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

Shadi Bagherzadeh-Azbari[1] | **Charlotte J. Lion**[2] | **Tilman Stephani**[3,4] | **Olaf Dimigen**[1] | **Werner Sommer**[1,5]

[1]Department of Psychology, Humboldt-Universität zu Berlin, Berlin, Germany

[2]Department of Neurology, University-Hospital-RWTH-Aachen, Aachen, Germany

[3]Department of Neurology, Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany

[4]International Max Planck Research School NeuroCom, Leipzig, Germany

[5]Department of Psychology, Zhejiang Normal University, Jin Hua, China

Correspondence

Shadi Bagherzadeh-Azbari and Werner Sommer, Department of Psychology, Humboldt University of Berlin, Unter den Linden 6, 10117 Berlin, Germany.
Email: shadi.bagherzadeh@cms.hu-berlin.de and werner.sommer@cms.hu-berlin.de

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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

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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

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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

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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.

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.

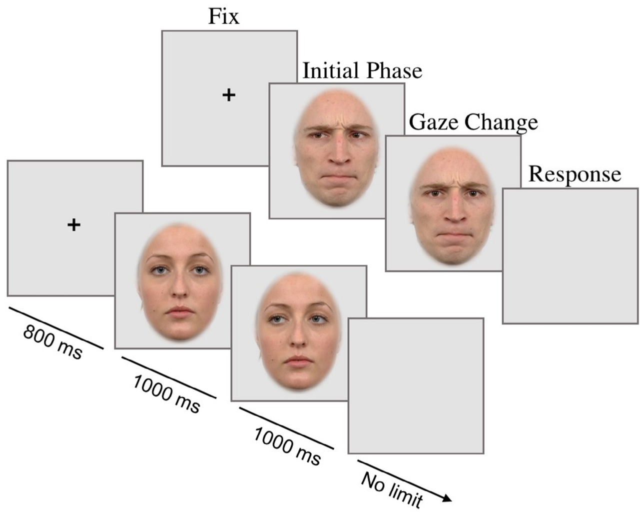

FIGURE 1 Trial structure, illustrated with two examples. A fixation cross (fix) was presented for 800 ms, followed by a first face image (initial gaze phase) for 1000 ms, and a second image (gaze change phase) for another 1000 ms. the second image involved a gaze change in 50% of the trials (as shown 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).

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)

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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).

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

[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.

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.

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

	Emotion		
Gaze	**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

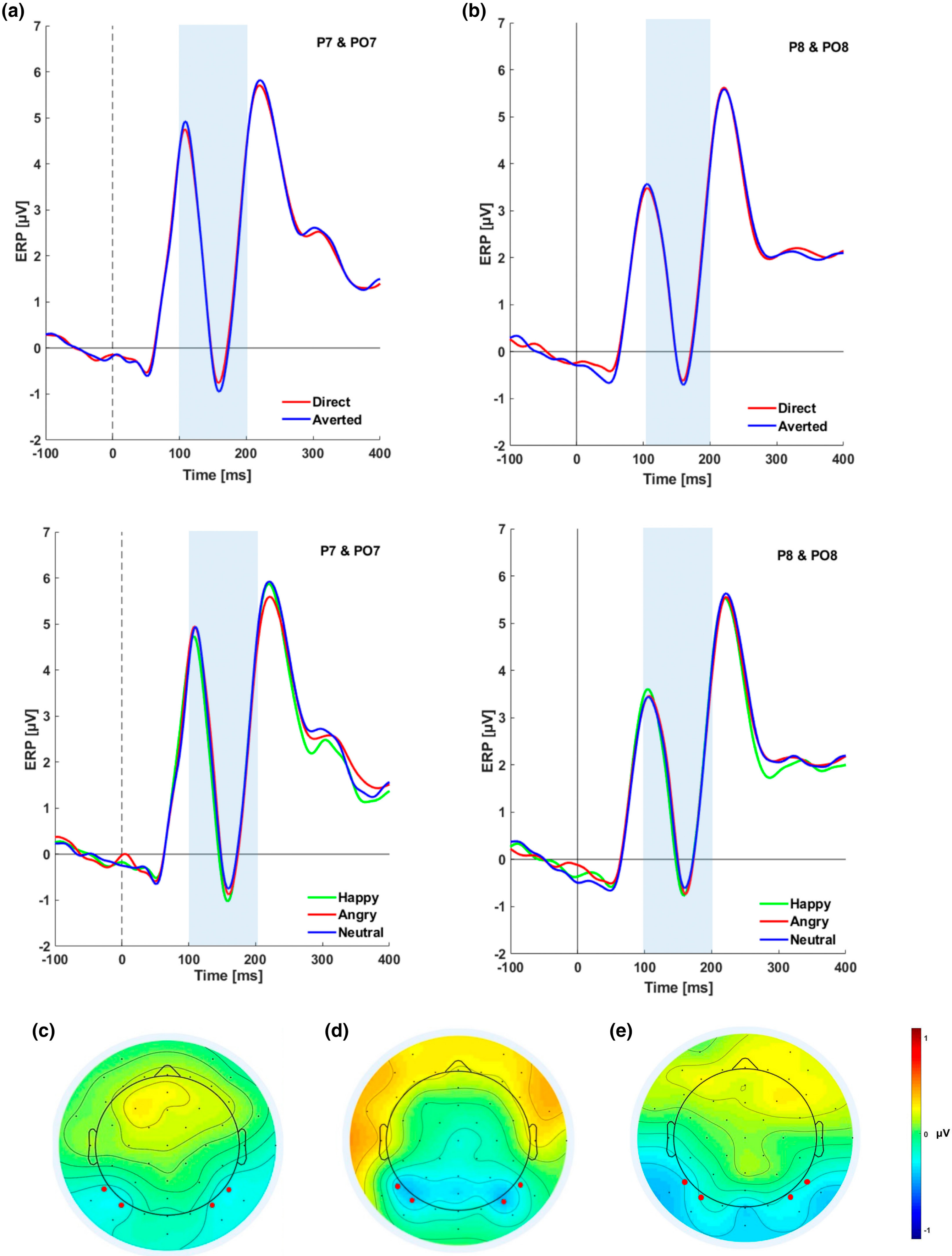

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FIGURE 2 Effects of gaze direction and emotion on the N170 component in the initial gaze phase. Top: Grand mean ERPs for the N170 region of interest (consisting of left hemisphere electrodes P7 and PO7 and right-hemisphere electrodes P8 and PO8); the 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 ($M = 0.17\,\mu V$, $SD = 3.34$) eliciting a more negative-going N170 amplitude than faces showing a direct gaze ($M = 0.40\,\mu V$, $SD = 3.25$) (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 ($M = 0.55\,\mu V$, $SD = 3.21$), both angry faces ($M = 0.26\,\mu V$, $SD = 3.29$) and happy faces ($M = 0.04\,\mu V$, $SD = 3.37$) 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 ($M = 7.08\,\mu V$, $SD = 4.46$) and angry faces ($M = 6.75\,\mu V$, $SD = 4.62$). A significant difference was also found between neutral and happy faces ($M = 6.68\,\mu V$, $SD = 4.58$). 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 ($M = 4.98\,\mu V$, $SD = 3.71$) differed from both angry ($M = 4.60\,\mu V$, $SD = 3.86$) and happy faces ($M = 4.15\,\mu V$, $SD = 3.80$), as well as happy from angry faces.

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

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

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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

*$p < .05$.

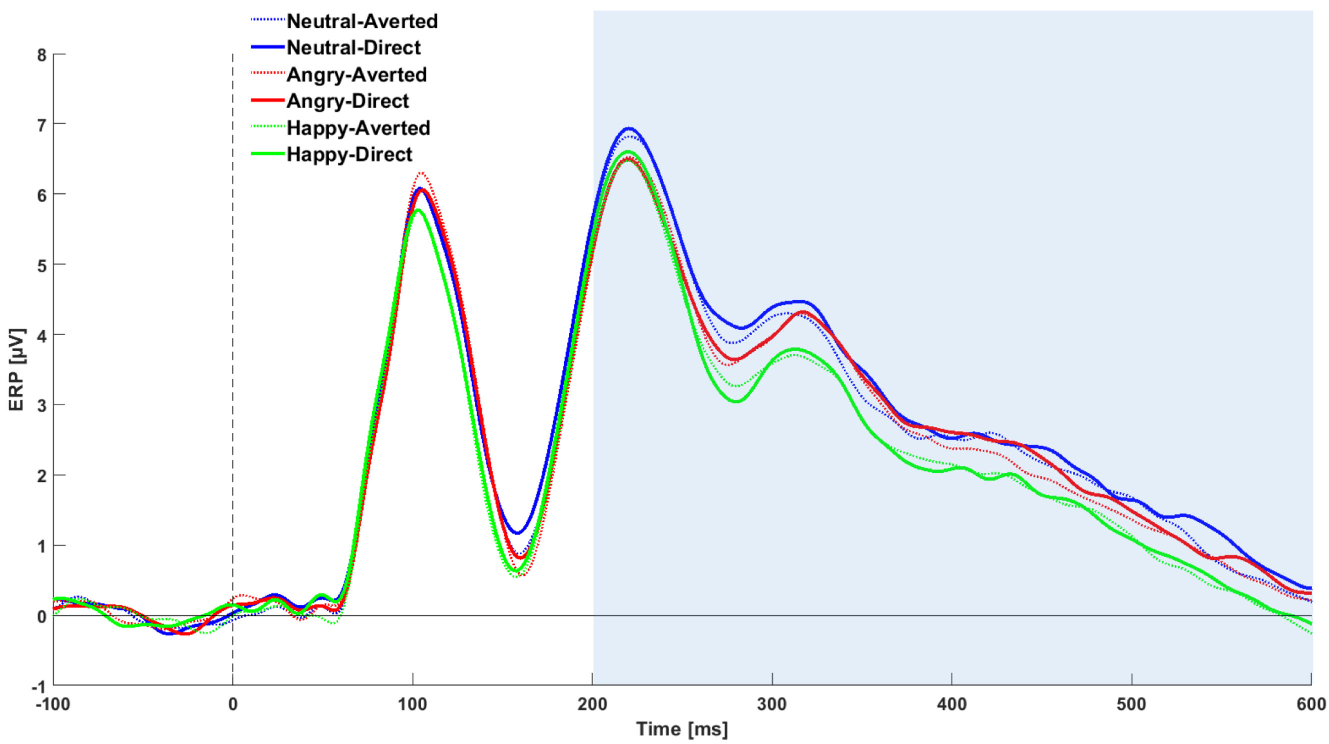

FIGURE 3 Effects of gaze and emotion on the EPN component for the initial gaze phase. ERPs are averaged across the electrodes of the EPN region of interest (P7, PO7, P8, PO8, PO9, PO10, O1, oz, O2, Iz). Shading indicates the time window that was defined for the EPN analysis. (effects of gaze and emotion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

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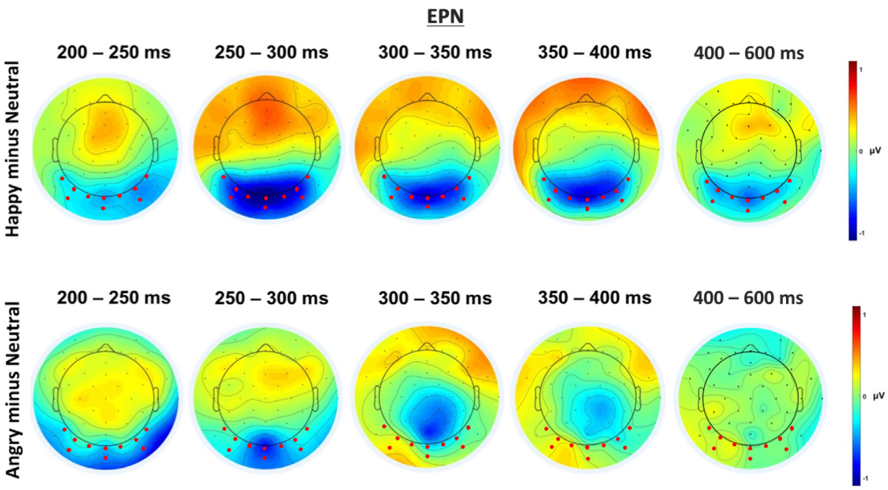

FIGURE 4 Difference topographies of the emotion effects in the initial gaze phase between 200 and 600 ms after face onset for the EPN component. The electrodes for the EPN ROIs are marked as thick red dots.

(M = 3.37 µV, SD = 3.71) was significant, as was the contrast between happy and angry faces (M = 3.39 µV, 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 µV, SD = 2.72), and neutral faces (M = 1.96 µV, SD = 2.75) was significant. However, the EPN amplitude to neutral and angry (M = 1.81 µV, 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 µV, SD = 3.38) than over the left hemisphere (M = −4.08 µV, 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 µV, SD = 3.78) than for averted-to-direct changes (M = −4.51 µV, 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 µV, SD = 2.72) differed significantly from neutral faces (M = −0.68 µV, SD = 2.73), when the gaze changed from averted to direct. The contrast between neutral and angry faces (M = −0.96 µV, SD = 2.74) was not significant (p > .05). For the time window 400–600 ms, the contrast between happy (M = 0.45 µV, SD = 2.09) and neutral faces (M = 0.75 µV, 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 µV, 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

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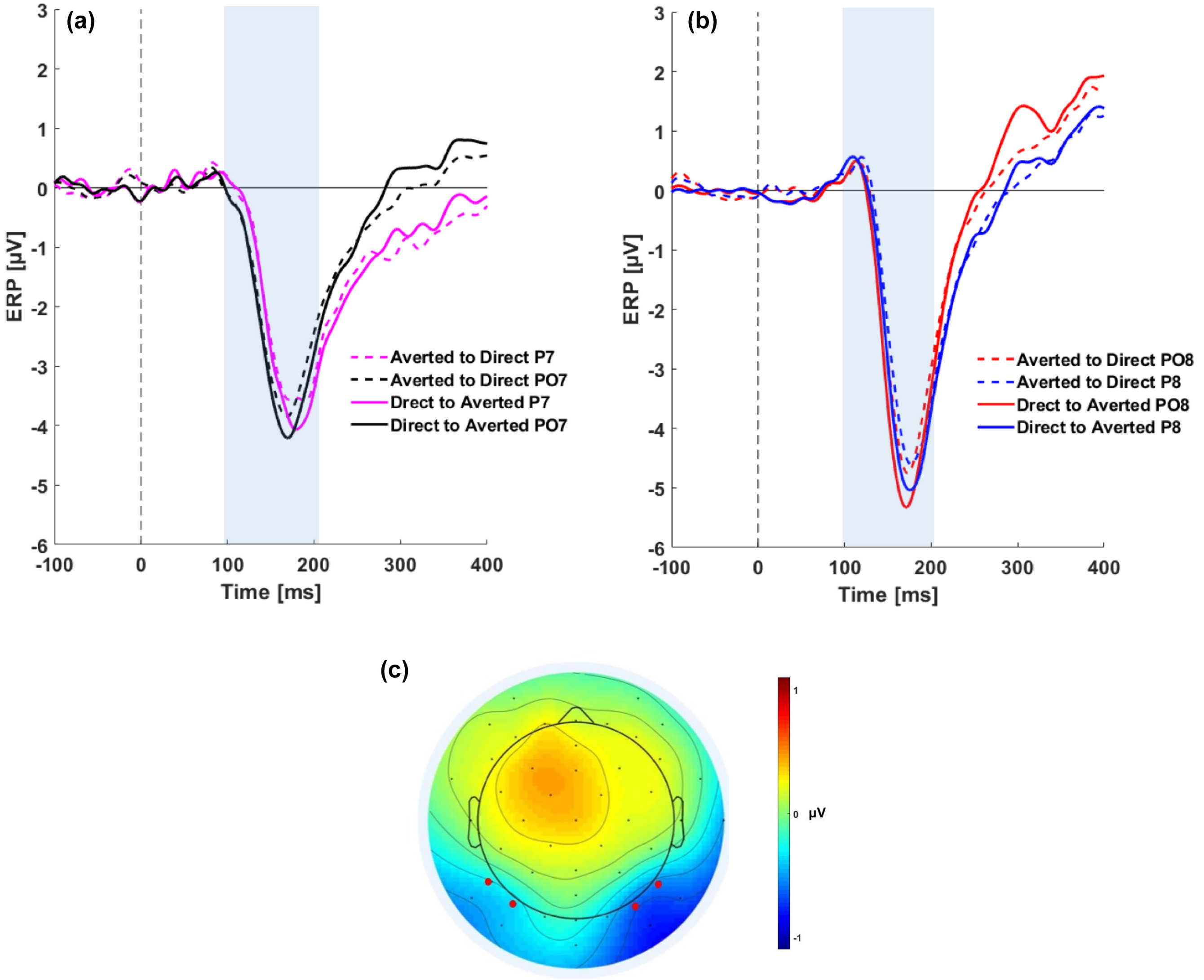

FIGURE 5 Effects of gaze and hemisphere on the N170 component in the gaze change phase. ERP waveforms of gaze effects for the (a) left hemisphere (electrodes P7 and PO7), and (b) right hemisphere (electrodes P8 and PO8). (c) Grand average ERP scalp map in the interval from 125 to 225 ms after the gaze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

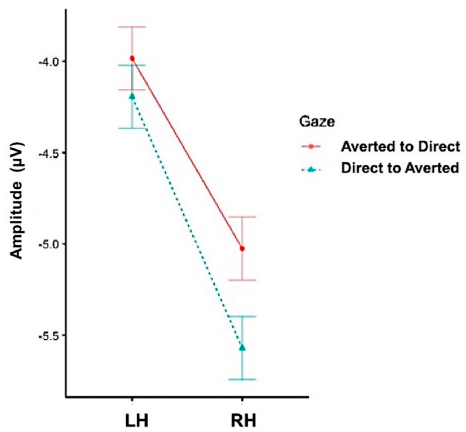

FIGURE 6 Effects of gaze direction and hemisphere on N170 amplitudes in the gaze change phase. Levels of the x-axis: Hemisphere (LH = left hemisphere, RH = right hemisphere). Error bars indicate Fisher's least significant difference.

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

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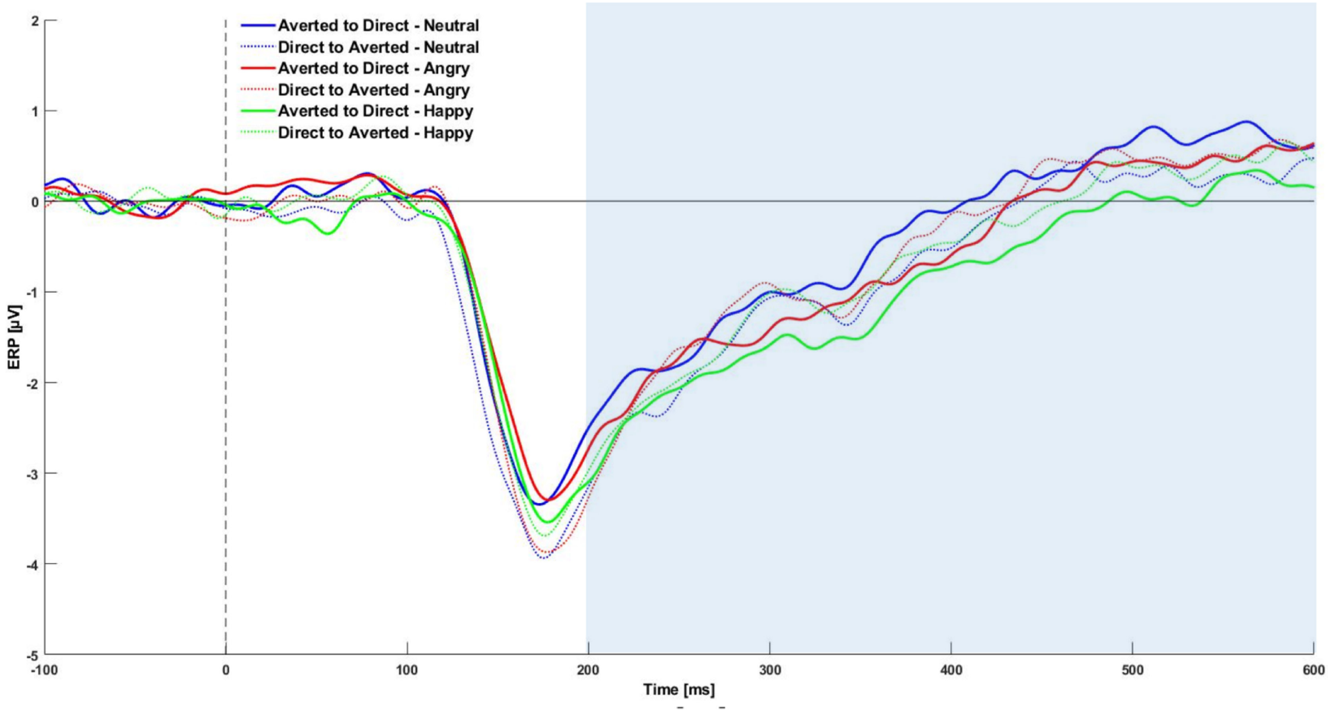
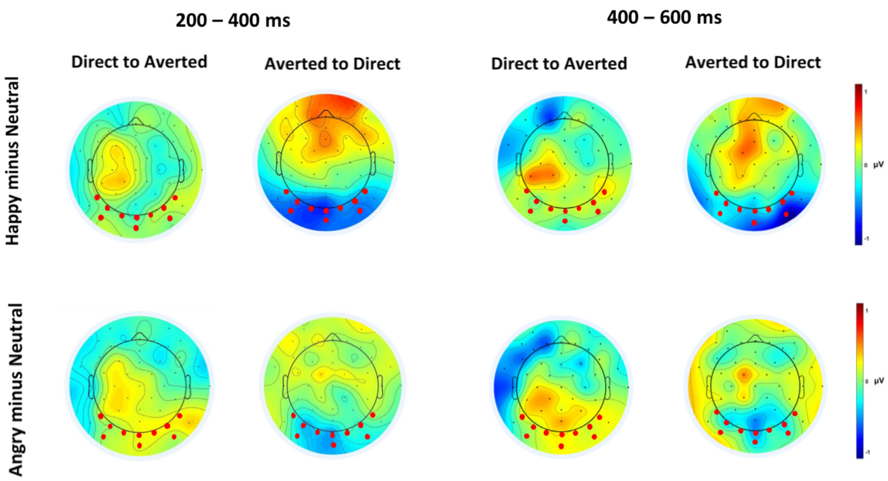


FIGURE 7 Effects of gaze change direction and emotion on the EPN component in the gaze change phase, averaged across the electrodes of the EPN region-of-interest. The shading indicates the time window pre-defined for the analysis. Thick lines indicate the significant emotion effect of happy faces in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

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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

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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.

ORCID

Shadi Bagherzadeh-Azbari https://orcid.org/0000-0002-1994-5261
Charlotte J. Lion https://orcid.org/0000-0002-5318-0266
Tilman Stephani https://orcid.org/0000-0003-3323-3874
Olaf Dimigen https://orcid.org/0000-0002-2507-2823
Werner Sommer https://orcid.org/0000-0001-5266-3445

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Appendix S1

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