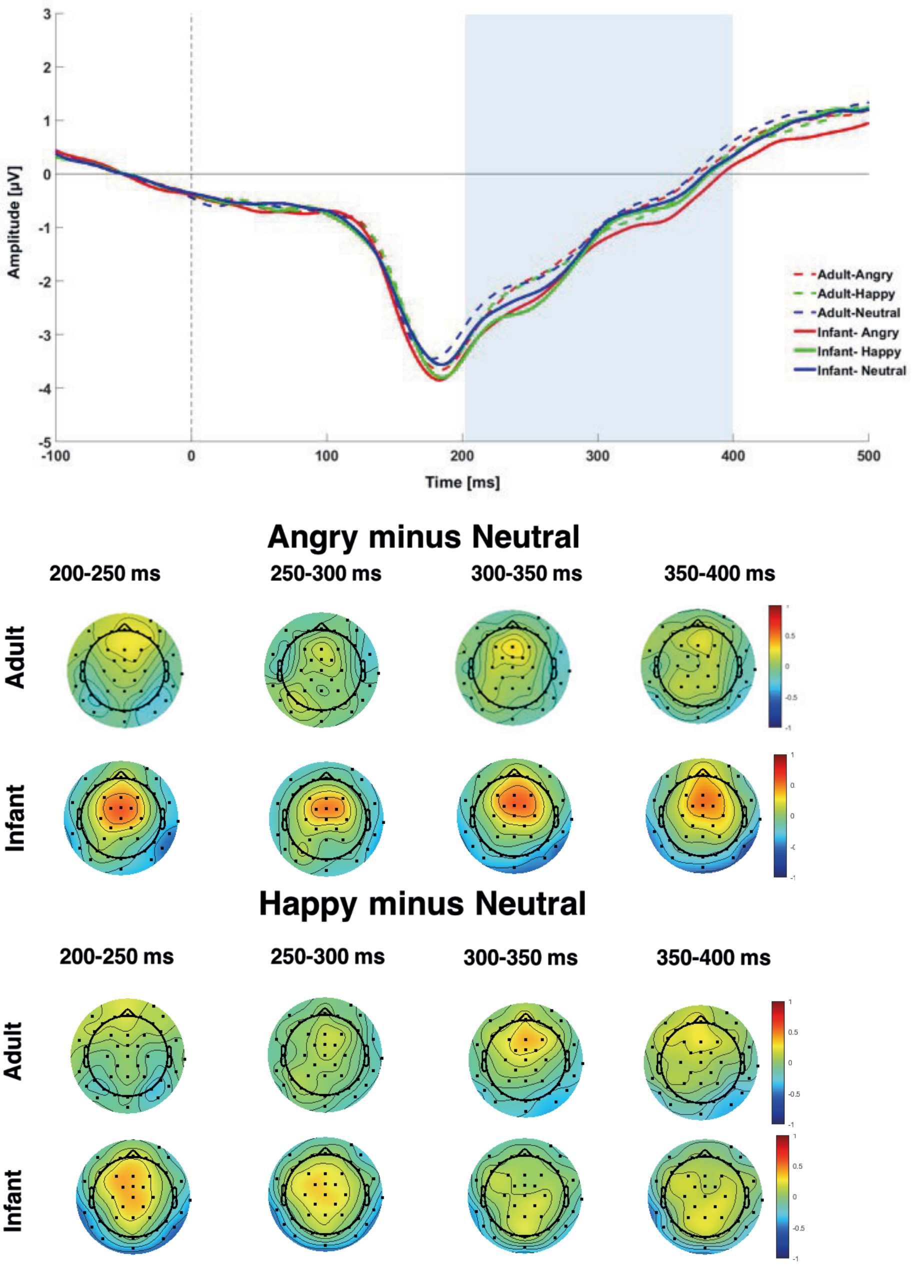
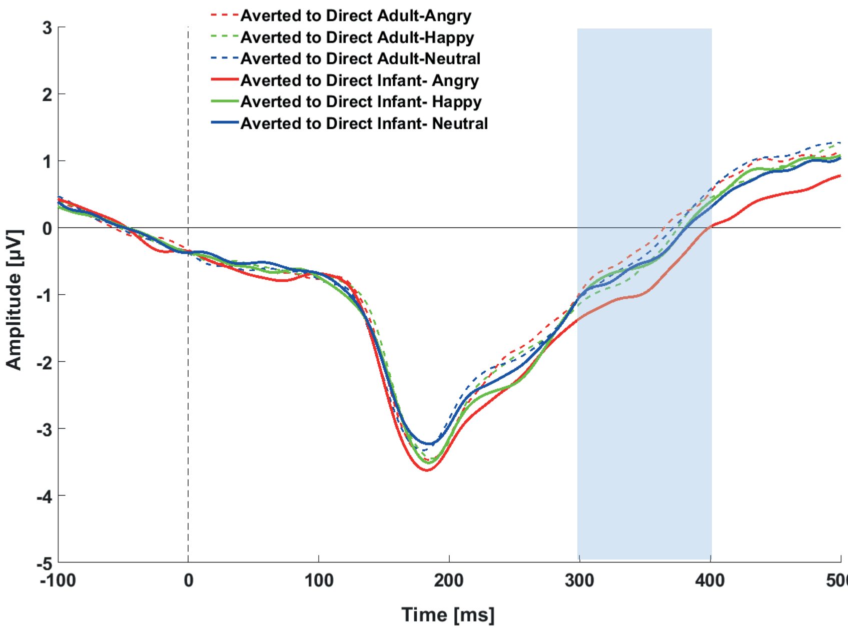
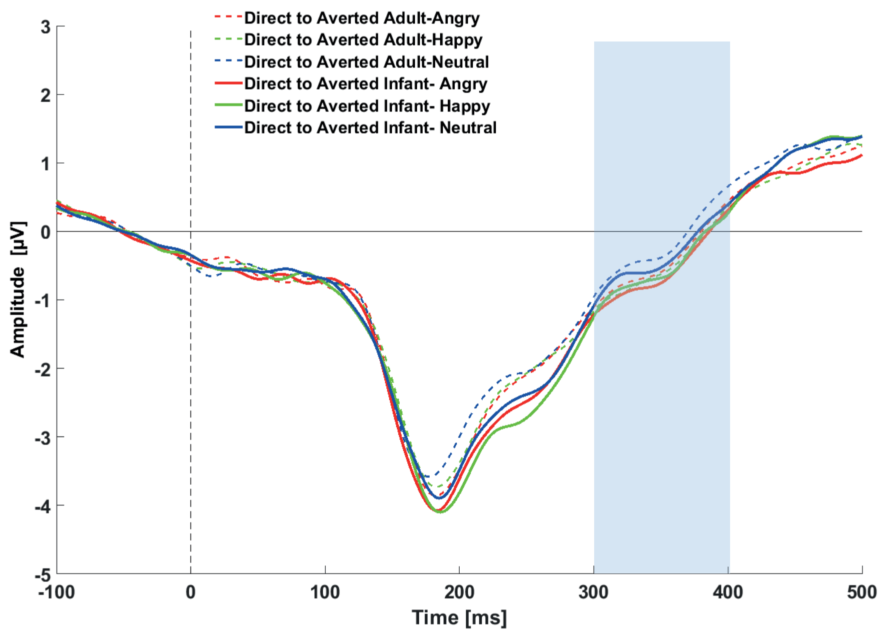


Figure 11. Gaze change phase: Interaction of emotion and stimulus age in the EPN (time window 300-400 ms). A: Grand mean ERPs of emotion x stimulus age for the EPN ROI (average of electrodes P7 / P8, PO9 / PO10, PO7 / PO8, O1 / O2, Oz, and Iz); 300-400 ms time window is shaded. C: Topographies of the emotion effect for infant and adult faces.

A


Averted to Direct Adult-Angry
Averted to Direct Adult-Happy
Averted to Direct Adult-Neutral
Averted to Direct Infant- Angry
Averted to Direct Infant- Happy
Averted to Direct Infant- Neutral
Amplitude [µV]
3
2
1
0
-1
-2
-3
-4
-5
-100
0
100
200
300
400
500
Time [ms]

B


Direct to Averted Adult-Angry
Direct to Averted Adult-Happy
Direct to Averted Adult-Neutral
Direct to Averted Infant- Angry
Direct to Averted Infant- Happy
Direct to Averted Infant- Neutral
Amplitude [µV]
3
2
1
0
-1
-2
-3
-4
-5
-100
0
100
200
300
400
500
Time [ms]

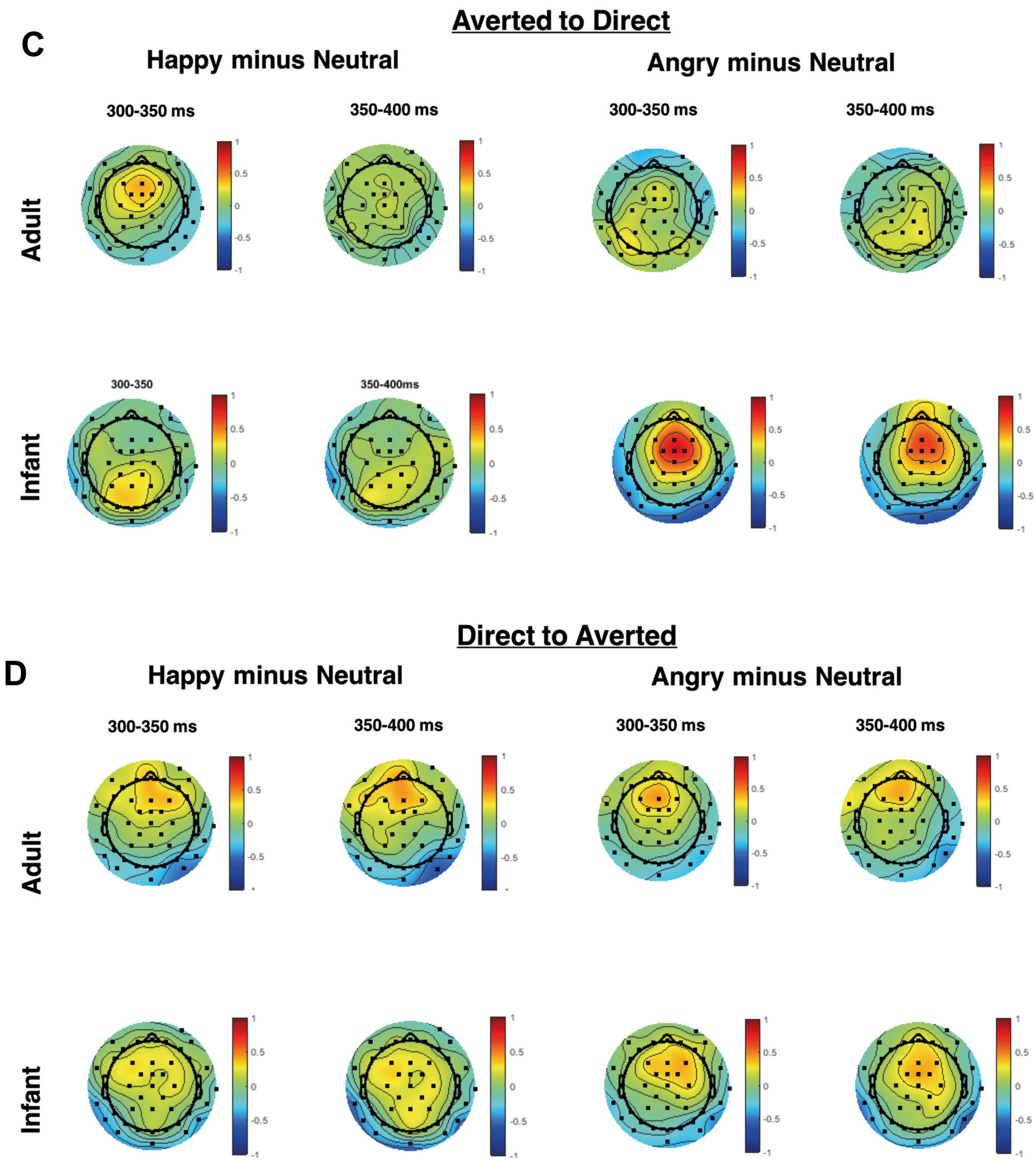

C
Averted to Direct
Happy minus Neutral
Angry minus Neutral
300-350 ms
350-400 ms
300-350 ms
350-400 ms
Adult
Infant
300-350
350-400ms
D
Direct to Averted
Happy minus Neutral
Angry minus Neutral
300-350 ms
350-400 ms
300-350 ms
350-400 ms
Adult
Infant

Figure 12. EPN, Gaze change phase: interaction of gaze change direction, emotional expression and stimulus age for the EPN (time window 300-400). A and B: Grand mean ERPs for the EPN ROI (average of electrodes P7 / P8, PO9 / PO10, PO7 / PO8, O1 / O2, Oz, and Iz); 300-400 ms time window is shaded. C: Topographies of the emotion effects (angry minus neutral and happy minus neutral) for infant and adult stimuli for the direction averted to direct. D: Same as C for change direction direct to averted.

Table 4. Test statistics of post-hoc pairwise comparisons of experimental effects on the EPN component in the gaze change phase.

	Contrasts	Effect Magnitude (μV)	*95% CI*	*t*-statistic *(df = 113)*	*p*	*Cohen's d*
	Emotion					
200-250 ms	Angry - Neutral	-0.17	[-0.28, -0.06]	3.83*	< 0.001	0.09
	Happy - Neutral	-0.18	[-0.31, -0.07]	4.68*	< 0.001	0.07
	Happy - Angry	-0.01	[-0.98, -0.12]	0.25	0.96	0.05
250-300 ms	Angry - Neutral	-0.12	[-0.14, -0.07]	0.13*	< 0.001	0.08
	Happy - Neutral	-0.18	[-0.21, -0.08]	1.58	0.01	0.04
	Happy - Angry	-0.14	[-0.19, 0.05]	1.28	0.21	0.11
300-350 ms	Angry - Neutral	-0.16	[-0.28, -0.04]	3.46*	0.01	0.02
	Happy - Neutral	-0.13	[-0.24, -0.01]	2.81*	0.02	0.04
	Happy - Angry	-0.03	[-0.14, -0.08]	0.61	0.81	0.07
350-400 ms	Angry - Neutral	-0.15	[-0.27, 0.03]	3.23*	< 0.001	0.15
	Happy - Neutral	-0.12	[-0.24, -0.01]	2.62	0.04	0.03
	Happy - Angry	-0.03	[-0.15, 0.08]	0.64	0.81	0.01
	Stimulus age x Gaze direction					
200-250 ms	Di → Av – Av → Di (Adult)	-0.15	[-0.29, -0.02]	18.61*	0.02	0.08
	Di → Av – Av → Di (Infant)	-0.34	[-0.48, -0.21]	14.13*	< 0.001	0.05
	Stimulus age x Emotion					
300-350 ms	Happy – Neutral (Adult)	-0.21	[-0.42, -0.02]	11.21*	0.02	0.01
	Angry – Neutral (Infant)	-0.28	[-0.49, -0.08]	14.92*	< 0.001	0.12
350-400 ms	Happy – Neutral (Adult)	-0.18	[-0.39, -0.01]	8.09	0.09	0.17
	Angry – Neutral (Infant)	-0.23	[-0.44, -0.03]	12.01*	0.02	0.15

	Stimulus age x Gaze direction x Emotion					
300-350 ms	**Adult: Di → Av (Happy) – Di →Av (Neutral)**	-0.28	[-0.55, -0.01]	12.91*	0.04	0.03
	Infant: Av > Di (Angry) – Av > Di (Neutral)	-0.35	[-0.65, -0.05]	16.72*	0.01	0.02
350-400 ms	**Adult: Di →Av (Happy) – Di → Av (Neutral)**	-0.29	[-0.58, -0.01]	14.13*	0.03	0.06
	Infant: Av →Di (Angry) – Av → Di (Neutral)	-0.33	[-0.62, -0.04]	6.34*	0.01	0.08

*$p < 0.05$

4. Discussion

In order to better understand the maternal neurocognitive system, the present study investigated associations between motherhood and brain activity during the processing of facial expressions and eye gaze cues from adult and infant faces. Specifically, we measured the electrophysiological responses to gaze direction and emotion expressions in stimuli representing adults and infants and their interplay. We distinguished two trial phases, the initial presentation of a face with a given emotion and gaze direction and a subsequent phase where gaze changed direction, whereas the emotional expression remained unaltered. A relatively large sample - in comparison to studies hitherto published in this field - of mothers and nulliparous women were enrolled in the study. In addition to replicating previous findings of gaze direction and emotion, we showed that stimulus age has strong effects on both the N170 and EPN and interacts with motherhood and gaze direction.

4.1 N170

For the N170 component of the ERP in initial gaze phase, we obtained larger responses to infant than adult face stimuli. In line with previous reports of increased neural responses to infant stimuli reviewed by Maupin et al. (2015) and Vuoriainen et al. (2022), this finding indicates increased neural activity required to structurally encode infant faces. Similarly, infant faces have been previously found to activate brain regions involved in face perception like fusiform gyrus as a likely generator of N170. These activities have been suggested to reflect the encoding of “baby schema” meaning facial features that are indicators of infant faces such as round face, big eyes (Glocker et al., 2009; Luo et al., 2015). These features are typically perceived as more cute and attractive, thus prompting a differing response in comparison to adult faces in N170 (e.g., Endendijk et al., 2018; Glocker et al., 2009; Lobmaier et al., 2010). Therefore, the increased response to infant faces at the early visual processing could potentially reflect increased encoding of distinct infant facial features. Alternatively, the increased N170 to infant faces might reflect an increased difficulty of structural encoding or, more specifically configural processing, as compared to adult faces, resembling the effects of face inversion, which can also increase the N170.

In line with Weisman et al. (2012) who compared the responses to infant stimulus of mothers and non-mothers and found no effect in the N170 amplitude, the increase of N170 amplitude to infant faces observed here was not significantly modulated by motherhood. Considering the relatively large sample size in our study, motherhood does not seem to modulate the structural encoding of faces – whether of adults or infants.

The N170 was also sensitive to emotion, in line with many previous reports (e.g., Rellecke et al., 2011). Since the emotion effect in the N170 was similar in topography to the emotion effect in the EPN (cf. Fig. 3 and Fig. 8), it cannot be ruled out that this early emotion effect in the N170 is an early effect of reflexive attention commonly ascribed to the EPN. Whatever the underlying cause for the emotion effect in the N170, it was more pronounced to angry infant faces than to any other combination of emotion and stimulus age. Importantly, this remarkable effect of angry or distressed infant faces was indistinguishable between mothers and nullipara.

Hence, at this early stage, the absence of group differences indicates that infant faces in general and angry infant faces in particular elicit larger perceptual brain responses regardless of the parental status of our female participants. The present results are in line with Raz (2014) who found increased N170 amplitudes to angry compared to neutral infant faces in mothers during pregnancy compared to non-mothers. Regarding the reported group difference in the study by Raz (2014), it might be important if the participants are expected to differentiate between "face" stimuli and "shape stimuli" and the contrast to our results are essentially due to differences in task and stimuli. Despite our non-social task design in which our participants were only presented with "face stimuli". The enhanced N170 to angry as compared to happy infants is in agreement with the results of Rodrigo et al. (2011) who also found this effect in their control group of non-neglectful mothers. However, they did not find the effect in neglectful mothers. Because in the present nulliparous group, matched in many respects to the mother's group, the N170 response to angry infant faces was unmitigated relative to mothers, the findings of Rodrigo et al. (2011) in neglectful mothers may be specific to individuals with low empathy and high anhedonia.

Our results of increased N170 amplitudes to angry infant faces is in some contrast with the report of Rutherford et al. (2017). Whereas in our data from the initial gaze phase the N170 was larger to angry than happy infant faces by about 0.6 µV, Rutherford et al. found the N170 to be smaller to angry faces by 0.2 µV. Since their effect was at the border of significance, we tend to trust the present results, based on a larger sample, until further evidence on this apparent discrepancy is available.

Independent of stimulus age, we found significant group difference was shown with larger N170 amplitudes to angry faces in mothers as compared to nulliparae. This effect could be associated with greater maternal sensitivity to emotional expressions in general and in particular to negative stimuli meaning the allocation of perceptual encoding towards angry emotion. Although the N170 is often enhanced in response to negative stimuli of any kind compared to neutral ones, evidence suggests that the mother's sensitivity may have a special significance. As an example, prenatal exposure to maternal cortisol, known to be altered in depression, may program the developing stress response system, contributing to true increases in processing negative affect (Davis et al., 2007; Maupin et al., 2015).

For the gaze change phase, we also obtained an effect of gaze direction with larger N170 amplitudes for gaze changes from direct to averted than in the opposite direction. This gaze effect was larger in the right than in the left hemisphere. These results are in line with previous findings (Bagherzadeh-Azbari et al., 2022; Latinus et al., 2015) for dynamic gaze changes, and for gaze-contingent stimulus presentations (Stephani et al., 2020), where N170 amplitude was larger when the eyes were looking away from the observers than when aiming at them. Presumably this was due to the challenge of structurally encoding an altered face configuration, which may be even more challenging when gaze averts rather than when it is aimed at the observer (Bagherzadeh-Azbari et al., 2022).

Importantly for present purposes, these direction effects in the gaze change phase were not significantly modulated by stimulus age, motherhood or emotion or any interactions of these factors. Although, regarding the emotion effect on N170, similar to initial gaze phase, both mothers and nulliparae indistinguishably responded to angry faces with larger N170 amplitudes. Thus, angry faces may represent particularly salient stimuli requiring a significant allocation of perceptual resources that has led to significantly larger N170 amplitudes in both phases.

The effects on N170 in the change phase are of interest also from a different perspective. In the change phase, only the gaze direction changed while the other properties of the face, especially expression and age were the same as before the change. This caused an interesting dissociation. Whereas face age effect, which had been so dominant in the N170 of the initial phase, was absent in the change phase, there was still an emotion effect, albeit no expression change outside of the eye area had occurred. In our opinion these effects indicate that face age is independent of gaze direction and when only gaze direction changes, face age is irrelevant. In contrast, gaze direction may be perceptually integrated with the emotional expression. Hence, when gaze changes, the effects depend on the emotional expression of the face as a whole. Please note, this interpretation is independent of the underlying sources of the emotion effect in the N170.

4.2 EPN effects

As outlined in the introduction, the EPN is robustly sensitive to emotional contents that reflexively catch the attention of the observer. These effects may occur for different qualities (valence) of emotional content and sometimes even for non-emotional factors such as large versus small non-emotional facial movements. Therefore, it was of special interest to what degree, infant faces would catch reflexive attention above adult faces and how this would depend on the emotion displayed by the infant and on the motherhood status of the participants.

In the initial gaze phase, we observed the expected emotion effects in the EPN and time windows of 200 to 400 ms. The emotion effects correspond to reports from many studies (e.g., Bagherzadeh-Azbari et al., 2022; Itier & Neath-Tavares, 2017; Rellecke et al., 2011; Schacht & Sommer, 2009b) and show the typical posterior negativity, for both the expressions of anger and happiness. Interestingly, similar to the preceding N170 component, the emotion effect was most pronounced for angry infant faces, indicating the special attentional engagement with (angry) infant stimuli. Emotion effects to adult stimuli were comparatively small and only present for happy expressions, underscoring the special status of angry infant faces in their ability to trigger reflexive attention.

Importantly, in the time window of 250-300 ms the EPN to angry infant faces was especially pronounced in mothers. This is reminiscent of the enhanced emotion effect of angry faces (irrespective of face age) in mothers in the N170. Here in the EPN, however, the effect is even more specific to angry infant faces. Again, it is suggested that the larger EPN amplitude to angry (infant) faces in mothers is associated with greater maternal sensitivity and attentional encoding of negative stimuli. Importantly, the group difference for angry faces was observed. only in the initial gaze phase but was absent in the gaze change phase,

Moreover, in the initial gaze phase, EPN amplitudes were larger for infant faces relative to adult faces regardless of the emotion shown by the face. This indicates that infant faces not only induce more structural encoding (N170) but are also more likely to catch the attention of the observer (EPN). The fact that this is independent of emotion is in line with findings by Recio et al. (2014) who showed EPN-like effects of small versus large non-emotional facial movements. Hence, it seems that infant-faces are not only more effortful to structurally encode, as indicated by the N170, but also more attention-catching than adult faces.

In terms of obtained interactions in the initial gaze effect, from the time window of 200-350 ms the groups responded similarly to both stimulus ages, while specifically for the time window of the 250-300 ms a group difference was to be seen based on the emotion expressed on the stimuli. Specifically, mothers responded to angry infant faces with larger EPN amplitudes than nulliparae. This is in line with the study by Peltola et al. (2014), which showed larger EPN amplitudes to distressed infant faces compared to infant faces displaying pleasure but only in mothers and not in non-mothers. Here our results substantiate the functional significance of increased neural activity in response to infant emotion expressions in mothers given the continuous need to promptly respond to distress signals in order to mitigate infants' negative arousal.

In the gaze change phase, we observed similar emotion effects in the EPN as in the initial gaze phase. Given that in this phase only the gaze moved but emotion was invariant, it may be surprising to find an EPN; however, as discussed in the context of emotion effects in the gaze-change elicited N170, it may indicate the close relationship of gaze and emotional expression. Thus, the gaze change may have rekindled the emotional analysis of the – unchanged – facial expression; this analysis seemed to have been modulated even by stimulus age, albeit only in a short time segment after 300 ms.

In the gaze change condition, averted-to-direct rotation of gaze in angry infant face stimuli elicited larger EPN amplitudes in comparison to adult faces. Thus, a gaze change in an invariant (angry) facial expression of infant faces can trigger an EPN, that is, reflexive attention. Therefore, it seems that when an angry infant face turns its gaze towards the observer, stronger attention is reflexively elicited as compared to when gaze averts or when the stimulus is an adult face.

In line with our previous study, in which a gaze and emotion interplay was observed in the late time window of the gaze change EPN (Bagherzadeh-Azbari et al., 2022), in the current study a three-way interaction of emotion and gaze and stimulus age was observed. In details, EPN to angry infant faces was larger when gaze was directed toward the observer and it was larger to happy adult faces when the gaze was averted. This means, the present emotion by gaze interaction results for the adult faces is opposite to the results from our previous study, which found larger EPN to happy faces when gaze moved towards rather than away from the observer. Given that the present study had replicated many results of the previous one, we consider it unlikely that the discrepancy of these particular results is due to a lack of power or otherwise faulty procedural details. Instead, we suggest that the discrepancy is due to using only adult faces in the previous study and a randomized mixture of adult and infant faces with different emotional expressions in the present one. This procedural difference may have induced different range effects (Poulton, 1973) in the repeated measures designs of the two studies. The presence of the infant faces that strongly attract attention, especially when displaying negative emotions may have provided a very different context for the adult faces as compared to the previous study where adult faces were the only ones. Future research using blocked presentation of adult and infant faces may assess this suggestion.

In line with the parental ERP literature the present results support the view (e.g., Maupin et al. (2015) that ERP responses to child-related stimuli may provide useful information for assessing the parental neurocognitive system. In the current study, we aimed to investigate ERP responses to children's faces in motherhood to elucidate whether infant faces in general and emotional infant face in particular elicit larger perceptual and attentional brain responses in mothers than in nulliparae. The findings from this relatively large sample suggest that ERPs in the later processing stage (EPN) could be relevant indicators for assessing attentional-motivational factors related to parenting, since these responses were found to be consistently larger for infant faces and, in the initial gaze phase, were associated with group differences. Moreover, our findings suggest that increased attentional allocation to infant distress may be an essential part of the parent-child interaction, as it allows the mother to prioritize relevant infant signals and subsequently react in a sensitive and appropriate way to resolve the source of distress. Attention to distress is important not only in the immediate moment of caregiving, but also in the formation of long-term mother-child attachment and overall development of the child. As an example, another study from our lab conducted with the same participants using a Stroop paradigm, has also suggested that especially in mothers, negative deliberate facial expressions like frowns when facing infants is offset by an automatic caregiving response (Recio et el., 2022).

5. Limitations and Perspectives

The present study has advanced our knowledge about the maternal neurocognitive system and could be directly applied in different populations and setting. In some respects, the study has its limitations, which suggest further improvements. For example, we included gaze changes but no emotion changes between the initial and the following picture. Hence, a steps toward more natural and mutual human interactions measurements may be to implement a task where dynamic eye gaze is combined with dynamic facial expressions. This will allow to remedy a further limitation, that is, using tasks where emotion (and possibly also gaze direction) is task relevant. In present work, associations are derived from cross sectional observations which may not be the best indicator of causal effects and limits for causal inferences about motherhood; hence pre and post motherhood (longitudinal) observations would be an exciting yet challenging perspective.

6. Conclusions

The present study replicated the effects of gaze direction and gaze change but also uncovered some variability. We also confirmed that infant faces pose higher demands on structural face encoding and extended these findings to show stronger reflexive attention to infant faces in general and to angry infant faces in particular. These emotional effects of infant faces are further modulated by dynamic gaze direction. Interestingly, this was only observed in the gaze change phase, emphasizing the importance of dynamic movements for the interplay of emotional expression and gaze direction for angry infant and happy adult faces. In the early face processing stage mothers were more sensitive to stimulus age and showed stronger effects of anger expressions than nulliparae. Furthermore, mothers showed stronger reflexive attention to angry infant faces, especially when being looked at by these faces. Hence, mothers show greater sensitivity to emotional infant's faces at the level of structural face encoding and reflexive attention which may be an important element of caregiving behavior in mothers toward their infants.

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We have no known conflict of interest to disclose.

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S. B-Azbari: Conceptualization, Methodology, Investigation, Formal analysis, Writing - original draft. **A. Hildebrandt**: Conceptualization, Investigation, Writing - review & editing. **O. Dimigen**: Conceptualization, Methodology, Writing - review & editing. **W. Sommer**: Conceptualization, Supervision, Resources, Writing - review & editing.

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Supplementary Figures

Figure S1. EPN, initial gaze phase. A: Effects of emotion averaged across the electrodes of the EPN ROI (P7, PO7, P8, PO8, PO9, PO10, O1, Oz, O2, Iz). Shading indicates the time window of the EPN.

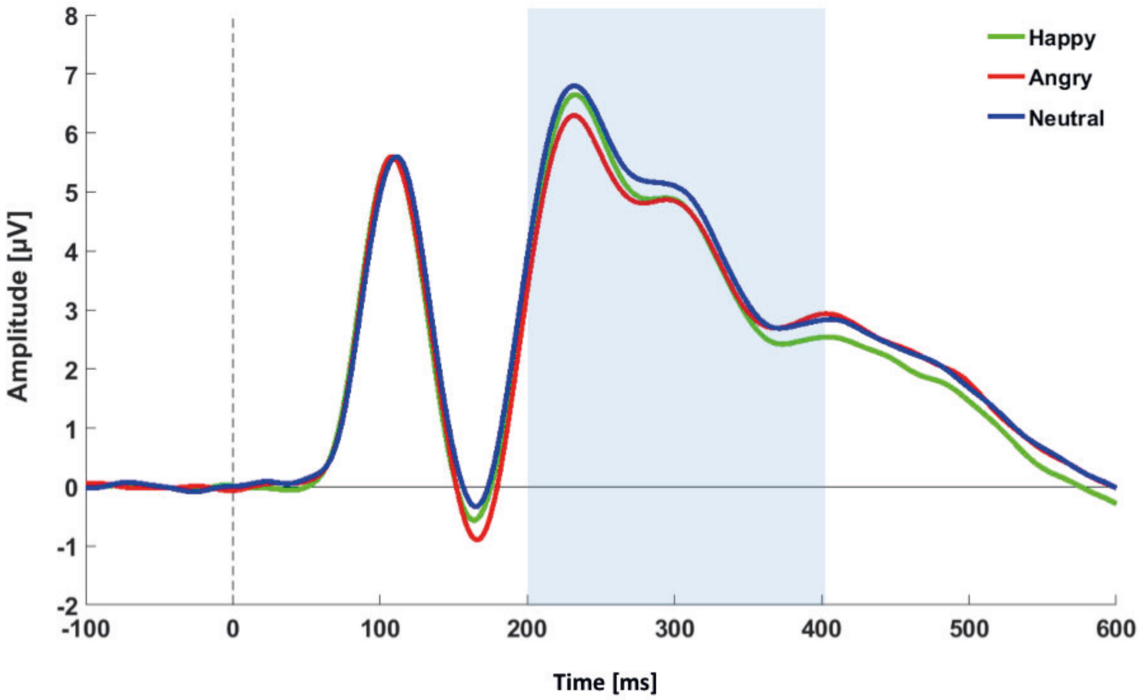

Figure S2. EPN, initial gaze phase: Grand mean amplitudes for EPN ROI (average of electrodes P7 / P8, PO9 / PO10, PO7 / PO8, O1 / O2, Oz, and Iz) presented in 50-ms intervals. A: interaction of emotional expression and group. B: interaction of emotional expression and stimulus age.