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How the visual brain detects emotional changes in facial expressions: Evidence from driven and intrinsic brain oscillations

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Abstract

The processing of facial expressions is often studied using static pictorial cues. Recent work, however, suggests that viewing changing expressions more robustly evokes physiological responses. Here, we examined the sensitivity of steady-state visual evoked potentials and intrinsic oscillatory brain activity to transient emotional changes in facial expressions. Twenty-two participants viewed sequences of grayscale faces periodically turned on and off at a rate of 17.5 Hz, to evoke flicker steady-state visual evoked potentials (ssVEPs) in visual cortex. Each sequence began with a neutral face (flickering for 2290 ms), immediately followed by a face from the same actor (also flickering for 2290 ms) with one of four expressions (happy, angry, fearful, or another neutral expression), followed by the initially presented neutral face (flickering for 1140 ms). The amplitude of the ssVEP and the power of intrinsic brain oscillations were analyzed, comparing the four expression-change conditions. We found a transient perturbation (reduction) of the ssVEP that was more pronounced after the neutral-to-angry change compared to the other conditions, at right posterior sensors. Induced alpha-band (8–13 Hz) power was reduced compared to baseline after each change. This reduction showed a central-occipital topography and was strongest in the subtlest and rarest neutral-to-neutral condition. Thus, the ssVEP indexed involvement of face-sensitive cortical areas in decoding affective expressions, whereas mid-occipital alpha power reduction reflected condition frequency rather than expression-specific processing, consistent with the role of alpha power changes in selective attention.

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face processing; EEG; ssVEP; alpha-band oscillations; facial expressions

INTRODUCTION

As social animals, humans continuously search for social information to improve the prediction and interpretation of behavior shown by conspecifics, as well as guide their own behavior. Facial expressions are an important source of social information, conveying nonverbal signals about others' disposition and intentions, thus facilitating proper social interactions (Smith, Cottrell, Gosselin, & Schyns, 2005). Consequently, pictures showing different facial expressions are used in a wide range of studies of emotion and social perception (Wieser, Miskovic, & Keil, 2016). Consistent with their wide use and evolutionary relevance, viewing emotional faces prompts robust hemodynamic engagement of brain structures involved in higher-order perception, salience detection, and emotion (for a meta-analysis, see Sabatinelli *et al.*, 2011). However, the electrocortical and autonomic correlates of emotional face processing have been less consistent across the published literature: Emotional faces engage little or no motivational system activity as assessed by autonomic activity, defensive reflex modulation, or facial EMG (e.g., Alpers, Adolph, & Pauli, 2011), and effects of emotional expression on event-related potentials (ERPs) are still subject to considerable debate. In the following, we briefly review electrophysiological studies of emotional expression processing, with a focus on processing changes in expression.

The presentation of a face stimulus elicits a negative-going ERP in adult observers that is most prominent over right occipito-temporal visual areas and peaks at approximately 170 milliseconds following stimulus onset, therefore termed the N170 (Bentin, Allison, Puce, Perez, & McCarthy, 1996; Rossion & Jacques, 2011). Recently, evidence has accumulated that this early component may also be modified by the emotional expression of the face (for reviews, see Eimer, 2011; Vuilleumier & Righart, 2012): Several studies have reported a relative enhancement of the N170 evoked by pleasant or unpleasant compared to neutral facial expressions (Batty & Taylor, 2003; Blau, Maurer, Tottenham, & McCandliss, 2007; Caharel *et al.*, 2002; Kolassa, Kolassa, Musial, & Miltner, 2007; Pizzagalli, Lehmann, Koenig, REGARD, & Pascual-Marqui, 2000; Rossignol, Philippot, Douilliez, Crommelinck, & Campanella, 2005; Williams, Palmer, Liddell, Song, & Gordon, 2006; Wronka & Walentowska, 2011). Also, the nature of the task (e.g., passive viewing as opposed to identification, detection, or classification) affects the N170 component: For example, heightened N170 amplitudes for emotional, compared to neutral, expressions were selectively observed when faces were classified as "emotional" by the participants (Smith, 2012). The modulation of ERPs by facial expressions has also been examined using components such as the early posterior negativity (EPN), and the late positive potential (LPP). Both components tend to be enhanced in response to static emotional faces (e.g., Mühlberger *et al.*, 2009; Wieser, Klupp, *et al.*, 2012; Wieser, McTeague, & Keil, 2012), and index relatively early selection processes (EPN) as well as sustained widespread brain activity (LPP) in response to salient stimuli (Guerra *et al.*, 2011, 2012; Schupp *et al.*, 2004;

Wieser, Klupp, *et al.*, 2012; Wieser, McTeague, *et al.*, 2012; Wieser, Pauli, Reicherts, & Mühlberger, 2010). Several reviews and meta-analytic considerations have concluded, however, that effect sizes or ERP effects to facial expressions appear small and the specific effects tend to be variable across studies (Hinojosa, Mercado, & Carretié, 2015; Rellecke, Sommer, & Schacht, 2013), also may depend on the face stimulus collection used (Adolph & Alpers, 2010). The question arises to what extent more naturalistic stimuli would prompt robust electrophysiological differences.

It has become evident that situational and temporal context has massive influence on face perception and electrocortical processing (for a review, see for example Wieser & Brosch, 2012). Specifically, facial expressions in a natural context unfold in time. A growing literature has explored the effects of naturalistic, more dynamic displays of facial emotion on behavioral and physiological measures: Dynamic facial expressions, often shown as short movie clips, are rated as more arousing (Sato & Yoshikawa, 2007; Weyers, Mühlberger, Hefele, & Pauli, 2006), elicit larger facial mimicry (Sato, Fujimura, & Suzuki, 2008; Weyers *et al.*, 2006), stronger ERP responses (Recio, Sommer, & Schacht, 2011; Reicherts *et al.*, 2012; Trautmann-Lengsfeld, Domínguez-Borràs, Escera, Herrmann, & Fehr, 2013), and stronger amygdala activity (e.g. (LaBar, Crupain, Voyvodic, & McCarthy, 2003; Sato, Kochiyama, Yoshikawa, Naito, & Matsumura, 2004; van der Gaag, Minderaa, & Keysers, 2007). Furthermore, subjective valence and threat ratings of dynamic facial expressions seem to depend on the direction of change (i.e. from neutral to emotional or from emotional to neutral (Mühlberger *et al.*, 2011). Overall, these studies support the notion that changes in facial expressions are potentially more evocative than viewing static images of facial expressions (see Krumhuber, Kappas, & Manstead, 2013). This notion is supported by ERP work showing that the EPN component was enhanced *and* prolonged due to dynamic displays (Recio *et al.*, 2011) relative to static displays. The present study addresses the question of how changes in emotional expression are processed by the visual brain. Specifically, we examine to what extent changes in facial expression modulate face-evoked luminance responses generated low in the visual hierarchy, measured by flicker ssVEPs.

Electrophysiological studies of changing facial expressions confront the difficulty that any expression-related effects make up a small portion of the recorded signal, which to a large extent is determined by the luminance and/or contrast changes occurring at face onset. Although this problem can be addressed by comparing suitable control conditions (Recio *et al.*, 2011), it is difficult to use the spatio-temporal dynamics reflected in ERPs to continuously quantify brain responses to dynamic displays in a specific, constant set of cortical regions. To address these challenges and to maximize the specificity of the neural response to face-specific processing, Rossion and collaborators have developed the fast periodic visual stimulation (FPVS) paradigm (see Rossion, 2014, for a review). The FPVS technique typically embeds a feature of interest (an oddball) at regular intervals into a rapid periodic stream of faces (or other objects). The rationale of this procedure is that any brain response that is specific to the intermittently repeated feature of interest (e.g. a given face identity, gender, race, etc.) will elicit regular brain responses at a sub-harmonic frequency of the primary driving stream, which can be captured by Fourier-based techniques. By contrast, any face-unspecific brain responses to changes in luminance and contrast will be present at the driving frequency at which faces are presented. Using this method, Dzhelyova, Jacques,

& Rossion (2017) showed that a brief change of expression inserted in a dynamic stimulation sequence elicited specific occipito-temporal responses between 100 and 310 ms, indicating a rapid change detection process followed by a long integration period of facial expression information in the human brain. In a similar vein, Zhu, Alonso-Prieto, Handy, & Barton (2016) demonstrated less adaptation of the FPVS signal when emotional expressions were varied, compared to when they were kept constant, an effect maximally pronounced over right posterior sensors. Importantly, the FPVS technique allows for quantification and separation of the brain response to the changes in luminance and contrast (maximal over mid-occipital sensors) from the “oddball” response maximal at sensors that are specifically sensitive to the oddball stimulus dimension (e.g., right posterior sensors in the case of face-specific processing). The present study also relies on periodic stimulation, but uses luminance modulation of the stimulus display at a rapid rate to examine the response of luminance-sensitive neurons low in the visual hierarchy to changing facial expressions. Building on the research described in the next paragraph, we aimed to characterize the time course and topography of change-induced responses in the flicker ssVEP. Using this method, the present research examines the overarching hypothesis that luminance sensitive populations of neurons are modulated by higher-level stimulus properties such as facial expression.

A widely-used approach for continuously quantifying the brain response to an ongoing stimulus stream is to measure the time-varying envelope of the luminance-evoked (flicker) or contrast-evoked (reversal) steady-state visual evoked potential (ssVEP; for a review see Norcia, Appelbaum, Ales, Cottareau, & Rossion, 2015). The ssVEP appears as an oscillatory brain response when observers view rapid (> 3 Hz) and periodical flicker or pattern reversal (e.g., Regan & Spekreijse, 1986). It thus reflects temporally sustained lower-tier visuocortical responses to luminance (flicker ssVEP) or local contrast (pattern reversal ssVEP). Given these properties, the ssVEP is suitable to examine questions regarding the modulation of early visual cortical neurons by experimental tasks (i.e., selective attention, Müller, Trautmann, & Keitel, 2016) or by stimulus content (Keil, Moratti, Sabatinelli, Bradley, & Lang, 2005). The FPVS, by contrast, typically focuses on an oddball stimulus embedded in a fast-periodic information stream, where a deviant stimulus (i.e. face) is regularly introduced within a sequence of standard stimuli. Thus, ssVEP and FPVS use different approaches, with the former being luminance or contrast-sensitive while the latter is sensitive to the feature of interest (i.e. the feature that distinguishes the oddball from the standards). Importantly, the time-varying ssVEP amplitude may be perturbed by changes of the stimulation stream that do not alter the luminance or contrast input, i.e., changes in the predictive value of the driving stimulus, or subtle changes in the direction of its visual motion (Deweese, Müller, & Keil, 2016). In line with these findings, the scalp topography of ssVEP amplitude modulations, their estimated sources (Wieser, McTeague, *et al.*, 2012), and their correspondence with concurrent fMRI (Petro *et al.*, 2017) suggest that changes in the visuo-cortical ssVEP amplitude likely reflect modulations in more widespread stimulus-sensitive cortical networks. Findings with face-evoked ssVEPs support this notion: Amplification of the ssVEP signal evoked by flickering emotional faces (compared to neutral expressions) was found in participants reporting high, but not low social anxiety (Gruss, Wieser, Schweinberger, & Keil, 2012; McTeague, Shumen, Wieser, Lang, & Keil,

2011; Wieser *et al.*, 2014). Furthermore, emotional facial expressions reduce the neural adaptation effect to face identity (Gerlicher, Van Loon, Scholte, Lamme, & Van der Leij, 2014). Paralleling work with the FPVS paradigm, the ssVEP differences discussed above tend to show maximum energy over mid-occipital sensors, but condition-related differences are often observed over right occipito-temporal sites, known to possess maximum sensitivity to face-specific visual processing (Rossion & Boremanse, 2011). The present research aims to leverage the time and topography information inherent in ssVEP time courses to characterize the visuo-cortical processing of changes in emotional expression.

In addition to the research reviewed above, electrophysiological studies have examined changes in intrinsic brain oscillations when viewing different facial expressions. In these studies, changes in the alpha frequency band (8–13 Hz) have emerged as a signal of interest (Balconi & Pozzoli, 2009; Girges, Wright, Spencer, & O'Brien, 2014; Güntekin & Başar, 2007). In studies with visual stimuli, decreases in alpha power reliably occur in response to task relevant stimuli (Bollimunta, Mo, Schroeder, & Ding, 2011; Keil, Mussweiler, & Epstude, 2006), and the degree of reduction has been viewed as an inverse measure of cortical arousal (Aftanas, Reva, Varlamov, Pavlov, & Makhnev, 2004; De Cesarei & Codispoti, 2011; Neuper, Grabner, Fink, & Neubauer, 2005). In terms of behavioral correlates, alpha signals traditionally have been regarded as an inverse index of attentive external stimulus processing, with greater midline posterior alpha reductions thought to index heightened attention and active visual processing (Pfurtscheller, 1992). Although emotionally engaging naturalistic scenes are typically followed by greater alpha power reduction compared to neutral pictures (De Cesarei & Codispoti, 2011), findings regarding alpha power changes in response to emotional facial expressions have been mixed (Güntekin & Başar, 2014). One reason for this discrepancy may be — as stated above — that static faces may not strongly engage motivational circuits and their associated attention mechanisms. Alpha oscillations have also been studied as participants monitored visual (Petro & Keil, 2015) and auditory stimulus streams (Weisz & Obleser, 2014) for target events, pertinent to the present study design. In sequence processing, relative increases of alpha power prior to a target event, along with heightened alpha power reduction following target events, have been associated with attentive monitoring of a stream, measured by means of detection accuracy and/or response time (Obleser, Henry, & Lakatos, 2017). The present study examines alpha power changes in response to a temporally distinct, temporally localized change in facial expression. This approach allows us to test two competing hypotheses regarding expression-related alpha power reductions: (1) if salient facial expression changes (from neutral to emotional) engage selective attention mechanisms, then these changes should prompt greater alpha power reduction, across midline posterior sensors, compared to neutral-neutral changes. By contrast, (2) if rare and subtle changes prompt greater attentive engagement as reflected in alpha power reduction, then we would expect greater power decrease in the neutral-neutral condition.

The present study assesses changes in oscillatory brain activity, with a focus on changes in the face-evoked ssVEP and alpha-band power changes. Specifically, we test whether ssVEPs and intrinsic oscillations are modulated by changes from an initial neutral expression to an emotional expression, and back to a neutral expression. If changes from a neutral expression to an emotional expression (happy, fearful, angry) prompt heightened processing of the

stimulus stream compared to less motivationally salient expressions, then we expect a commensurably stronger perturbation of the ssVEP signal and a more pronounced reduction in the alpha band in response to the change. If transient changes in facial expression affect visual areas more broadly, we expect effects to display a midline posterior topography. By contrast, if expression changes prompt altered processing primarily in face-sensitive areas of the right ventral stream, then we expect right posterior topographies of the change-related differences in alpha power as well as ssVEP amplitude.

METHODS

Participants

Twenty-two participants were recruited for the experiment. Participants were undergraduate and graduate students from the University of Florida as well as participants recruited from the community through flyers and advertisements. Students were given course credits for participation. Analysis included all 22 participants (13 women; $M = 20.77$; $SD = 2.74$), ranging from 18 to 29 years of age, 21 of whom reported being right-handed. All participants had normal or corrected-to-normal vision and reported no personal or family history of seizures. Each participant completed the Liebowitz Social Anxiety questionnaire (Heimberg *et al.*, 1999) prior to participating. With a mean of 15.50 ($SD = 11.53$), and a range between 2 and 39, all participants scored in what is considered the low social anxiety range (see McTeague *et al.*, 2011). Previous work (McTeague *et al.*, 2018, 2011; Wieser, McTeague, *et al.*, 2012) has demonstrated that people high in social anxiety as measured by the Liebowitz Social Anxiety questionnaire show heightened flicker ssVEP amplitudes to emotional expressions, whereas low-anxious observers do not. Thus, we employed this questionnaire as an exclusion criterion, in order to assure no high anxiety person would be included in this sample. The study was approved by the Institutional Review Board of the University of Florida and was in accordance with the Declaration of Helsinki. All participants provided informed consent following a short description of the study.

Stimuli

Eighty (80) pictures from the Karolinska Directed Emotional Faces (KDEF) database (Lundqvist, Flykt, & Öhman, 1998) were selected. Stimuli consisted of faces of 20 different actors (10 females, 10 male) with frontal gaze, displaying each of four emotional expressions (neutral, happy, angry, and fearful; see Figure 1B, for example stimuli). Additionally, 20 different neutral expressions from the same actors were also selected to accommodate the fully crossed experimental design described below. Pictures of the KDEF database are standardized regarding the eye position and were additionally converted to grayscale and standardized using programs from the image processing toolbox in MATLAB (MathWorks, Natick, MA, USA). After standardization, pictures had equal average luminance (49 cd/m^2 , measured by a Gossen MavoSpot luminance meter) and contrast (measured as the standard deviation of grayscale values across the picture).

Experimental Design and Procedure

Upon arrival at the laboratory, participants were briefly given an overview of the study and then provided written informed consent. The experiment was conducted in a sound-

attenuated and electrically shielded room under dimmed light. Participants were instructed that they would be viewing a series of flickering pictures of faces with different emotional expressions. They were asked to keep their eyes comfortably focused on the center of each face throughout the duration of a trial. Participants were explicitly told to minimize the occurrence of eye blinks while the faces were on the screen and to avoid head movements during the entire recording session.

Stimuli were presented on a 27" CRT monitor (ViewSonic GS815) with a vertical refresh rate of 70 Hz, 1.5 m away from the participant. Pictures spanned a visual angle of 7° vertically and 5° horizontally. Stimuli were delivered using Psychtoolbox running on MATLAB (Brainard, 1997). Pictures were displayed in a flickering fashion at a rate of 17.5 Hz in the center of the screen with a black background. These settings led to a cycle (one flicker) duration of 57.14 ms, with the face picture on the screen for 28.57 ms followed by 28.57 ms of black screen. The duration of one face presentation was 5714 ms (100 cycles), with the first picture within the trial always being a neutral face (displayed for 40 cycles, lasting from 0 ms to 2.29 seconds). Subsequently, the picture changed to an expression by the same actor with one of the three emotional expressions (happy, angry, or fearful) or a different neutral face (again 40 cycles, from 2.29 seconds to 4.57 seconds). The trial concluded with the initially presented neutral picture (20 cycles, shown from 4.57 seconds to 5.71 seconds). The second change was added primarily to end each trial on a comparable stimulus, avoiding carry-over effects to subsequent trials, and because of its short duration and proximity to the offset potential was not a target for ssVEP analyses. Using 40 cycles (i.e. flicker responses), for the two initial phases of each trial allowed us to assess the extent to which a robust, temporally stable measurement of the ssVEP was achieved with the present trial count (40 trials per condition, see below). Relatively long trial durations also facilitated the interpretation of slow neural responses such as alpha power changes as prompted by the expression change. By contrast, shorter trial durations may result in overlapping neural responses to the onset and change events, making interpretation more difficult. A fixation cross was presented between trials, to facilitate that participants maintain gaze at the center of the screen. Because the KDEF faces used are standardized relative to eye position, the fixation cross was always located at a position that corresponded to the midpoint between the eyes of each poser. The inter-trial interval varied between 2 to 4 seconds, drawn from a rectangular distribution. For an illustration of the experimental design, see Figure 1A.

The total number of trials was 160, with each condition comprising 40 trials. Given previous methodological work with ssVEP signals, these trial counts, especially when using higher driving frequencies above the alpha range, tend to result in excellent signal-to-noise ratios, and allow estimation of ssVEP amplitudes at high re-test reliability and internal consistency (Keil *et al.*, 2008; Miskovic & Keil, 2014). The experiment lasted approximately 25 minutes and the total experimental session lasted about 1 hour, after which participants were debriefed.

EEG Recording and Data Collection

The electroencephalogram (EEG) was continuously recorded from 129 channels using a HydroCel high-density Geodesic Sensor Net (Electrical Geodesics, Eugene, Oregon, USA) equipped with Ag/AgCl sensors (see Figure 2 for the sensor recording montage). The vertex sensor (Cz) served as the recording reference. Continuous EEG was recorded using NetStation software on a Macintosh computer, digitized at a rate of 250 Hz. All channels were preprocessed online by means of a 0.1 Hz high-pass filter and a 48 Hz low-pass elliptical filter. Impedance for each sensor was kept below 60 K Ω , as recommended for this high (200 M) input impedance amplifier. Trigger pulses synchronized to the screen retrace were delivered through Psychtoolbox to the EEG amplifier and co-registered with the online EEG signal.

The EEG signal was segmented from the continuously recorded data relative to the onset of each trial. Epochs of 6800 ms length were extracted from the continuous signal (800 ms pre and 6000 ms post-stimulus onset). Data were low-pass filtered offline at a frequency of 40 Hz (cutoff at 3 dB point; 45 dB/octave, 18th order Butterworth filter). Subsequently, artifact rejection was conducted using EMEGS software (Peyk, De Cesarei, & Junghöfer, 2011). This procedure identifies artifacts in individual recording channels using the recording reference (Cz), based on the distribution of the absolute value, standard deviation, and temporal gradient of the voltage amplitude across trials and channels. Such channels were replaced by spline-interpolated data, using the full channel set. Then, statistical parameters were used to identify and remove artifact-contaminated trials (Junghöfer, Elbert, Tucker, & Rockstroh, 2000). These steps were repeated after re-referencing the data to the average reference. After this artifact correction procedure, trials of the same condition were averaged together to form specific time domain representations of the visual evoked activity. An average of 71% of the total trials were retained for further analyses. The average percentage of trials per condition comprised: 69% for happy, 74% for neutral, 70% for angry, and 72% for fearful expression change conditions.

Steady-state Visual Evoked Potentials (ssVEP)

Artifact-free EEG segments were averaged in the time domain for each participant and condition separately. To extract the time-varying amplitude envelope of the ssVEP, a 14th order Butterworth filter (3 dB corner frequencies of 17.0 and 18.0 Hz) was applied to the averaged data, and an analytic, phase-shifted (by 90 degrees) signal of the band-pass filtered data was generated by means of the Hilbert transform, using standard MATLAB functions. The ssVEP envelope was then obtained as the modulus of the original and phase-shifted data, computed for each time point, resulting in a time-varying ssVEP amplitude measure at each sensor and for each facial expression condition. Measured as the full width at half maximum of the impulse response, this time-varying amplitude had a time resolution of 162 ms.

Time-Frequency Analysis of Intrinsic Oscillations

Temporal dynamics of intrinsic oscillatory brain activity were investigated using convolution of the artifact-free single trials and a family of complex Morlet wavelets. Using a Morlet parameter of 7 (see, e.g., Bartsch, Hamuni, Miskovic, Lang, & Keil, 2015; Tallon-Baudry &

Bertrand, 1999) resulted in a frequency resolution of 0.1471 Hz and a time resolution of 111 ms (full width at a half maximum) at a center frequency of 10 Hz. Complex wavelets were calculated for frequencies between 2.94 Hz and 41.19 Hz in steps of 1.47 Hz, aiming to obtain wide coverage of the lower-frequency spectrum of interest in the present study. Gamma range oscillations (> 40 Hz), which tend to be small in amplitude, were not considered (Keil, 2013).

For each trial, the time-varying total power was computed as the absolute value of the convolution of the EEG data, tapered by a cosine-square window (ramping up/down over 200 ms) with the wavelet. The resulting time-by-frequency matrices for each trial were averaged by condition, for each participant. Time-varying amplitudes were divided from the mean of a baseline segment between 600 and 200 ms prior to stimulus onset, and expressed as percent change for each frequency. Baseline corrected time-varying spectral amplitudes were then used for statistical analyses throughout. In the present study, the alpha band was defined as the power captured by wavelets with center frequencies between 9.30 and 12.24 Hz.

Statistical Analyses

A two-pronged approach was used for statistical analysis. The first set of analyses leveraged an ANOVA approach to test the main hypotheses of the study for specific time ranges and scalp locations. A second set of exploratory analyses was conducted using permutation-controlled t-tests comparing emotional and neutral expression conditions for all time points, frequencies, and scalp locations, to fully use the temporal and spatial information inherent in the data and generate hypotheses for future work. Separate analyses were conducted for ssVEPs and alpha power. No part of the study analyses was pre-registered prior to the research being conducted. All significance levels were applied in a two-tailed fashion, with the significance level of $p < 0.05$.

Steady-State Visual Evoked Potential (ssVEP)

Analysis of Variance.—Given the present focus on mid-occipital versus right-posterior (occipito-temporal) effects, the time-varying ssVEP amplitudes were averaged across sensors in two different clusters, which contained sensors Oz and PO8 of the international 10–20 system, and their six nearest neighbors, respectively¹. See Figure 2 for an illustration of the sensor clusters. These clusters allowed discrimination between mid-occipital and right-lateralized effects, central to the hypotheses tested in the present study. A 2×4 repeated-measures ANOVA using Time Window (ONSET and CHANGE) and Facial Expression (angry, fearful, happy, and neutral) as factors was applied to investigate each sensor cluster location separately. To quantify effects of stimulus train onset and of the first change on the ssVEP envelope, we measured the mean ssVEP amplitude in two time windows of 1000 ms length, following the ONSET (756 to 1756 ms post-stimulus onset), and first CHANGE (2452 to 3452 ms post-stimulus onset). These time windows maximized sensitivity to sustained effects, specifically sustained changes in ssVEP amplitude after the

¹The left-posterior (occipito-temporal) cluster, which comprised sensor PO7 and its six nearest neighbors (see Figure 2 for mirrored sensor cluster location) was not included in the analysis because there was no hypothesis regarding left posterior sites. However, results are reported below in footnotes, accordingly.

change in facial expression. They also eliminated potential spurious effects due to rapid fluctuations in noise. The time segment following the return to the original neutral expression was not considered in this analysis because this final time segment was too short to discriminate true perturbations in the ssVEP envelope from artefactual responses of the Hilbert transform to transient (event-related) components, and because the study as planned did not include hypotheses regarding the ssVEP modulation by the change back to neutral. Two-tailed paired t-tests were employed as follow-up comparisons whenever appropriate. Analyses of variance were corrected for non-sphericity using the Greenhouse-Geisser method. Frequentist statistics were supplemented by Bayesian ANOVAs implemented in JASP (JASP Team, 2018), where appropriate, to seek converging evidence. For Bayesian ANOVAs, the default priors (equal prior likelihood for each main effect and interaction model) were used and estimation errors are reported throughout.

Permutation controlled t-tests.—In a second set of analyses, permutation t-tests were used to quantify the fine-grained spatial and temporal structure of any effects identified by ANOVA analysis, and to explore effects that were not anticipated. Paired t-tests were used, comparing the neutral-neutral-neutral condition to the three remaining conditions at each sensor and time point, correcting for multiple comparisons by means of the algorithm proposed by Blair & Karniski (1993). To this end, the data were shuffled across conditions, and t-value matrices (sensor by time) were re-calculated 8000 times. For each random shuffle (permutation) and time point, the minimum and maximum t-value (corresponding to the extreme t-values in each topography) entered a t-max (t-min) distribution. This procedure yields highly conservative thresholds, identifying effects that are consistently in the tails of the reference distribution, across all sensors (Karniski, Blair, & Snider, 1994). The 0.025 and 0.975 tails of these distributions were used as thresholds for determining statistical significance (cf., Keil *et al.*, 2005; McTeague, Gruss, & Keil, 2015). This resulted in critical t-values of -2.86 and 2.89 , meaning that values below and above these thresholds reached statistical significance at the 0.05 percent level, controlled for multiple comparisons.

Intrinsic brain oscillations

Planned analysis of variance on alpha power.—Alpha power was averaged across sensors in each of the two sensor clusters described above (mid-occipital, right occipito-temporal, see Figure 2) and across time points within three time windows. These windows comprised the following time intervals: (i) ONSET: 300 to 700 ms; (ii) CHANGE: 2600 to 3000 ms; (iii) RETURN: 4700 to 5100 ms, relative to stream onset. The time windows of 400 ms length were chosen according to the transient nature of the brain oscillation changes to these stimuli. For each cluster separately, a 3×4 repeated-measures ANOVA was conducted, with factors of Time Window (ONSET, CHANGE, RETURN) and Facial Expression (angry, fearful, happy, and neutral). Follow-up ANOVAs and two-tailed paired t-tests were employed as follow-up comparisons whenever appropriate and deviations from sphericity corrected using the Greenhouse-Geisser method. Again, frequentist statistics were supplemented by Bayesian ANOVA, where appropriate.

Permutation controlled t-tests across the entire time-by-frequency plane.—Paralleling the analysis of ssVEP envelope, permutation t-tests corrected for multiple

comparisons were performed to assess the time point and scalp locations at which t-values reached significance. Differing from the permutation tests described for ssVEP envelope (above), additional t-tests were also calculated for each frequency. As a consequence, the permutation distribution (generated by 8000 random permutations of conditions within participants) consisted of the maximum and minimum of each sensor by frequency t-value plane, for each time point. Again, the 0.975 and 0.025 tails of the resulting t-max (t-min) distributions were used as thresholds for statistical analysis. Because of the greater number of possible comparisons, the critical values for time-frequency planes were more conservative than for time-varying ssVEP amplitude: Paired t-values below -3.73 and exceeding 3.69 were considered statistically significant at the permutation corrected p-value of 0.05.

RESULTS

Steady-State Visual Evoked Potentials (ssVEPs)

Figure 3 represents the time-locked averages of the cortical activity over representative sensors Oz and PO8, averaged across all conditions and all 22 participants. The ssVEP envelope is perturbed by the transient changes of the facial expressions within the trials, visible in the time domain by disruption of periodic modulation after the first and the second facial expression change. This disruption is most evident at right occipito-temporal sensors. An ERP is visible, consistent with an N170 component linked to face processing. Note that the present trial count, while sufficient for analysis of ssVEP and alpha power changes, does not allow for reliable measurement of the N170.

To examine the signal quality, we computed the frequency spectrum of the averaged ssVEP signal for each participant. Grand mean spectra were calculated at the condition level to establish the extent to which the trials contained in one condition were sufficient to produce satisfactory SNRs in the ssVEP, separately for each condition. As visible in the grand mean averaged Fourier spectrum across participants for the neutral condition, a pronounced peak was observed at 17.5 Hz (Figure 4, left), with the power maximum located at occipital pole sensors (Figure 4, right).

Time-varying ssVEP amplitudes (envelopes obtained through Hilbert transform) were then compared across experimental conditions using repeated-measures ANOVA, with factors of Time Window and Facial Expression. Grand mean ssVEP envelopes are shown in Figure 5, top panel, with each line representing the envelope of the ssVEP at the driving frequency (17.5 Hz) for one of the four expression change conditions. The bottom left panel of Figure 5 shows topographical maps of the differential ssVEP amplitude (emotional minus neutral) for each condition during the CHANGE time period, when the facial expression changes from neutral to an emotional or another neutral expression of the same actor.

ANOVA results: ssVEP envelope²

Mid-occipital cluster.—The temporal dynamics of the ssVEP amplitude were not modulated by expression at the mid-occipital cluster: The interaction between Time Window and Facial Expression did not reach the significance threshold ($F(3,63) = 0.48$, $p = 0.68$, n.s.).

There was, however, a main effect of Time Window ($F(1,21) = 7.17$, $p = 0.014$, $\eta_p^2 = 0.25$), again showing that there was lower evoked oscillatory amplitude for the CHANGE time window ($M = 0.17 \mu V$, $SE = 0.043$) compared to the ONSET time window, across all expressions ($M = 0.20 \mu V$, $SE = 0.043$). No main effect was observed for Facial Expression ($F(3,63) = 1.77$, $p = 0.17$, n.s.), with angry faces ($M = 0.18 \mu V$, $SE = 0.038$), fearful faces ($M = 0.18 \mu V$, $SE = 0.037$), happy faces ($M = 0.20 \mu V$, $SE = 0.040$), and neutral faces ($M = 0.18 \mu V$, $SE = 0.037$) showing similar ssVEP amplitudes. The Bayesian ANOVA with the same design converged with the frequentist analysis and showed that the data were most likely to arise under a selective effect of Time Window, $BF_{10} = 1551.4$, estimation error = 2.3%, providing decisive support for the hypothesis that the transient change in facial expression disrupts the ssVEP responses irrespective of facial expression.

Right-posterior cluster.—In the repeated-measures ANOVA on ssVEP amplitudes at the right-posterior (occipito-temporal) cluster, a main effect of Time Window ($F_{(1, 21)} = 12.77$, $p = 0.002$, $\eta_p^2 = 0.38$) emerged: Paralleling the mid-occipital cluster, lower amplitudes were observed in the CHANGE time window compared to the ONSET ($M = 0.20 \mu V$, $SE = 0.029$ versus $M = 0.17 \mu V$, $SE = 0.022$). No main effect of Facial Expression was observed ($F_{(3, 63)} = 0.79$, $p = 0.47$, n.s.; $M_{Angry} = 0.18 \mu V$, $SE_{Angry} = 0.025$; $M_{Fearful} = 0.18 \mu V$, $SE_{Fearful} = 0.023$, $M_{Happy} = 0.19 \mu V$, $SE_{Happy} = 0.029$; and $M_{Neutral} = 0.18 \mu V$, $SE_{Neutral} = 0.027$). Importantly, an interaction between Time Window and Facial Expression was observed ($F(3, 63) = 3.20$, $p = 0.049$, $\epsilon = 0.69$, $\eta_p^2 = 0.13$; Figure 5, bottom right). A post-hoc ANOVA of this interaction effect using differences between the CHANGE time window and the ONSET time window, for each expression, showed a main effect of Facial Expression ($F_{(3,63)} = 3.20$, $p = 0.049$, $\epsilon = 0.69$, $\eta_p^2 = 0.13$). Followed up by paired t-tests, this main effect reflected the selective decrease in ssVEP amplitude when changing to angry, compared to when changing to neutral expressions, $t_{(21)} = 2.33$, $p = 0.03$, and compared to fearful expressions, $t_{(21)} = 4.14$, $p < 0.01$, with the other expression conditions not differing in terms of the change from ONSET to CHANGE. The Bayesian ANOVA model comparison also favored the interaction model, $BF_{10} = 3.34$, estimation error = 2.9%, under which the data were 3.34 times more likely than the null model combined with the models without the interaction (i.e. when the main effect of Time Window model and the main effect of Facial Expression model were added to the null model). This supports the notion of stronger perturbation of the ssVEP by changes to angry, compared to other expressions. Thus, substantial evidence for the interaction model was provided by the Bayesian ANOVA.

Permutation-controlled t-tests.—Time-varying paired t-tests for each time-point and sensor reached the significance level only at right-posterior sensors corresponding to PO8 and one neighboring sensor, for the comparison between neutral and angry expressions. Paralleling ANOVA findings, the ssVEP envelope reduction prompted by the change to an

²A 2 X 4 repeated-measures ANOVA on ssVEP amplitudes for the left-posterior (occipito-temporal) cluster, using Time Window (ONSET, CHANGE) and Facial Expression (happy, neutral, angry, fearful) as factors showed a main effect of Time Window ($F_{(1, 21)} = 4.54$, $p = 0.045$, $\eta_p^2 = 0.18$). Lower amplitudes were observed in the CHANGE time window compared to the ONSET ($M = 0.16 \mu V$, $SE = 0.021$ versus $M = 0.18 \mu V$, $SE = 0.030$, respectively). No main effect of Facial Expression was observed, showing similar oscillatory amplitudes ($F_{(3, 63)} = 1.00$, $p = 0.39$, n.s.; $M_{Angry} = 0.17 \mu V$, $SE_{Angry} = 0.027$; $M_{Fearful} = 0.17 \mu V$, $SE_{Fearful} = 0.026$, $M_{Happy} = 0.18 \mu V$, $SE_{Happy} = 0.026$; and $M_{Neutral} = 0.16 \mu V$, $SE_{Neutral} = 0.025$). No interaction between Time Window and Facial Expression was observed ($F_{(3, 63)} = 1.37$, $p = 0.26$, n.s.).

angry face was greater compared to the change to a neutral expression, between 2676 and 2908 ms after stimulus onset, which corresponds to a time range of 386 to 618 ms after the change in expression. Considering the temporal smearing of the Hilbert transform (162 ms), the window containing significant ssVEP modulation thus maximally extended from 224 ms to 780 ms following the change in expression.

Time-Frequency Analysis of Alpha Oscillations³

ANOVA results midline occipital cluster.—Means of the alpha power amplitudes as a percentage of the signal change for each cluster of sensors are given in Tables 1 and 2. For the midline occipital cluster (see Figure 6), alpha power following the onset, change, and return events displayed a significant interaction between Time Window and Facial Expression ($F_{(6, 126)} = 2.49$, $p = 0.037$, $\epsilon = 0.82$, $\eta_p^2 = 0.11$). No main effects of Time Window ($F_{(2, 42)} = 0.86$, $p = 0.43$, n.s.) or Facial Expression ($F_{(3, 63)} = 1.53$, $p = 0.22$, n.s.) were observed. Follow-up analyses of the interaction showed that mean alpha power changes in response to the four expression conditions differed from each other only during the RETURN time window, i.e. after the second change, back to the original neutral expression ($F_{(31, 63)} = 4.43$, $p = 0.013$, $\epsilon = 0.78$, $\eta_p^2 = 0.17$). Two-tailed paired t-tests showed that neutral faces elicited greater alpha reduction during the RETURN time window compared to all other expressions (Happy: $t_{(21)} = -2.79$; $p = 0.011$; Angry: $t_{(21)} = -2.21$; $p = 0.038$; Fearful: $t_{(21)} = -4.27$; $p < 0.001$). As expected, no differences between emotional facial expression conditions were found for the ONSET window with a neutral face present in each condition ($F_{(1, 3)} = 0.50$, $p = 0.66$, n.s.). Furthermore, the mean alpha reduction following the change also did not show differential modulation by expression ($F_{(1, 3)} = 0.56$, $p = 0.61$, n.s.), in the mid-occipital cluster of sensors.

Complementing frequentist ANOVA, the Bayesian ANOVA on the same overall model indicated that the data were most likely to arise from a main effect of Facial Expression, $BF_{10} = 4.28$, estimation error = 1.3%. Bayesian post-hoc t-tests corresponded with frequentist ANOVA in that they only found the neutral expression to be different from all other expressions, all $BFs > 4.4$.

ANOVA results right-occipital cluster.—For the right occipito-temporal cluster, there was no significant interaction between Time Window and Facial Expression ($F_{(6, 126)} = 2.10$, $p = 0.078$, $\epsilon = 0.76$, $\eta_p^2 = 0.09$). Also, no main effects of Time Window ($F_{(2, 42)} = 1.16$, $p = 0.32$, n.s.) or Facial Expression ($F_{(3, 63)} = 1.22$, $p = 0.31$, n.s.) were observed. Correspondingly, the Bayesian ANOVA resulted in a $BF_{01} = 281.79$, estimation error = 1.0%, providing strong support for the overall null model, in which conditions did not differ.

Permutation-controlled t-tests.—Insets in Figure 6 show time periods in which the paired t-tests comparing each emotional expression condition with the neutral change condition exceeded the permutation-controlled t-threshold of 3.72, at site Oz. Alpha oscillatory activity, measured by the wavelet with a center frequency of 9.3 Hz, was reduced

³A 3×4 repeated measures ANOVA on alpha oscillatory activity for the left-posterior (occipito-temporal) cluster showed no significant interaction between Time Window and Facial Expression ($F_{(6, 126)} = 1.58$, $p = 0.178$, $\epsilon = 0.76$, $\eta_p^2 = 0.07$). Also, no main effects of Time Window ($F_{(2, 42)} = 0.77$, $p = 0.47$, n.s.) or Facial Expression ($F_{(3, 63)} = 0.40$, $p = 0.72$, n.s.) were observed.

for neutral faces compared to all other expressions at sensor Oz, in a time segment preceding, during, and following the return to the original neutral expression. Within this time interval and limited to sensor Oz and two of its nearest neighbors, the greatest t-value was 5.02 ($p < 0.05$). Only sensor Oz consistently exceeded the threshold for all three comparisons during this time range (see Figure 7). No significant effect was observed for any of the other frequency bands.

DISCUSSION

In the present study, we assessed the effects of transient changes in facial expressions on induced (alpha power) and evoked (ssVEPs) brain oscillations. Specifically, we tested the overarching hypotheses that changes in facial expressions (1) prompt modulation of luminance driven population activity in visual cortex, measured using flicker ssVEPs, and (2) engage attention mechanisms reflected in alpha power reduction. It was observed that changes from neutral to angry facial expressions selectively perturbed the time-varying ssVEP amplitude evoked by the rapid face stream. This effect was seen only over right occipito-temporal regions, consistent with involvement of face-sensitive cortices in this modulation. In addition, we found pronounced mid-occipital alpha power reductions in response to each change event. Changes from neutral to neutral expressions prompted the greatest reduction in alpha power. These findings suggest that induced and evoked brain oscillations can be used to examine different aspects of dynamic expression processing, including face-specific and attentive selection processes.

Steady-State Visual Evoked Potentials (ssVEPs)

In an online rating study (see McTeague *et al.*, 2017), observers recruited from the same population as the present sample ($n = 242$), indicated that the angry faces used in the present study were associated with greater emotional arousal and displeasure, resulting in greater motivational intensity (calculated as the vector length of emotional arousal and pleasure-displeasure scores) compared to the other expressions. As such, the change from neutral to angry expressions could be considered the most motivationally salient, and was accompanied by the greatest perturbation of the face-evoked ssVEP envelope, at the right occipito-temporal sensors typically associated with early face processing (Bentin *et al.*, 1996). This location is also consistent with findings from studies using periodic stimulation with faces (Boremanse, Norcia, & Rossion, 2014; Rossion, Prieto, Boremanse, Kuefner, & Van Belle, 2012).

It is now well-established that the time-varying ssVEP is disrupted by transient events, and that this perturbation is enhanced as a function of the emotional or motivational relevance of the transient stimulus (Bekhtereva & Müller, 2017; Ben-Simon *et al.*, 2015). It has been speculated that these perturbation effects are caused by transient brain responses disrupting the phase of the ongoing driven oscillation, as the driven circuits receive additional afferent input (Moratti, Clementz, Gao, Ortiz, & Keil, 2007; Müller, Andersen, & Keil, 2008). Applied to the present paradigm, this would imply that the response of face-sensitive areas in right occipito-temporal cortex prompts modulation of contrast-sensitive neurons in lower-tier visual cortex, and that this modulation interferes with the regular driving of visual

neurons that results in the ssVEP signal. Alternatively, the observed disruption may be related to the transient response in face-sensitive neural tissue itself interfering with the ongoing ssVEP. Future work may use multimodal imaging or more advanced signal processing techniques to address these alternative hypotheses.

Previous studies have consistently reported absence of support for a modulation of the luminance-evoked or contrast-evoked ssVEP by static facial expression in healthy young observers (McTeague *et al.*, 2011; Wieser, McTeague, & Keil, 2011). For example, McTeague *et al.* (2011; 2017) found sustained amplification of the time-varying ssVEP amplitude for emotionally expressive faces only in individuals showing clinically-significant levels of social anxiety, but not in those low in social anxiety. Across multiple ssVEP studies, angry faces from the Karolinska data set resulted in the most pronounced, and most replicable effects on the flicker-ssVEP, in those high in social anxiety (McTeague *et al.*, 2011; Wieser, McTeague, & Keil, 2011), but pronounced effects of fearful expressions were also found, for example in a trans-diagnostic patient sample (McTeague *et al.* 2018). The fact that participants low in self-reported social anxiety responded differentially to angry expressions in the present study is consistent with the notion that changing faces may be more emotionally evocative owing to their heightened biological significance and ecological validity (Weyers *et al.*, 2006). In line with this notion, Mayes and colleagues (Mayes, Pipingas, Silberstein, & Johnston, 2009) found differences in latency and frontal amplitude of ssVEP signals elicited by ambient flicker, while observers view foreground videos of dynamic, compared to static, facial expressions.

A number of functional magnetic resonance imaging (fMRI) studies (Foley, Rippon, Thai, Longe, & Senior, 2012; LaBar *et al.*, 2003; Sato *et al.*, 2004; Trautmann, Fehr, & Herrmann, 2009) and a positron emission tomography (PET) study (Kilts, Egan, Gideon, Ely, & Hoffman, 2003) have also converged to show stronger activation for dynamic, compared to static, faces in early visual areas such as the inferior occipital gyrus and in higher-order visual areas including the cuneus and the fusiform gyrus, as well as in widespread temporal, parahippocampal, premotor, and peri-amygdaloid regions. More recently, Trautmann-Lengsfeld *et al.* (2013) examined the spatio-temporal dynamics of emotional facial expression processing for static and dynamic stimuli, using a combined EEG-fMRI approach. Using fMRI-constrained source analysis, these authors found that viewing dynamic facial expressions prompted relatively heightened source activity for emotional compared to neutral conditions in fusiform gyrus and ventromedial prefrontal cortex, as well as medial and inferior frontal cortex. In line with these results, the present ssVEP results highlight the sensitivity of driven oscillations to subtle dynamic changes in facial expressions, which are consistent with the extant literature in terms of their topographical distribution and in terms of being specific to the most motivationally salient (angry) expression change used in the present stimulus set. Given the recent surge in interest in objective measures of social perception (Morrison & Heimberg, 2013), future work may examine the neural origin of the perturbation effects observed here, along with systematically assessing their sensitivity to inter-individual differences.

Alpha Oscillations

The present study also examined intrinsic (as opposed to periodically-driven) brain oscillations, induced by the dynamic face stimuli. Specifically, we focused on how reductions in alpha-band power evoked by the expression changes in the stimulus stream varied by emotional expression. Changes in time-varying alpha power have recently garnered attention because of their sensitivity to a variety of experimental manipulations in cognitive and affective tasks (Anderson, Serences, Vogel, & Awh, 2014; Bartsch *et al.*, 2015). Based on a rapidly growing literature on the role of alpha oscillations during cued attention paradigms (Snyder & Foxe, 2010), one would predict larger alpha power decreases following salient changes (between emotionally intense and neutral expressions), compared to neutral-to-neutral changes. As an alternative hypothesis, work in speech stream monitoring suggests that attentive tracking of a dynamically changing stream should be accompanied by relatively heightened alpha-power (Wöstmann, Lim, & Obleser, 2017). Such findings would be consistent with a study by Popov *et al.* (Popov, Miller, Rockstroh, & Weisz, 2013), who also found lower alpha power during the neutral-to-neutral, compared to neutral-to-emotional continuous transitions between morphed facial expressions.

Together, the present findings are not consistent with the notion that changes from a neutral to an emotional expression engage attention mechanisms to a larger extent than neutral-to-neutral changes: The rare neutral-to-neutral changes were associated with greater midline alpha power reductions, suggesting that they prompted a stronger change in attentive processing, potentially owed to their oddball properties. Conversely, the finding of relatively heightened alpha power during large portions of the neutral-to-emotional trials, compared to neutral-to-neutral trials (see Figure 6) is also consistent with the idea that successfully detecting changes in a stream (Petro & Keil, 2015) and tasks that require top-down control (Klimesch, Sauseng, & Hanslmayr, 2006; Wöstmann *et al.*, 2017) are both associated with relatively heightened alpha power.

Relation of Alpha Power and ssVEP Amplitude

One may argue that the effects found for ssVEP and for brain oscillations could be intrinsically correlated to one another. To address this notion, we conducted a correlation analysis linking ssVEP and alpha power differences. Across participants and conditions, none of the effects in either measure were related to the other. Thus, it is unlikely that the perturbation of the ssVEP and the alpha power reduction induced by changes in emotional expression are epi-phenomena or reflect overlapping processes. Given the lack of correlation, the non-overlap of the topography of the differences, and the differential sensitivity to facial expression changes, the present results suggest that the two measurements reflect distinct brain processes. Thus, combining ssVEP analyses with analyses of induced alpha power might be an attractive approach for investigating the effects of dynamic face processing.

Limitations and Conclusions

Although our findings contribute to the electrophysiological understanding of the processing of emotional facial expressions through a dynamic fashion, several limitations need to be taken into account. First, our experimental design comprised a limited number of emotional

facial expressions (angry, happy, fearful). It will be important to extend these findings by testing a wide range of emotional stimuli to corroborate the conclusions of the present work. Second, our sample comprised mainly college students and few individuals recruited from the community, which prevents us from generalizing the present findings to community or patient samples.

Only one discrete change of the facial expression was displayed in the present study, interspersed with neutral expressions. This is distinct from the facial stimuli presented as incrementally dynamic morphs of facial expressions (Harris, Young, & Andrews, 2012). The ssVEP technique is amenable to dynamic changes and ultimately can be used to assess gradual changes between morphed expressions.

In conclusion, information on another person's affective state as communicated through facial expressions is a crucial element which is constantly monitored, for social and survival purposes (Wieser *et al.*, 2016). The findings related to the ssVEP showed modulation consistent with involvement of higher-order, face-sensitive visuo-cortical areas in affective expression decoding, whereas alpha-band changes varied with perceptual similarity and condition frequency, consistent with its role in selective attention. Taken together, the present findings provide new and complementary electrophysiological evidence for a better understanding of the processing of changing facial expressions, which are more ecologically valid than static pictures of facial expressions.

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Highlights:

- Changes in facial expressions modulate evoked and intrinsic brain oscillations.
- Transient perturbation of evoked oscillations occur after salient changes.
- This perturbation (reduction) was specific to right occipito-temporal sensors.
- Mid-occipital alpha power reductions occurred after each expression change.
- Lower alpha power during neutral-to-neutral compared to neutral-to-emotional changes.

Figure 1.

(A) Schematic of the experimental design. Each trial began with a neutral face presented on the screen for the initial 2.29 seconds (ONSET time window). Subsequently, the picture changed to a happy (H), angry (A), fearful (F), or a different neutral (N) expression of the same actor from 2.29 to 4.57 seconds (CHANGE time window). The trial ended with the initial neutral expression presented from 4.57 to 5.71 seconds (RETURN time window). The stimuli flickered at 17.5 Hz throughout the trial. A variable inter-trial interval (2–4 seconds) separated trials. (B) Example of happy, angry, fearful, and neutral stimuli are presented in a clockwise fashion.

Figure 2.

The 128-sensor HydroCel GSN recording montage. The highlighted gray sensors represent the selected mid-occipital cluster, comprising Oz and the six nearest neighbors. The highlighted black sensors represent the right occipito-temporal cluster, with PO8 and the six nearest neighbors.

Figure 3.

Grand mean time-locked averages of the voltages of the ssVEP over sensors Oz and PO8 across all the conditions and all the 22 participants. Facial expressions evoked pronounced 17.5 Hz oscillations, which are abruptly disrupted by the transient change of facial expressions within the trials. The beginning of each change period is represented by the vertical lines in the graphs. Note that the amplitude of the steady-state potential evoked in the representative PO8 right occipito-temporal sensor is higher compared to the Oz mid-occipital sensor.

Figure 4.

Frequency spectrum and topographical map of the steady-state visual evoked potential at the 17.5 Hz-driven frequency. Individually computed spectra were averaged across participants for each condition separately to obtain the grand mean frequency spectrum (neutral condition shown). Note the pronounced peak at the 17.5 Hz-driven frequency (left). The topographical map shows that the peak of the evoked 17.5 Hz response is focally localized around the occipital pole (right).

Figure 5.

Time-varying ssVEP amplitude averaged over seven occipital sensors for the angry, fearful, happy, and neutral facial expressions for all the participants (N=22) for the mid-occipital cluster and the right occipito-temporal cluster. **Top:** Hilbert waveforms show differences only for the right occipito-temporal cluster during the first change. The black line at the bottom of the top right plot represents the t-values for the comparison of the ssVEP amplitudes of angry minus neutral facial expressions at the right occipito-temporal cluster. The gray-shaded area shows the permutation-controlled t-threshold of -2.86. **Bottom left:** Topographical maps of the ssVEP differential amplitude (emotional minus neutral) are represented for the CHANGE time period, ranging from 2700 ms to 2900 ms. The ssVEP amplitude evoked after the change to angry faces were significantly reduced when compared to neutral dynamic faces. **Bottom right:** The bar plot illustrates the means during the first change window, with the ssVEP amplitude decreased more in response to angry faces compared to the other expressions, over the right occipito-temporal cluster. No significant effect was found for the mid-occipital cluster.

* represents $p < 0.05$.

Figure 6.

Grand mean evolutionary spectra for sensor Oz, shown for each facial expression. Plots show time-varying amplitudes for frequencies varying from 1.94 Hz up to 22.54 Hz, and for the time range from –600 ms to 5800 ms relative to picture onset. White boxes indicate the time periods used for ANOVA (ONSET, CHANGE, and RETURN). Results are plotted as the percentage of the signal change, relative to pre-stimulus baseline. The white dashed lines represent 9.3 Hz, the center frequency of the wavelet showing differences in permutation controlled t-tests: Time periods that exceeded the critical t-threshold are illustrated by showing the t-values as black areas, comparing each emotional expression condition compared to the neutral condition. Note that significant differences between neutral and emotional expressions arise after the change and are sustained throughout the RETURN time window. An example topography of the alpha amplitude reduction following the RETURN from neutral to neutral is shown at the top right (4700 ms to 5100 ms, center frequencies, 9.30 to 12.24 Hz).

Figure 7.

Topographical distribution of t-values comparing alpha amplitude for the neutral-neutral condition with the remaining conditions, shown here for the wavelet centered at 9.3 Hz, and a time point in the RETURN window (5080 ms post-onset). Note that the maximum t-values are located near the midline, at parietal and occipital sensor locations, not at right-occipital locations.

Table 1.

Means and standard deviations of the alpha power amplitudes as a percentage (%) of the signal change (relative to the baseline) for the midline posterior cluster.

	Midline Posterior Cluster					
	Onset		Change		Return	
	Mean	SD	Mean	SD	Mean	SD
Happy	-3.0	± 21	-5.4	± 19	-4.5	± 18
Neutral	-7.0	± 18	-9.3	± 19	-15.1	± 9
Angry	-6.7	± 18	-7.5	± 20	-8.4	± 16
Fearful	-6.6	± 18	-7.2	± 18	-5.4	± 13

Table 2.

Means and standard deviations of the alpha power amplitudes as a percentage (%) of the signal change (relative to the baseline) for the right posterior cluster.

	Right Posterior Cluster					
	Onset		Change		Return	
	Mean	SD	Mean	SD	Mean	SD
Happy	-7.2	± 19	-9.5	± 22	-8.7	± 16
Neutral	-8.8	± 20	-13.3	± 16	-15.8	± 11
Angry	-12.4	± 17	-13.3	± 20	-10.9	± 18
Fearful	-8.1	± 19	-11.1	± 17	-6.7	± 15