

Emotion

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Increasing Perceived Happiness in Neutral Faces by Posing a Smile: An Electroencephalography (EEG) Frequency-Tagging Study

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Previous research using electroencephalography has so far failed to provide strong and convincing evidence for the effects of facial feedback on the visual processing of emotional facial expressions. To fill this gap, we harnessed the power of electroencephalography frequency tagging, which offers excellent objective indication of implicit stimulus processing with high signal-to-noise ratio. Healthy adult participants ($N = 47$) from diverse backgrounds (tested in 2023/2024) viewed rare happy and angry oddball faces, interspersed with frequent neutral faces, while either producing a smile or keeping a neutral face. Smiling resulted in reduced neural discrimination of happy versus neutral faces over the left occipitotemporal region, as shown by decreased power at the oddball frequency. These findings could reflect that voluntary smiling, and the associated change in facial feedback, leads to neutral faces being perceived as happier, providing evidence for the facial feedback hypothesis.

Keywords: emotion, facial expression, facial feedback, electroencephalography, frequency tagging


The interpretation of others' facial expressions is mainly based on vision but is also influenced by other sensory signals, such as proprioceptive feedback from our own facial muscles (Efthimiou et al., 2024; Korb et al., 2014; Wood et al., 2016), especially when expressions are ambiguous (Green & Angelaki, 2010). In line with the "Facial Feedback Hypothesis" (Tomkins, 1962), the simulation of observed expressions can facilitate emotional understanding (Gallese, 2006). A number of studies have indeed demonstrated an effect of blocking facial mimicry—the spontaneous imitation of others' facial expressions—on the processing of emotional facial and vocal expressions (Borgomaneri et al., 2020; Rychlowska et al., 2014; Vilaverde et al., 2024; Wood et al., 2016) and that artificially inducing facial expressions (e.g., by using props or simply asking participants to pose a smile) can change the way we interpret emotional facial expressions (Marmolejo-Ramos et al., 2020). Facial muscle activation is, however, most likely to have the greatest effect on the interpretation of emotionally neutral or ambiguous stimuli. In line with this, it was recently demonstrated that electrical stimulation of the bilateral zygomaticus major (the main smiling muscle) can induce a happiness bias during the categorizing of ambiguous facial expressions (Efthimiou et al., 2024).

Few studies have examined the influence of facial feedback on emotional face processing at the electrophysiological level. These studies have primarily focused on the time domain and have sometimes reported effects on event-related potentials such as an increase in N170 amplitude to neutral faces when smiling (Sel et al., 2015) and an increase in N400 amplitude to faces displaying happiness and disgust when manipulating lower face muscles (Davis et al., 2017). Overall, effects of facial feedback manipulations on face processing in the time domain seem weak and hard to pinpoint.

Regarding the frequency domain, a desynchronization of the cortical mu rhythm can be observed during the viewing of emotional facial expressions (Ensenberg et al., 2017; Moore et al., 2012), highlighting the role of the motor system in emotional face perception. In a recent study, mu desynchronization was found to be modulated by facial feedback, whereby blocking certain movements of facial muscles reduced mu desynchronization (Birch-Hurst et al., 2022). Though this highlights the susceptibility of the *motor* system to facial feedback, it does not inform us on how facial feedback may influence the *visual* processing of emotional facial expressions.

A powerful technique to examine the automatic visual processing of faces is to measure steady-state visual evoked potentials

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Joshua Baker played a lead role in data curation, formal analysis,

visualization, writing—original draft, and writing—review and editing and an equal role in conceptualization, investigation, resources, and software. Stephanie Van der Donck played an equal role in conceptualization, formal analysis, methodology, software, and writing—review and editing. Bart Boets played a supporting role in supervision and an equal role in conceptualization, methodology, and writing—review and editing. Sebastian Korb played a lead role in conceptualization, funding acquisition, methodology, project administration, and supervision and an equal role in formal analysis, investigation, writing—original draft, and writing—review and editing.

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(SSVEPs) during a fast-paced visual oddball paradigm. By presenting emotionally expressive “oddball” faces (at a low frequency, e.g., 1.2 Hz) among a train of neutral “standard” faces presented at a higher frequency (e.g., 6 Hz), an induced entrainment can be observed in the brain at the same frequencies (Regan, 1966). If a peak at the “tagged” oddball frequency is observed, then this indicates that the expressive and neutral faces were consistently and reliably discriminated. By implementing this “frequency-tagging” approach, one is able to obtain an objective measure of neural sensitivity for stimulus discrimination, across different experimental conditions (Norcia et al., 2015; Wieser et al., 2016).

A number of studies have used this technique in the context of face perception. SSVEPs have been demonstrated to be a reliable and consistent means of studying how the brain discriminates between specific facial expressions (Poncet et al., 2019) and are even able to quantify the extent to which certain expressions (e.g., fearful faces) are differentiated more than others (Luo & Dzhelyova, 2020). SSVEPs have also been used to demonstrate a reduced sensitivity to fearful faces in children with autism (Van der Donck et al., 2020) and a reduced response for inverted faces (Yan & Rossion, 2020). These studies typically reveal a strong response at the base frequency at medial-occipital electrodes (indicative of low-level visual processing in the primary visual cortex) and a response at the oddball frequency originating from neural populations in the lateral inferior occipital and fusiform gyri (Rossion et al., 2020). As such, this lateralization of the oddball response suggests the recruitment of higher order face processing operations that are independent from the processes involved in unpacking low-level features such as changes in luminance and shape. Frequency tagging has also been demonstrated in other sensory modalities (Drijvers et al., 2021; Vos et al., 2023); however, to our knowledge, no study has yet explored the impact of facial feedback manipulations on SSVEPs.

In this preregistered study, we aimed to examine whether activations of facial muscles modulate the neural sensitivity for facial expression discrimination, as measured by SSVEPs. Participants viewed sequences containing fast-changing (6/s, 6 Hz) neutral faces (standards) and happy or angry faces oddballs (presented every fifth image, at 1.2 Hz) while posing a smile or keeping a relaxed neutral expression. An emotion-orthogonal task ensured attention was kept on the center of the screen. Based on the assumption that facial muscle configurations contribute to the differentiation of emotional facial expressions, we expected that derived power at the oddball frequency (and harmonics) would differ over occipitotemporal electrodes as a function of the facial manipulation (smile, neutral) and the oddball category (happy or angry, depending on the sequence). Note that an increase or decrease in power at the frequency at which the oddballs are presented indicates, respectively, the brain’s increased or decreased ability to discriminate between neutral standards and emotional oddballs.

Power for happy oddballs was expected to change in one of two directions. Posing a smile could make neutral faces look somewhat happier (see Efthimiou et al., 2024) and thus more similar to the happy oddballs. As a result, the oddball response would diminish (for a similar finding, see Kuehne et al., 2019). Alternatively, the processing of happy expressions might become elevated (they become more salient), given the congruency/incongruency of the posed and seen expression. As a result, happy and neutral expressions would appear more different, resulting in an increase of the happy oddball response. Similarly, power for angry oddballs was

expected to become larger or remain unchanged, when posing a smile. The former case occurs if neutral faces appear somewhat happier and thus more different to angry faces. The latter can occur if posing a smile enhances the processing of congruent (happy) but not incongruent (angry) expressions. Finally, power at the base frequency was not expected to differ between conditions, as it reflects the contrast between the background and the face stimuli, and is a mixture of low-level and high-level processes (see, e.g., Dzhelyova & Rossion, 2014).

Method

Research Transparency

Data (electroencephalography [EEG] and behavioral), experiment file, and analysis scripts are made publicly available on the Open Science Framework (<https://osf.io/8qcw9/>). We report how we determined our sample size, all data exclusions (if any), all manipulations, and all measures in the study.

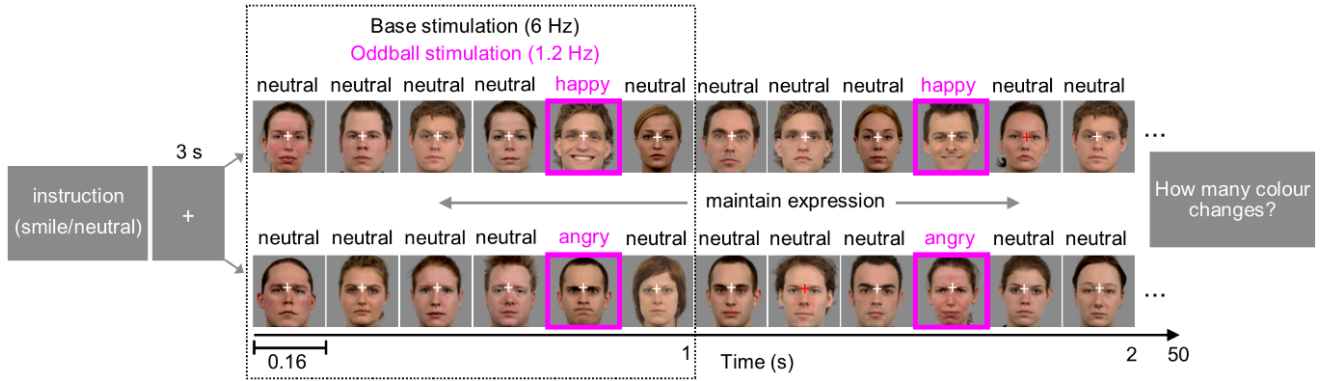
Participants

To determine an appropriate sample size, an a priori power analysis using Superpower (Lakens & Caldwell, 2021) was conducted based on data from Van der Donck et al. (2020), which used a similar design and stimulus set (see preregistration for specific details). The power analysis revealed that including at least 40 participants would achieve 88% power for an interaction between pose and emotion. The participants were 47 adults (25 female, $M_{\text{age}} = 22.9$, $SD = 3.65$, range 18–33, 61% non-White) tested in 2023 and 2024, with normal or corrected-to-normal vision, no current use of prescribed medication or history of illicit drug use, and no history of neurological or psychiatric illness. Participants were recruited through a number of channels (e.g., flyers, email lists, social media) and were financially compensated at a rate of £10/hr. They gave written informed consent before taking part and were debriefed at the end of the testing session. The study was approved by the local ethics committee (ETH2223-1598).

Stimuli, Experimental Procedure, and Task Design

The stimulus pool consisted of a total of 60 images (front-facing neutral, happy, and angry facial expressions, from 10 male and 10 female identities) from the Radboud Face database (Langner et al., 2010). Faces were presented (horizontal = 10.88° and vertical = 13.28° of visual angle) in the center of a 24.5 in. screen (Alienware aw2521h) with a resolution of $1,920 \times 1,080$ pixels and a 60 Hz refresh rate. The task was programmed and run using Psychopy3 (v3.2.4) for Windows (Peirce et al., 2019) and consisted of 16 sequences of images, each lasting 50 s. Each sequence consisted of 300 images of faces: 240 neutral faces (standard stimuli) and 60 angry or happy faces (oddball stimuli), depending on the sequence type. Faces were presented in a pseudorandom order using a boxcar function, ensuring that the identity of each face changed on every image and, importantly, that every fifth image in a sequence was that of a happy or an angry face (only one type of oddball stimuli was presented within a given sequence; Figure 1). All other face stimuli in a sequence were neutral faces. Each face was presented for 166.66 ms (base frequency of 6 Hz), with oddball

Figure 1
Oddball Paradigm



Note. Each sequence started with an instruction to pose and maintain a facial expression (either smile or neutral expression). Following a 3 s fixation cross, images of faces were presented at a rate of 6 Hz (base frequency), with every fifth image presenting an expressive (happy or angry) face (oddball frequency = 1.2 Hz). Each sequence lasted 50 s, and participants were monitored via webcam to ensure that the instructed pose was maintained throughout the entire sequence. A White fixation cross was superimposed over all faces and occasionally (5–10 times per sequence) changed to red. Participants were asked to keep a mental tally of the number of color changes and to report this number at the end of each sequence. Faces are taken from the Radboud Face database (Langner et al., 2010). See the online article for the color version of this figure.

stimuli being presented every 833.33 ms (oddball frequency of 1.2 Hz).

In order to assess differences in low-level visual features between stimulus categories, the spatial frequency composition of the face stimuli was analyzed by comparing power at low (<1 cycles/degree), medium (1–4 cycles/degree), and high (4–20 cycles/degree) spatial frequencies. This analysis revealed that the difference in power at medium spatial frequencies between neutral and happy faces approached significance ($p = .059$), whereas no differences were found between neutral and angry faces in any frequency band (all $p > .487$).

Four types of sequences were presented to participants (each presented four times): neutral-pose happy oddballs, neutral-pose angry oddballs, smile-pose happy oddballs, and smile-pose angry oddballs. Prior to the start of each sequence, participants received a written instruction to produce an expression (either a neutral expression or to pose a smile with the mouth closed) and were asked to maintain said expression for the entire upcoming sequence. Half of the sequences required participants to maintain a smile, with the other half requiring a neutral expression. Half of the sequences presented happy faces as oddballs, with the other half presenting angry faces as oddballs. Sequences were presented in a pseudorandom order, ensuring that no two consecutive sequences required participants to maintain the same expression (to avoid muscle fatigue). A webcam was used to ensure that participants were correctly following the pose instructions during the experiment, and acquired video data were later analyzed to compare smiling across conditions.

During each sequence, participants were required to fixate on a White fixation cross (horizontal = 0.47° and vertical = 0.47° of visual angle) that was superimposed over the nasion of each face. In order to ensure that participants remained engaged and focused on the center of the screen, an orthogonal task was implemented by which participants had to report the number of times the fixation cross briefly turned red (for 166.66 ms). The number of color changes was random (between 5 and 10) and could occur any time

after 20 images or before 240 images were presented (with at least four images presented in between each color change). At the end of each sequence, participants used the mouse to select the detected number of color changes from a list (ranging from 5 to 20). Feedback was then presented indicating whether the participant had accurately detected the correct number of color changes.

EEG Data Acquisition and Signal Processing

EEG data were acquired with 64 Ag/AgCl electrodes in the international 10–20 configuration using an eego sports amplifier (ANT Neuro, Netherlands) at 512 Hz and digitized with 24-bit resolution. Data were referenced online to electrode CPz, with the ground electrode at AFz. For further analyses, EEG data were imported and processed using functions from the EEGLAB (v2022.1) environment (Delorme & Makeig, 2004) for MATLAB (The Mathworks, Inc.). Continuous data were high-pass filtered at 0.1 Hz (filter order = 16,897; -6 dB at 0.05 Hz) and low-pass filtered at 100 Hz (filter order = 69; -6 dB at 112.5 Hz) using zero-phase, noncausal linear finite impulse response filters. Continuous data were then segmented into 48 s epochs, starting from the first image of each sequence (generating 16 epochs). Epochs of EEG data were subjected to independent component analysis decomposition (Infomax independent component analysis; Bell & Sejnowski, 1995) using the EEGLAB's *runica* function to remove the contribution of blink components to the observed data. A component was labeled for removal if it presented low-frequency non-time-locked fluctuations with strong power toward the front of the head. Following the removal of blinks, channels that were considered noisy (e.g., containing extreme values or long periods of high-frequency noise) were interpolated using spherical interpolation (average of 4.85 per participant). Epochs were then visually inspected for artifacts and were removed if they were considered to contain low-frequency drifts and/or large periods of unusual high-frequency activity. A small number of epochs were rejected, leaving on average 3.96 ($SD = 0.17$)

sequences per condition. Data were finally referenced to an average reference.

Analysis of SSVEPs

Spectral analysis was performed in MATLAB using bespoke scripts. Preprocessed EEG epochs were first trimmed to contain an integer number of 1.2 Hz cycles, resulting in an epoch length of 47.998 s. Epochs of the same type were then averaged in the time domain prior to the derivation of single-sided amplitude spectra for each channel using a fast Fourier transform, resulting in derived amplitudes for frequencies between direct current and 256 Hz. For each channel, the amplitude at each individual frequency bin was then baseline-subtracted by subtracting the mean amplitude of the 20 surrounding frequency bins from said bin, excluding immediately neighboring bins, and one bin either side of the targeted frequency that had the highest amplitude from the range selected (Van der Donck et al., 2020). In order to define the number of base and oddball harmonics to include in the analysis, Z-scores were computed using the mean and standard deviation of the 20 surrounding bins for each base and oddball harmonic separately, for the mean of a selected number of channels in each region of interest (ROI; see below), and for each condition separately. Harmonics were considered significant and were included in the analysis as long as the Z-score for two consecutive harmonics across all ROIs and conditions was above 1.64 ($p < .05$, one-tailed). As a result, the oddball response was quantified as the sum of amplitudes of the oddball frequency (1.2 Hz) and harmonics up to and including 7.2 Hz, excluding the 6 Hz general response. For the base response, 6 Hz and harmonics up to and including 36 Hz were included.

Determination of ROIs

ROIs were selected based on both previous literature (e.g., Van der Donck et al., 2020) and scalp topographies displaying the summed power of the base frequency and harmonics and oddball frequency and harmonics separately. Defined ROIs were as follows: left occipitotemporal (LOT; including TP7, P7, P5, PO7, PO5, PO3), right occipitotemporal (ROT; including TP8, P8, P6, PO8, PO6, PO4), and medial-occipital (MO; including POz, Oz, O1, O2).

Analysis of Video Data

Continuous video files of the participants were first segmented into 48 s videos (one per sequence, 15 frames/s, 640 × 480 pixels), starting from the onset of each sequence. Videos were analyzed using FaceReader 8.1 (Noldus Information Technology BV, Wageningen, Netherlands), set to analyze every frame, in order to quantify the presence of “happiness” in each sequence. To minimize person-specific biases (e.g., naturally looking more happy or more angry), each participant’s facial expressions were calibrated against their neutral expression by using the first 2 s of a single neutral expression sequence for that participant. Due to failures to detect or model the face, analysis was not possible for seven participants, and so a total of 40 participants were included in the analysis of the video data. The magnitude of a smile in each sequence was taken as the mean value of the extracted continuous “happiness” intensity score (ranging between 0 and 1) across the length of each video. Finally, values were averaged across sequences of the same condition and

were used to both compare the extent of smiling in each condition and to correlate with SSVEP values.

Statistical Analysis

All statistical analyses were performed in SPSS 28 (IBM). For the analysis of the behavioral data, the number of correct sequences (for which the correct number of color changes was reported) was entered into a 2 (pose: neutral, smile) × 2 (emotion: happy, angry) repeated measures analysis of variance (ANOVA; four being the maximum accuracy in each condition, due to four repetitions). For the analysis of the video data, a 2 (pose: neutral, smile) × 2 (emotion: happy, angry) repeated measures ANOVA was used to compare the extent of smiling in each condition. In addition, a Spearman’s correlation was used in order to assess whether the extent of smiling was associated with any significant SSVEP changes across conditions. For the analysis of SSVEPs, summed baseline-subtracted amplitudes for the base frequency and harmonics, and oddball frequency and harmonics, were entered separately into a 2 (pose: neutral, smile) × 2 (emotion: happy, angry) × 3 (ROI: LOT, ROT, MO) repeated measures ANOVA. Post hoc comparisons were performed using a series of paired-sample *t* tests with Bonferroni correction applied to *p* values.

Results

Behavioral Accuracy

Accuracy was generally high in all conditions (happy neutral: $M = 3.47$, $SD = 0.69$, happy smile: $M = 3.36$, $SD = 0.67$, angry neutral: $M = 3.43$, $SD = 0.65$, angry smile: $M = 3.45$, $SD = 0.72$). No significant main effects nor interactions were observed (all $p > .05$). As such, accuracy on the behavioral task was not modulated by pose type or oddball type.

Extent of Smiling

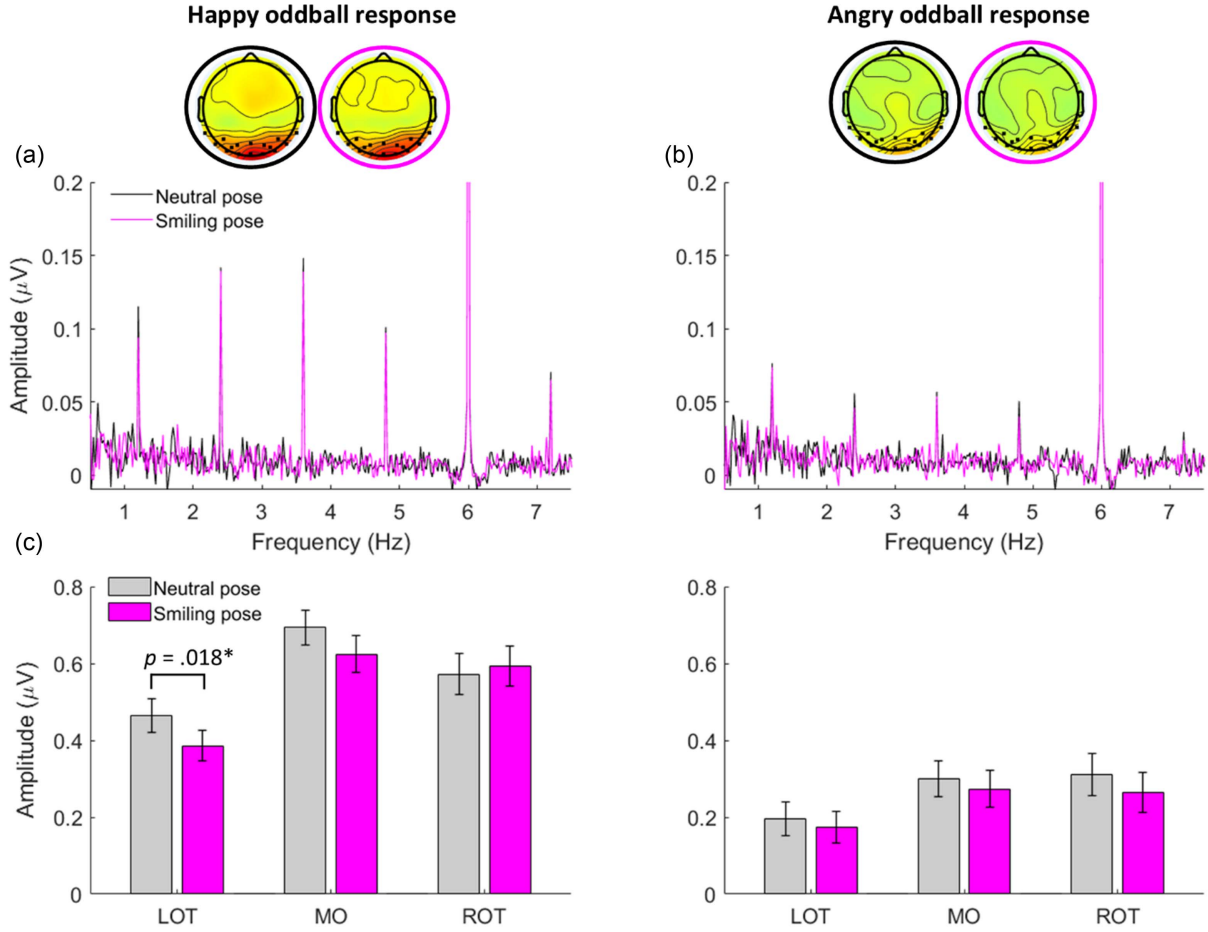
A main effect of pose, $F(1, 27) = 53.39$, $p < .001$, $\eta_p^2 = .664$, confirmed that participants smiled more during the smiling conditions ($M = 0.370$, $SD = 0.30$, 95% CI [0.268, 0.471]) than during the neutral-pose conditions ($M = 0.008$, $SD = 0.019$, 95% CI [0.002, 0.014]). No main effect of emotion nor interaction between pose and emotion was found (all $p > .05$). As such, the emotion type of the oddball stimuli did not influence the extent of smiling.

Steady-State Visual Evoked Potentials

Oddball Response

Channel spectra from the three ROIs showed clear peaks at the oddball frequency (1.2 Hz) and harmonics in all conditions, indicating that the brain was able to automatically discriminate between the standard (neutral) stimuli and the emotionally expressive (oddball) stimuli (Figure 2). The repeated measures ANOVA showed a significant main effect of emotion, $F(1, 46) = 89.21$, $p < .001$, $\eta_p^2 = .660$, whereby the oddball response to happy expressions ($M = 0.556$, $SD = 0.23$, 95% CI [0.487, 0.624]) was greater than to angry expressions ($M = 0.253$, $SD = 0.17$, 95% CI [0.202, 0.304]). A main effect of pose was also found, $F(1, 46) = 4.92$, $p = .031$, $\eta_p^2 = .097$, whereby the oddball response was lower while posing a smile

Figure 2
Oddball Response



Note. Panels (a) and (b) show baseline-subtracted spectra (average across ROIs) during sequences containing happy (a) and angry (b) facial expressions while either smiling (magenta) or maintaining a neutral expression (black). Clear peaks can be identified at the oddball frequency (1.2 Hz) and harmonics up to 7.2 Hz. Note the response at 6 Hz (base frequency) is clipped in order to preserve visualization of the oddball response. Panel (c) shows the summed baseline-subtracted oddball response for happy (left) and angry (right) expressions in each of the three ROIs during smiling (magenta) and maintaining a neutral expression (gray). Smiling significantly reduced the oddball response to happy expressions in the LOT ROI. Error bars show standard error. Topographic map shows the distribution of power at the oddball frequency and significant harmonics in the happy (left pair) and angry (right pair) oddball sequences in the smile (magenta) and neutral (black) pose conditions. LOT = left occipitotemporal; MO = medial-occipital; ROT = right occipitotemporal; ROI = region of interest. See the online article for the color version of this figure.

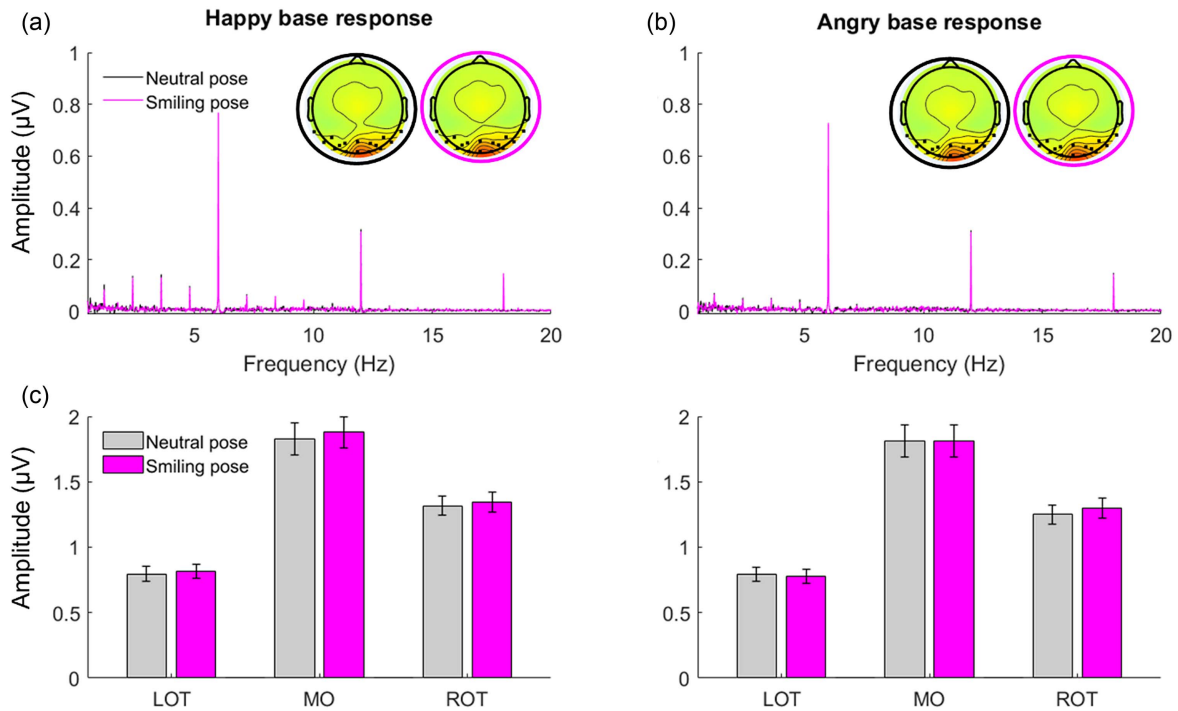
($M = 0.386$, $SD = 0.17$, 95% CI [0.334, 0.438]), relative to maintaining a neutral expression ($M = 0.423$, $SD = 0.18$, 95% CI [0.368, 0.478]). In addition, a significant main effect of ROI, $F(2, 92) = 15.34$, $p < .001$, $\eta_p^2 = .250$, indicated that the oddball response in the LOT cluster ($M = 0.305$, $SD = 0.17$, 95% CI [0.248, 0.361]) was smaller than in the MO cluster, $M = 0.473$, $SD = 0.24$, 95% CI [0.407, 0.539]; $t(46) = 5.27$, $p < .001$, and the ROT cluster, $M = 0.435$, $SD = 0.19$, 95% CI [0.369, 0.501]; $t(46) = 3.58$, $p < .001$. The MO and ROT cluster did not significantly differ ($p > .05$). Finally, a significant three-way interaction was found between emotion, pose, and ROI, $F(2, 92) = 3.92$, $p = .023$, $\eta_p^2 = .079$. In order to unpack this interaction, paired-sample t tests were performed on each Emotion \times Pose combination within each ROI separately. For the LOT cluster, the oddball response to happy expressions was significantly reduced, $t(46) = 3.08$, $p = .018$,

during a smiling pose ($M = 0.386$, $SD = 0.27$, 95% CI [0.304, 0.468]), relative to maintaining a neutral expression ($M = 0.463$, $SD = 0.30$, 95% CI [0.375, 0.552]). No other significant differences were found in any other ROI nor any effects of pose on the oddball response to angry (all $p > .05$).

Base Response

As expected, large peaks at the base frequency (6 Hz) and harmonics were observed in the channel spectra, confirming that neutral faces were being presented (and perceived) at the intended 6 Hz frequency (Figure 3). The ANOVA showed a significant main effect of emotion, $F(1, 46) = 6.00$, $p = .018$, $\eta_p^2 = .115$, whereby the base response during sequences containing happy expressions

Figure 3
Base Response



Note. Panels (a) and (b) show baseline-subtracted spectra (average across ROIs) during sequences containing happy (a) and angry (b) facial expressions while either smiling (magenta) or maintaining a neutral expression (black). Clear peaks can be identified at the base frequency (6 Hz) and harmonics up to 18 Hz. Panel (c) shows the summed baseline-subtracted base response for happy (left) and angry (right) expressions in each of the three ROIs during smiling (magenta) and maintaining a neutral expression (gray). Power at the base frequency was significantly larger in the MO cluster relative to the lateralized clusters. Error bars show standard error. Topographic map shows the distribution of power at the base frequency and significant harmonics in the happy (left pair) and angry (right pair) oddball sequences in the smile (magenta) and neutral (black) pose conditions. LOT = left occipitotemporal; MO = medial-occipital; ROT = right occipitotemporal; ROI = region of interest. See the online article for the color version of this figure.

($M = 1.31$, $SD = 0.47$, 95% CI [1.18, 1.45]) was greater than during sequences containing angry expressions ($M = 1.27$, $SD = 0.46$, 95% CI [1.14, 1.41]). In addition, a main effect of ROI was found, $F(2, 92) = 70.86$, $p < .001$, $\eta_p^2 = .606$, whereby the base response was larger in the MO cluster ($M = 1.77$, $SD = 0.79$, 95% CI [1.55, 1.99]), compared to both the LOT cluster, $M = 0.788$, $SD = 0.35$, 95% CI [0.679, 0.896]; $t(46) = 10.10$, $p < .001$, and the right MO cluster, $M = 1.33$, $SD = 0.47$, 95% CI [1.17, 1.48]; $t(46) = 6.00$, $p < .001$. The LOT cluster also presented a lower base response than the ROT cluster, $t(46) = 7.49$, $p < .001$. No main effect of pose nor any interaction between pose and emotion or ROI was observed (all $p > .05$).

Relationship Between Smiling and SSVEPs

In order to examine whether the extent of smiling was associated with the extent of the observed reduction of amplitude during smiling in the happy oddball sequences (in the LOT cluster), a Spearman's correlation was performed using the FaceReader smile value in the smile-pose happy oddball sequences and the aforementioned difference in amplitude. No significant correlation was found, $r(40) = .021$, $p > .05$. As such, the extent of smiling was

not systematically associated with the observed reduction in amplitude.

Discussion

The present study examined the effects of posing a smile on the brain's ability to automatically discriminate between neutral and emotional facial expressions. In a fast-paced visual oddball paradigm, happy or angry faces were interspersed by neutral faces, while participants either smiled or maintained a neutral expression (confirmed by video analysis). Simultaneously, participants carried out a counting task, performance of which did not differ by type of pose or oddball stimulus.

As expected, producing and maintaining a smile modulated the brain's response to happy faces. Specifically, smile posing significantly reduced amplitude, in the LOT cluster, at the frequency (1.2 Hz and harmonics) at which happy faces were presented. No such modulation was found for the angry oddball response or for any response in the other ROIs. This is in line with the hypothesis that producing a smile "blurred" the perceived visual differences between happy and neutral expressions, but not the differences between angry and neutral expressions.

Previous work has demonstrated that proprioceptive feedback from the zygomaticus major muscle (either resulting from voluntarily smiling or from electrical stimulation) can modulate how we perceive neutral and emotionally ambiguous facial expressions (Efthimiou et al., 2024; Sel et al., 2015). That is, proprioceptive input from the zygomaticus major muscle can result in a happiness bias when labeling ambiguous facial expressions (Efthimiou et al., 2024) and in similar neural responses for neutral and happy faces (Sel et al., 2015). Moreover, greater spontaneous facial mimicry is related to smaller N170 amplitudes in response to happy facial expressions (Achaibou et al., 2008), suggesting a reduced involvement of the visual system in processing emotional facial expressions, when an alternative (proprioceptive) input is also available. We therefore propose that the facial feedback produced by smiling in the current study resulted in the neutral facial expressions being perceived as happier. As such, the oddball response became smaller during the happy oddball sequences, given that the two types of expressions were perceived as more similar. The lack of a correlation between the intensity of smile posing and changes in amplitude for happy oddballs could be due to the lack of sensitivity of our video analysis, which could have missed subtle differences in the intensities of smiles. In contrast, Achaibou et al. (2008) had used the more sensitive measure of facial electromyography. Moreover, it is unclear why an increase of power for angry oddballs was not observed. This could be addressed in future studies by implementing a condition in which participants are required to also maintain an angry expression.

A main effect of emotion was also found, reflecting a greater oddball response for happy than angry oddball images. This might be explained by the fact that happy (but not angry) faces differed from neutral ones in medium spatial frequencies—which have been demonstrated to play a critical role in face perception (Ruiz-Soler & Beltran, 2006)—and have been found to exert more of an influence on face recognition than lower and higher spatial frequency bands (Tieger & Ganz, 1979). Alternatively, the teeth shown in happy faces might have captured participants' attention to a greater degree. A way to control for that, which future studies might want to implement, is to assign neutral faces as oddball stimuli with happy and angry faces serving as standard stimuli (for a similar approach, see Poncet et al., 2019).

Frequency-tagging studies that use face stimuli typically find the largest oddball response at lateralized occipital channels, especially in the right hemisphere (Rossion et al., 2020). This is considered to reflect higher order face processing operations that are independent of the low-level processing of simple visual features such as luminance performed in the primary visual cortex. The specific roles of the left and right hemispheres for emotional face processing are still debated; however, a meta-analysis involving 105 functional magnetic resonance imaging studies revealed no such support for a right hemisphere dominance (Fusar-Poli et al., 2009). The left hemisphere, for example, has been associated with the processing of local elements of faces (Hillger & Koenig, 1991) and is perhaps a precursor to a “deeper” analysis performed on the right (Meng et al., 2012). The present study, although it demonstrated a significant effect of smiling on happy oddballs only in the left ROI, presented the largest overall oddball response in the MO cluster, particularly during happy oddball sequences. It is possible that the large oddball response in the MO cluster was driven by low-level differences (e.g., differences in medium spatial frequencies) between the neutral

and happy faces, rather than the perceived affective properties of the faces.

Sequences containing happy oddballs also resulted in a higher base response compared to those with angry oddballs. This was strongest in the MO cluster, as the base frequency rate response reflects the contrast between the background and the face stimuli, and is a mixture of low-level and high-level processes in the primary visual cortex (see, e.g., Dzhelyova & Rossion, 2014). Though the difference in the base response during happy and angry oddball sequences was unexpected, it is likely that the (same) difference observed for the oddball response (at 1.2 Hz) was contributing to the differences in the response at 6 Hz (as 1.2 Hz is a subharmonic of 6 Hz).

In sum, we found that producing and maintaining a smile reduces the brain's ability to automatically visually discriminate between neutral and happy facial expressions in the LOT cortex. We interpret this finding as a sign that neutral faces are perceived as slightly happier due to the proprioceptive feedback accompanying smiling. Importantly, however, these findings can also be explained by alternative theoretical frameworks and the notion that facial feedback context modulates the extent of parallel visual processing. Facial feedback accompanying smiling is either congruent or incongruent with the muscle activity presented in the oddball stimuli. The visual processing of happy faces is facilitated by the congruent facial feedback caused by posing a smile. This results in a reduction of the visual system's effort in processing the face. That is, smiling may activate motor representations associated with happy faces, allowing shared neural resources to process these faces with reduced perceptual effort (for a similar reasoning in the context of an EEG and facial electromyography study, see Achaibou et al., 2008). In contrast, the facial feedback context (posing a smile) is incongruent with the visual processing of angry oddballs, which should either not modulate visual processing or result in an even greater visual processing effort (as stipulated in our preregistration). Alternatively, the reduction of the oddball response to happy faces could be explained within the context of predictive coding (Friston & Kiebel, 2009; Gordon et al., 2017) and the mismatch between sensory input and sensory predictions (Brodski-Guerniero et al., 2017). Prediction errors, which indicate that something unexpected has occurred, are associated, for example, with larger evoked responses in the brain (Robinson et al., 2020). Within the context of the current findings, the facial feedback context accompanying a smile pose may form the neural prediction of a happy face. As such, when a happy face is indeed presented, the error signal is smaller, and thus the SSVEP amplitude is reduced. This would also predict that the oddball response becomes larger for angry faces when posing a smile, which however was not observed here.

Although this evidence supports the facial feedback hypothesis, future studies should both refine and extend the current design. For example, matching the magnitude of the oddball response in happy and angry sequences and including additional posing conditions, such as producing an angry expression—to examine the level of specificity of the influence of facial feedback on emotional face perception. It should also be noted that we cannot argue that participants truly perceived the neutral faces to be slightly happier when they themselves were smiling. The lack of a task-relevant behavioral measure therefore limits the interpretation of our findings to modulated sensitivities at the neural level. Indeed, behavioral measures would complement our findings. For example, future

studies could ask participants to count the number of happy/angry faces in a sequence. If smiling does indeed “color” neutral faces to be happier, then one might expect participants to report seeing more happy faces in the smile-pose condition relative to the neutral-pose condition. Alternative paradigms and analyses could also be useful in this respect, whereby the use of psychophysics and signal detection theory could shed light on how participants’ sensitivity to discrimination between happy and neutral faces is modulated by facial feedback. For example, facial feedback as induced by electrical stimulation of smiling muscles has been found to increase the likelihood of labeling ambiguous faces as happy (Efthimiou et al., 2024), and smiling has been found to increase cumulative time for happy faces in a binocular rivalry task (Quettier et al., 2024). This being said, we would like to emphasize that previous frequency-tagging EEG experiments using the same oddball paradigm with emotional faces have repeatedly found a tight link between neural and behavioral effects (Luo & Dzhelyova, 2020). Therefore, we are confident that our neural effect reported here would be in line with behavioral effects too.

To conclude, the present study is the first to demonstrate the effectiveness of employing frequency-tagging EEG in obtaining direct and objective measures of emotional face discrimination during the controlled influence of facial feedback. We provide evidence for the impact of facial muscle activations on automatic visual processing, which also has potential implications for understanding how mood disorders can result in emotion interpretation biases.

Constraints on Generality

We believe the findings of the present study are generalizable to the wider population. Over 60% of our participants were from a diverse range of ethnic backgrounds. It should be noted, however, that age can play a significant factor in emotional processing, and thus more work is needed to generalize the observed effects to other age ranges (e.g., children and older adults). It should also be noted that the stimuli used were of White individuals. Although emotional facial expressions are often considered to be universal, one might wish to include stimuli that depict individuals from non-White backgrounds.

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