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Oscillatory brain dynamics underlying affective face processing

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Abstract

Facial expressions are ubiquitous and highly reliable social cues. Decades of research has shown that affective faces undergo facilitated processing across a distributed brain network. However, few studies have examined the multispectral brain dynamics underlying affective face processing, which is surprising given the multiple brain regions and rapid temporal dynamics thought to be involved. Herein, we used magnetoencephalography to derive dynamic functional maps of angry, neutral, and happy face processing in healthy adults. We found stronger theta oscillations shortly after the onset of affective relative to neutral faces (0–250 ms), within distributed ventral visual and parietal cortices, and the anterior hippocampus. Early gamma oscillations (100–275 ms) were strongest for angry faces in the inferior parietal lobule, temporoparietal junction, and presupplementary motor cortex. Finally, beta oscillations (175–575 ms) were stronger for neutral relative to affective expressions in the middle occipital and fusiform cortex. These results are consistent with the literature in regard to the critical brain regions, and delineate a distributed network where multispectral oscillatory dynamics support affective face processing through the rapid merging of low-level visual inputs to interpret the emotional meaning of each facial expression.

Keywords: affective faces; magnetoencephalography; MEG; theta activity; gamma activity; beta desynchronization

Introduction

Facial expressions are ubiquitous social cues, predictive of others' intentions (Ekman and Friesen 1971, Frith 2009) and motivationally relevant variables in the environment (Phelps et al. 2006). The ability to efficiently identify and interpret facial expressions is essential for successful social cognition and behaviour (Nachson 1995, Matsumoto et al. 2008). Indeed, facial feature configurations are rapidly identified in perception (Bruce and Young 1986, Tanaka and Farah 1993) to aid a speeded interpretation of the expression's emotion and meaning (Calder and Jansen 2005, Tanaka et al. 2012). Moreover, this process appears to be facilitated for particularly arousing expressions, including those that convey imminent danger or reward (e.g. angry or happy faces; Öhman 1986, Öhman et al. 2001, Sweeny et al. 2013, Gregory et al. 2021). The processing of facial expressions has also been shown to be aberrant in multiple mental health disorders and tied to the severity of inherent symptomatology (Marwick and Hall 2008, Gentili et al. 2016, MacNamara et al. 2017, Pei et al. 2023, Doucet et al. 2024). Thus, understanding the neurobiological basis of affective face processing is of paramount importance, especially in terms of the spatial and temporal dynamics that unfold during these processes.

Affective face processing is thought to involve a distributed network of brain regions that transform low-level perceptual features into higher-order information which conveys emotional meaning (Gobbini and Haxby 2007). The inferior occipital gyrus, fusiform gyrus, and ventral temporal cortex are consistently active during face viewing regardless of expression (Fusar-Poli et al. 2009; Müller et al. 2018, Sabatinelli et al. 2011), and underlie the binding of low-level visual features into holistic perceptual face representations (Haxby et al. 2000, 2002, Rossion et al. 2003, Kanwisher and Yovel 2006, Blauch et al. 2022, Scott and Arcaro 2023). Affective compared to neutral expressions prompt stronger responses from the fusiform gyrus and temporal cortex (Allison et al. 2000; Müller et al. 2018, Puce et al. 1998, Sabatinelli et al. 2011), which is thought to reflect the identification of emotionally relevant expressions (Allison et al. 2000, Haxby et al. 2002) and facilitate their perceptual processing

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(Itier and Taylor 2004, Hinojosa et al. 2015). In addition to these visual regions, affective expressions also prompt activation of frontal cortical regions (Palomero-Gallagher and Amunts 2022, Pierce et al. 2023) and the amygdala (Fusar-Poli et al. 2009; Müller et al. 2018, Sabatinelli et al. 2011), in addition to other subcortical limbic regions (Apps et al. 2012, Mundy et al. 2013). Notably, parietal cortices serving attention are also frequently activated when participants identify affective expressions (Gobbini and Haxby 2007, Grill-Spector et al. 2017).

These distributed regions are thought to contribute, in part, to the transformation of perceptual information into complex representations that involve internal memory and mentalizing processes (Takahashi et al. 2015, Zeidman et al. 2015, Yordanova et al. 2017) to interpret the expression's meaning (Gobbini and Haxby 2007, Petro et al. 2018, 2021, Ilyka et al. 2021, Pierce et al. 2023), direct attention (LeDoux 2000, Vuilleumier et al. 2001, Pierce et al. 2022), and guide appropriate social behaviour (Adolphs 2003, Amaral 2004). However, frontal and parietal activity is not always observed and the specific regions have varied across studies, depending perhaps on specific task and stimulus parameters (Fusar-Poli et al. 2009, Lukito et al. 2023). Taken together, ventral visual regions are consistently observed across studies and are essential for processing faces and identifying their expressions, while the involvement of heterogeneous nonvisual cortical areas likely serve to help interpret the expression and its affective content. Crucially, the vast majority of neuroimaging work in this area has focused on using fMRI or EEG modalities, which have lent foundational insights, but are limited in resolving either spatial, temporal, or frequency specific neural dynamics.

Multispectral analyses of neural oscillatory activity measured by magneto- and electroencephalography (M/EEG) have been used to study low-level vision, attention, and high-order executive processes with excellent spatial and temporal precision, making it an excellent approach to study the dynamic, multifaceted components of affective face processing. Unfortunately, studies using oscillatory analysis approaches in the context of affective face processing are very limited. Across the limited number of studies, one consistent finding is stronger gamma-band activity for angry- compared to neutral- and/or happy-faces (Luo et al. 2007, 2009, Sato et al. 2011, Balconi and Bortolotti 2013, Weidner et al. 2024), which may reflect their facilitated perceptual processing. Similar effects have been observed in the theta (Balconi and Lucchiari 2006, Knyazev et al. 2009, 2010, Bocharov and Knyazev 2010, Zhang et al. 2012) and alpha ranges (Güntekin and Basar 2007, Balconi et al. 2009a, 2009b, Sollfrank et al. 2021), which have been linked to a variety of the components underlying affective face processing, ranging from low-level visual feature parcellation (Meehan et al. 2021), visual attention (Klimesch 2012, Wiesman et al. 2017), and working memory (Itthipuripat et al. 2013, Cavanagh and Frank 2014, Heinrichs-Graham and Wilson 2015), to more general emotion regulation (Ertl et al. 2013, Zouaoui et al. 2023). Notably, the effects in the alpha range are somewhat inconsistent (Codispoti et al. 2023), with some suggesting these responses reflect selective attention toward facial features rather than putative 'bottom-up' processing of emotional content (Campagnoli et al. 2019). Overall, while past M/EEG work has made important links between face processing and brain activity related to attention and social cognition, the relative sparseness of studies has limited the conclusions that can be drawn. The few studies that have source imaged face-induced oscillations focused on gamma-band activity (Luo et al. 2007, 2009, Sato et al. 2011, Weidner et al. 2024). Such anatomical information pertaining to the brain regions generating these spectral responses, particularly across multiple frequency bands, would help link M/EEG work more directly with animal models and the wealth of literature in fMRI-BOLD imaging and ultimately expand the field's ability to form deeper interpretations from the findings. Moreover, the temporal precision afforded by MEG would complement the findings from the relatively less temporally precise fMRI-BOLD signal.

The current study is the first to use source imaging on multispectral oscillatory responses during affective face processing. Specifically, our goal was to map the spatiotemporal oscillatory dynamics underlying affective face processing. To this end, we quantified neurophysiological activity using MEG as individuals viewed angry, neutral, and happy expressions. The MEG recordings were imaged in the time-frequency domain and compared voxel-wise across the affective and neutral expressions using a whole-brain, repeated measures ANOVA model. We predicted that, for affective compared to neutral expressions, we would find stronger oscillations in extended ventral visual and temporal cortex consistent with meta-analyses of affective face processing (Fusar-Poli et al. 2009; Müller et al. 2018, Sabatinelli et al. 2011). We expected these patterns to manifest in the gamma and theta spectral windows, given their frequent implication across the, albeit sparse, extant literature.

Methods

Participants

A total of 32 adults (19 females) with a mean age of 26.62 (s.d. = 4.11) years were included in this study. Enrolees were a subset of control participants from a larger study investigating the effects of drug use on neurocognitive activity. Participants were recruited from the local community and received monetary compensation for their participation. All participants were right-handed. Of the 32 participants, 9.38% were Black, 3.13% were American Indian/Alaska Native, 78.13% were Caucasian, and 6.26% were more than one race. This distribution corresponds closely to the racial demographics of the surrounding area. Exclusionary criteria included any medical illness affecting CNS function (e.g. HIV/AIDS and Lupus), any neurological or psychiatric disorder, cognitive impairment, history of head trauma, current substance abuse, and the standard exclusionary criteria related to MEG and MRI acquisition (e.g. ferromagnetic implants). The Institutional Review Board reviewed and approved this investigation. Each participant provided written informed consent following detailed description of the study.

Stimulus and apparatus

Stimuli consisted of angry, neutral, and happy expressions taken from the RADIATE face stimulus set (Conley et al. 2018), from 40 different actors (20 male, 20 female) contributing equally to each expression condition. The 40 actors consisted of an equal number of Asian, Black, Caucasian, and Hispanic/Latino individuals. The mean luminance of the images (Mean = 169 Luma) did not differ as a function of expression condition, $F(2157) = 0.296$, $P = .744$. The face images were presented using the Psychophysics Toolbox (Kleiner et al. 2007) and a PROPixx DLP LED projector (VPixx Technologies Inc., Saint-Bruno-de-Montarville, Canada), subtending to horizontal visual angles between approximately 3.6 and 4.6 degrees, which projected the stimuli from outside the magnetically shielded MEG room and onto a screen that was positioned 112 cm in front of the participant.

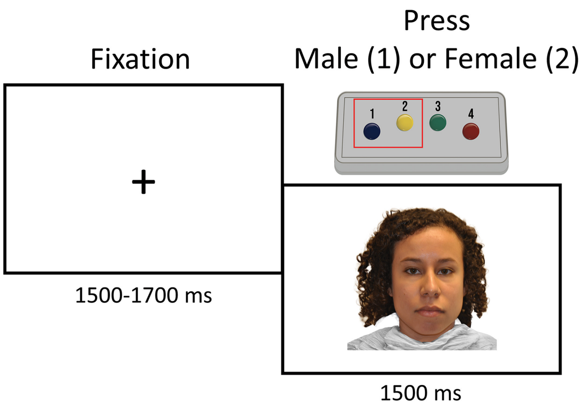

Figure 1. Task design. Face stimuli were presented centrally for 1500 ms and preceded by a fixation cross for a random duration between 1500 and 1700 ms. On each trial, participants were instructed to identify each face as either male or female using a button pad.

Experimental paradigm

During the MEG recording, participants sat in a nonmagnetic chair within a magnetically shielded room. The experiment consisted of 240 trials. In each trial, a face was presented centrally for 1500 ms and was preceded by a fixation cross for a duration between 1500 and 1700 ms (Fig. 1). Thus, the duration of the experiment was ∼12.4 min. Participants were instructed to fixate on each face and indicate whether it was a male or female face using a button press by either the index or middle finger, which the participants performed with a mean accuracy of 98.38% (s.d. = 1.3%). This behavioural task (i.e. sex attribution) was implemented primarily to ensure participants' attention toward the faces, while also being orthogonal to the faces' affect which was the effect of interest in the statistical analyses. Stimuli were presented in a pseudo-randomized order such that the same sex or affective expression condition were repeated in no more than two consecutive trials.

MEG data acquisition

All MEG recordings were conducted in a two-layer magnetically shielded VACOSHIELD room (Vacuumschmelze, Hanau, Germany). Neuromagnetic responses were sampled continuously at 1 kHz, with an acquisition bandwidth of 0.1–330 Hz, using a MEGIN Triux Neo MEG system with 306 magnetic sensors (Helsinki, Finland). During data acquisition, participants were monitored via real-time audio-visual feeds from inside the shielded room. Participant-wise MEG data were corrected for head motion and subjected to external noise reduction using signal space separation method with a temporal extension (Taulu and Simola 2006).

Structural MRI processing and MEG coregistration

Preceding MEG measurement, five head position indicator (HPI) coils were attached to the participant's head and localized, together with three fiducial points and at least 100 scalp surface points, with a 3D digitizer (Fastrak, Polhemus Navigator Sciences, Colchester, VT, USA). Once in the MEG, electrical currents with unique frequencies (e.g. 322 Hz) were fed into each of the HPI coils, which induced measurable magnetic fields, allowing the position of the coils to be actively tracked relative to the MEG sensors throughout the recording. Since the HPI coil locations were also known in head coordinates, all MEG measurements could be transformed into a common coordinate system. With this coordinate system, participant-wise MEG data were coregistered with the participant's high-resolution structural T1-weighted MRI data prior to source reconstruction using BESA MRI (Version 3.0, BESA GmbH, Gräfelfing, Germany). Structural MRI data were transformed into standardized space and aligned parallel to the anterior and posterior commissures. Following source analysis, each participant's MEG functional images were also transformed into standardized space and spatially resampled to enable comparison across participants.

MEG preprocessing, time-frequency transformation, and sensor-level statistics

Cardiac and ocular artefacts (blinks and eye movements) were removed from the data using signal-space projection (SSP), which was accounted for during source analysis (Uusitalo and Ilmoniemi 1997). A 0.5 Hz high-pass and a 150 Hz low-pass filter, in addition to a notch filter at 60 Hz and its harmonics, was applied to the continuous magnetic time series. The time series was divided into 3000 ms epochs (–1500 to 1500 ms surrounding stimulus onset), with the baseline period being defined as the 750 ms prior to the onset of the face stimulus (i.e. –750 to 0 ms). Subsequently, epochs with remaining artefacts were removed based on a fixed threshold method, supplemented with visual inspection. Briefly, the amplitude and gradient distributions across all trials were determined per participant and those trials containing the highest amplitude and/or gradient values relative to this distribution were rejected based on participant-specific thresholds. This approach was employed to minimize the impact of individual differences in sensor proximity to the brain and overall head size, which strongly affect MEG signal amplitude. Artefact-free epochs were then transformed into the time-frequency domain using complex demodulation (Papp and Ktonas 1977, Hoechstetter et al. 2004, Kovach and Gander 2016), with a resolution of 2 Hz and 25 ms between 4 and 100 Hz. Following time-frequency transformation, spectral power estimates per sensor were averaged across trials to generate plots of mean spectral density per sensor. These sensor-level data were then normalized to the baseline power within each frequency bin, which was calculated as the mean power for that 2.0 Hz bin during the –750 to 0 ms time period. The significant time-frequency windows used for source imaging were then determined by statistical analysis of the sensor-level spectrograms across the entire array of 204 gradiometers conducted in BESA Statistics (Version 2.1 T, BESA GmbH, Gräfelfing, Germany). Briefly, each pixel per spectrogram was initially evaluated using a mass univariate approach based on the general linear model, followed by cluster-based permutation testing to address the problem of multiple comparisons (Ernst 2004, Maris and Oostenveld 2007). This two-stage procedure was utilized to minimize false positive results while maintaining sensitivity, with the first stage consisting of paired-sample *t*-tests against baseline on each pixel per spectrogram and thresholding the output spectrograms of *t*-values at $P < .05$ to define time-frequency bins containing potentially significant oscillatory deviations from baseline. In stage two, the time-frequency bins that survived thresholding (at $P < .05$) were clustered with temporally and/or spectrally neighbouring bins that also survived, and cluster values were derived by summing all *t*-values within each cluster. Nonparametric permutation testing was then used to derive a distribution of cluster values and the significance level of the cluster(s) were tested directly using this permuted distribution, which was the result of 10 000 permutations. Based on this cluster-based permutation analysis, only the time-frequency windows that contained significant oscillatory deviations from baseline at the $P < .001$, corrected, threshold across all participants were subjected to source imaging (i.e. beamforming).

MEG source imaging

Cortical regions were imaged through a time-frequency-resolved extension of the linearly constrained minimum variance (LCMV) beamformer (Van Veen et al. 1997, Gross et al. 2001, Dalal et al. 2006). The images were derived from the cross-spectral densities of all combinations of MEG gradiometers averaged over the time-frequency range of interest, and the solution of the forward problem for each location on a grid specified by input voxel space. In principle, the beamformer operator generates a spatial filter for each grid point that passes signals without attenuation from a given neural region, while suppressing activity in all other brain areas. The filter properties arise from the forward solution (i.e. lead field matrix) for each location on a volumetric grid specified by input voxel space (at a 4mm^3 resolution), and from the MEG cross-spectral density matrix. Basically, for each voxel, a set of beamformer weights is determined, which amounts to each MEG sensor being allocated a sensitivity weighting for activity in that particular voxel. Following convention, the source power in these images was normalized per participant using a prestimulus period (i.e. baseline) of equal duration and bandwidth (Hillebrand et al. 2005). Such images are typically referred to as pseudo-t maps, with units (pseudo-t) that reflect noise-normalized power differences (i.e. active vs. passive) per voxel. MEG preprocessing and imaging used the Brain Electrical Source Analysis (version 7.1) software. Individual participant-level maps containing significant artefacts were excluded from further analysis.

In addition, we imaged the same time-frequency windows using the magnetometers to more specifically probe deeper brain structures that have been implicated in affective face processing, with the rationale that activity in such regions could be missed by the gradiometers. Indeed, by-design, magnetometers are more sensitive to distant sources than gradiometers, but are also more susceptible to noise (Wilson 2014, Wilson et al. 2016). Given the potential, albeit conditional, benefit of magnetometer data, we used the same beamformer pipeline as described above in an exploratory analysis that substituted the gradiometers for magnetometers.

Behavioural and neuronal mapping statistics

While the behavioural task of sex attribution was implemented primarily to ensure participants' attention toward the faces, previous studies indicate that affective expressions can improve detection of identifying facial features (Nummenmaa and Calvo 2015). To determine if the expression impacted the participants' ability to identify each face's sex, the average response speed for each expression and participant was submitted to a repeated measures ANOVA where expression (angry, neutral, happy) was the only factor.

To identify differences in neural oscillatory power during face processing as a function of affective expression, the whole-brain maps per oscillatory response were submitted to voxel-wise repeated measures ANOVAs, where expression (angry, neutral, happy) served as the within-subjects factor, computed in *R*. To account for multiple comparisons, a cluster forming threshold of $P < .005$ and cluster-extent threshold of $k > 10$ (i.e. at least 640 mm^3 of brain tissue, at a 4mm^3 resolution) were used, based on Gaussian random fields theory (Poline et al. 1995, Worsley et al. 1996). To determine the direction of the effect for any significant cluster, follow-up pairwise t-tests with Bonferroni correct were conducted on the voxel showing the peak-effect (i.e. the voxel with the highest statistical value per cluster).

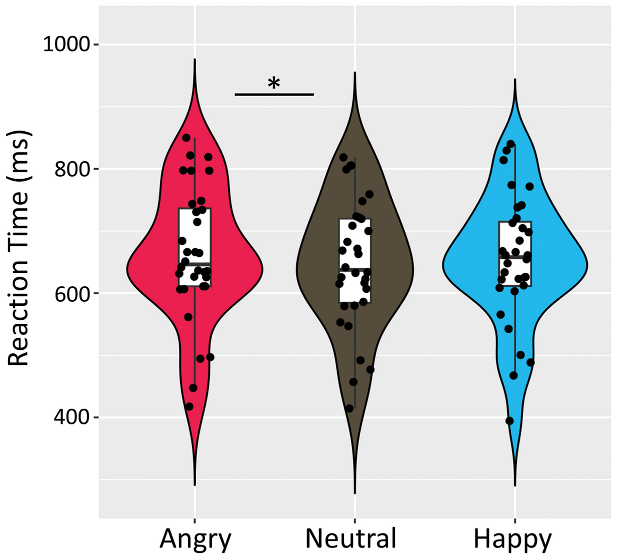

Figure 2. Behavioural results: reaction time differences across expressions. Participants exhibited slower responses during angry compared to neutral face trials. The dots represent the mean reaction time for each participant per affective expression. The box plots illustrate the mean, first, and third quartiles, and the whiskers indicate the minima and maxima. The violin plots illustrate the probability density. Horizontal bars depict the significant pairwise differences (* $P < .01$, Bonferroni corrected).

Results

Behavioural responses

The speed of the participants' responses to identify the sex of each face was submitted to an ANOVA with a within-subjects factor of expression (angry, neutral, happy). This analysis revealed an overall effect of affective expression, $F(2, 62) = 4.60$, $P = .014$ (Fig. 2). Follow-up pair-wise comparisons (all P's Bonferroni corrected) found that responses were faster for neutral compared to angry, $t(32) = 2.83$, $P = .024$, expressions, but did not differ between angry and happy, $t(32) = 1.66$, $P = .32$, nor between neutral and happy, $t(32) = 1.49$, $P = .44$.

Sensor-level neural responses

On average, 6.91% (s.d. = 10.49%) of trials in each expression condition were rejected for artefacts or an incorrect response. Thus, each participant had an average of 74.47 (s.d. = 8.39) trials per condition for beamforming. The number of retained trials did not differ across conditions, $F(2, 62) = 0.85$, $P = .432$. To derive the time-frequency bins for beamforming analyses, sensor-level spectrograms were probed using nonparametric permutation testing (see "Methods" section). These analyses revealed clusters of sustained decreases in the alpha (8–14 Hz) range from 250 to 600 ms and in the beta (20–26 Hz) band from 175 to 575 ms ($P < .001$, corrected; Fig. 3). These time windows were imaged using baselines of equal duration and bandwidth (alpha: –650 to –300 ms; beta: –650 to –150 ms). In addition, there were increases from baseline in the theta (4–8 Hz) band from 0 to 250 ms and in the gamma (74–90 Hz) range from 100 to 275 ms following stimulus onset ($P < 0.001$, corrected; Fig. 3). These two time-windows were imaged using baselines of –650 to –400 ms and

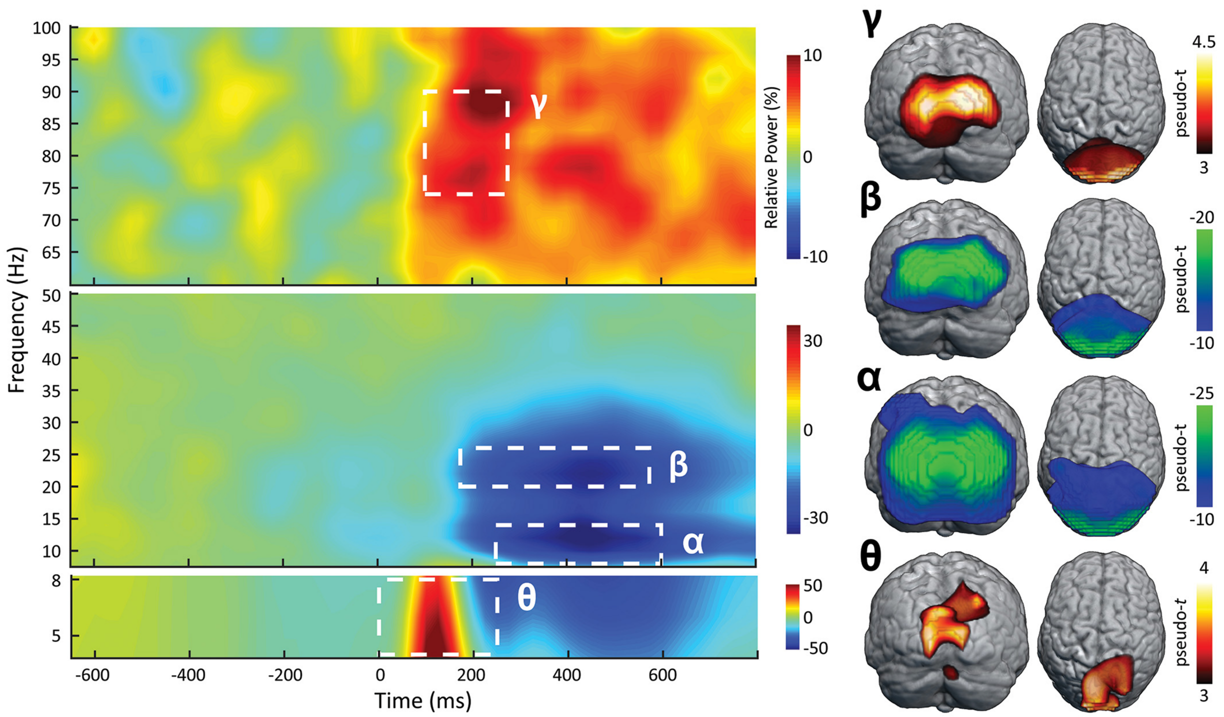

Figure 3. Sensor- and source-level oscillatory activity. (Left) Time-frequency spectrograms illustrate the oscillatory responses across all trials and participants from three representative sensors. Time (ms) is shown on the x-axis and frequency (Hz) on the y-axis, and the colour scale illustrates the change in oscillatory power relative to the baseline period. Strong increases in gamma (top; MEG1922, posterior sensor near occipital cortices) and theta (bottom; MEG2113, posterior sensor near occipital cortices) were observed, in addition to alpha and beta decreases (middle; MEG1623, sensor near left parietal cortex) from baseline. (Right) 3D renditions illustrate the mean images (pseudo-t; see colour bar) for each oscillatory response (i.e. time-frequency window).

–650 to –475 ms, respectively. Following imaging, each oscillatory response was grand-averaged across all participants and conditions to visualize the brain regions generating the strongest responses.

Functional mapping of oscillatory responses

The oscillatory maps for each condition were submitted to whole-brain repeated-measures ANOVA (see 'Behavioural and neuronal mapping statistics' section). Follow-up pairwise comparisons were all Bonferroni corrected. In the theta-band, there was an effect of expression in the left superior parietal lobule, *F*(2, 56) = 9.32, *P* < .001, precuneus, *F*(2, 56) = 9.64, *P* < .001, right inferior temporal gyrus, *F*(2, 56) = 6.58, *P* = .003, right anterior hippocampus, *F*(2, 56) = 7.25, *P* = .002, and right cerebellum, *F*(2, 56) = 6.31, *P* = .003 (Fig. 4). In the left superior parietal lobule, theta oscillations were stronger for angry, *t*(28) = 3.62, *P* = .004, and happy, *t*(28) = 3.96, *P* = .001, compared to neutral expressions, while angry and happy expressions did not differ, *t*(28) = 0.06, *P* = .999. In the precuneus, theta was stronger for angry compared to neutral expressions, *t*(28) = 5.96, *P* < .001, but did not differ between angry and happy expressions, *t*(28) = 2.05, *P* = .151, nor between happy and neutral expressions, *t*(28) = 1.91, *P* = .198. A similar pattern of effects was observed in the right inferior temporal gyrus, such that theta was stronger for angry compared to neutral expressions, *t*(28) = 3.78, *P* = .002, but did not differ between happy and angry, *t*(28) = 1.55, *P* = .399, nor between happy and neutral expressions, *t*(28) = 2.21, *P* = .107. Similarly, theta oscillations in the cerebellum were stronger for angry compared to neutral expressions, *t*(28) = 3.55, *P* = .004, but did not differ between angry and happy, *t*(28) = 2.20, *P* = .109, nor happy and neutral expressions, *t*(28) = 1.17, *P* = .754. In the anterior hippocampus, theta responses were stronger for angry compared to neutral, *t*(28) = 3.33, *P* = .007, and happy expressions, *t*(28) = 2.99, *P* = .017, but did not differ between happy and neutral expressions, *t*(28) = 0.82, *P* = .999.

In the beta-band, there was an effect of expression in the left middle occipital cortex, *F*(2,56) = 7.33, *P* = .001, and the left fusiform cortex, *F*(2,56) = 7.48, *P* = .001 (Fig. 5A). In the left middle occipital cortex, beta oscillations were stronger (i.e. a larger decrease from baseline) during neutral compared to angry, *t*(28) = 2.63, *P* = .041, and happy expressions, *t*(28) = 3.36, *P* = .007, and did not differ between angry and happy expressions, *t*(28) = 1.40, *P* = .518. The same pattern of effects were observed in the left fusiform cortex, such that beta oscillations were stronger for neutral compared to both angry, *t*(28) = 3.21, *P* = .010, and happy expressions, *t*(28) = 3.42, *P* = .006, but did not differ between angry and happy, *t*(28) = 0.98, *P* = 0999.

In the gamma-band, there was an effect of expression in the right presupplementary motor cortex (pre-SMA), *F*(2,54) = 8.71, *P* = .001, the right temporoparietal junction (TPJ), *F*(2,54) = 7.22, *P* = .002, and the right inferior parietal lobule, *F*(2,54) = 6.47, *P* = .003 (Fig. 5B). In the pre-SMA, gamma responses were stronger for angry compared to happy expressions, *t*(27) = 4.08, *P* = .001, but did not differ between angry and neutral, *t*(27) = 2.27, *P* = .095, nor between happy and neutral expressions, *t*(27) = 1.98, *P* = .175. The same pattern of effects was observed in the TPJ, with gamma oscillations being stronger for angry compared to happy expressions, *t*(27) = 4.12, *P* = .001, but not differing between angry and neutral expressions, *t*(27) = 2.26, *P* = .097, nor between neutral and happy expressions, *t*(27) = 1.39, *P* = .526. In the inferior parietal lobule, gamma oscillations were stronger for angry compared to both

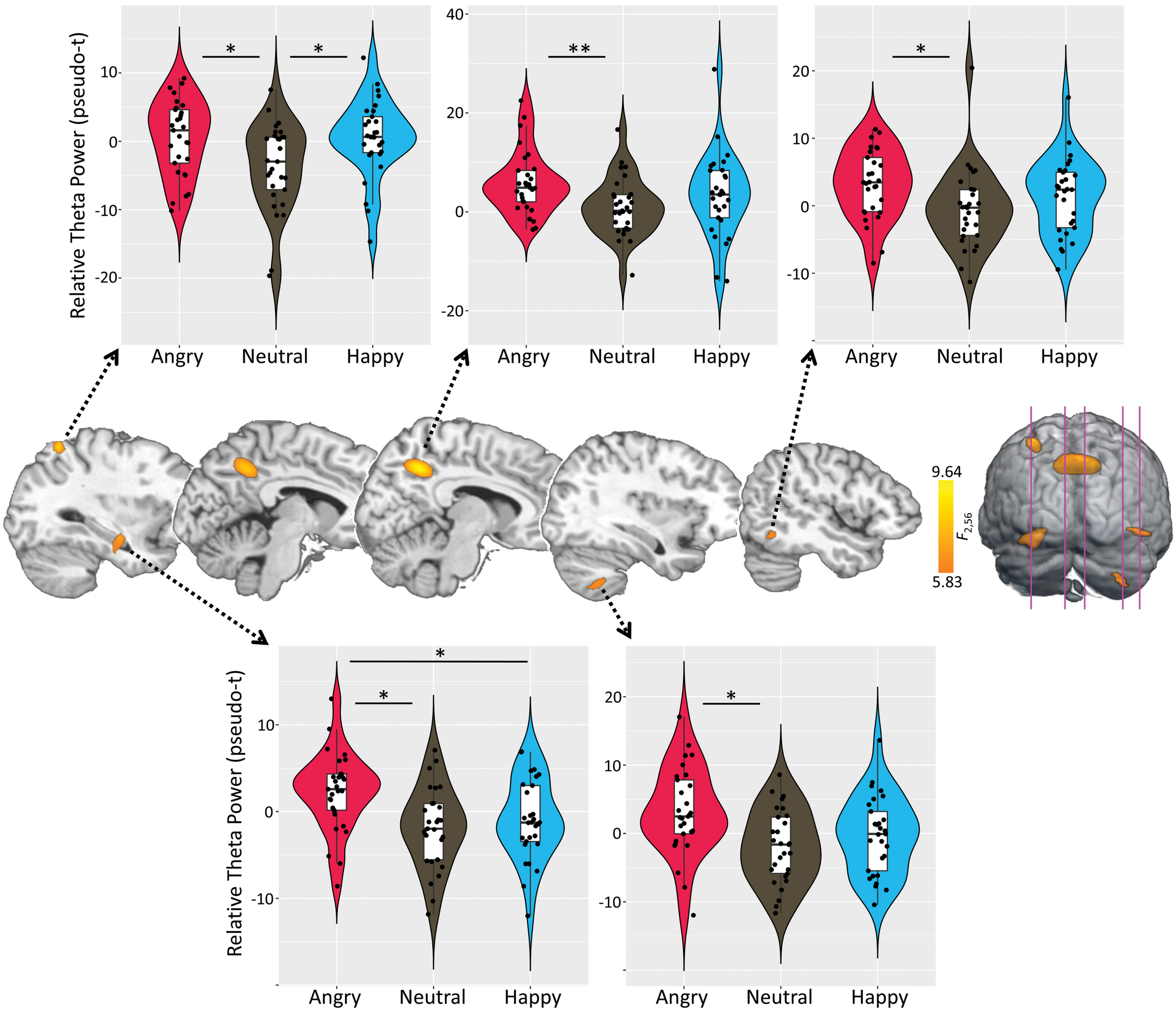

Figure 4. Differences in theta oscillatory activity between angry, neutral, and happy faces. In each panel, the brain images illustrate the *F*-values for facial affect differences thresholded at $P < .005$, corrected. In the data plots, the dots represent the relative oscillatory power for each participant per condition, taken from the peak-voxel in the corresponding clusters. The box plots show the mean, first, and third quartiles, and the whiskers indicate the minima and maxima. The violin plots illustrate the probability density. Horizontal bars depict the significant pairwise differences (** $P < .001$, * $P < .01$, all Bonferroni corrected).

neutral, $t(27) = 2.60$, $P = .045$, and happy expressions, $t(27) = 4.89$, $P < .001$, but did not differ between neutral and happy expressions, $t(27) = 0.47$, $P = .999$.

In the alpha range, no clusters showed an effect of expression. Lastly, our exploratory analysis of beamformer images calculated from the magnetometers revealed no effect of expression in subcortical regions, with similar but more limited findings in cortical regions.

Discussion

In the current study, we identified face expression related differences in theta immediately following stimulus onset (0–250 ms), during a sustained beta oscillatory response (175– 575 ms), and in gamma during an early time window (100–275 ms). The theta and gamma findings predominantly showed stronger oscillatory responses across relevant brain regions for the angry expressions compared to neutral, while beta activity was strongest for neutral relative to angry and happy expressions in other key regions. Most expression effects were found in occipital, parietal, and temporal regions implicated in visual attention and social cognition. In addition, angry faces elicited the strongest gamma responses in the pre-SMA, suggesting that emotional content conveyed through affective expressions involves motor planning brain systems (Pitcher et al. 2008). Collectively, the brain regions showing stronger oscillatory activity for angry (and happy) expressions are consistent with meta-analyses from functional neuroimaging (Fusar-Poli et al. 2009; Müller et al. 2018, Sabatinelli et al. 2011) and are thought to facilitate the identification and interpretation of emotional content in perceptual/attention, memory, and motor planning systems.

Theta activity immediately following face stimulus onset (0–250 ms) was stronger for affective compared to neutral expressions within parietal and ventral cortical regions. These effects are consistent with EEG studies showing stronger early (<250 ms) theta for affective compared to neutral expressions (Balconi and Lucchiari 2006, Knyazev et al. 2009, 2010, Zhang et al. 2012). Similar findings have shown that early theta activity has a role in guiding visuospatial attention (Wiesman et al. 2017, 2018, Wiesman and Wilson 2019, Meehan et al. 2021). Notably, the time window of these differences is broadly consistent with ERP findings (Hinojosa et al. 2015, Schindler and Bublatzky 2020).

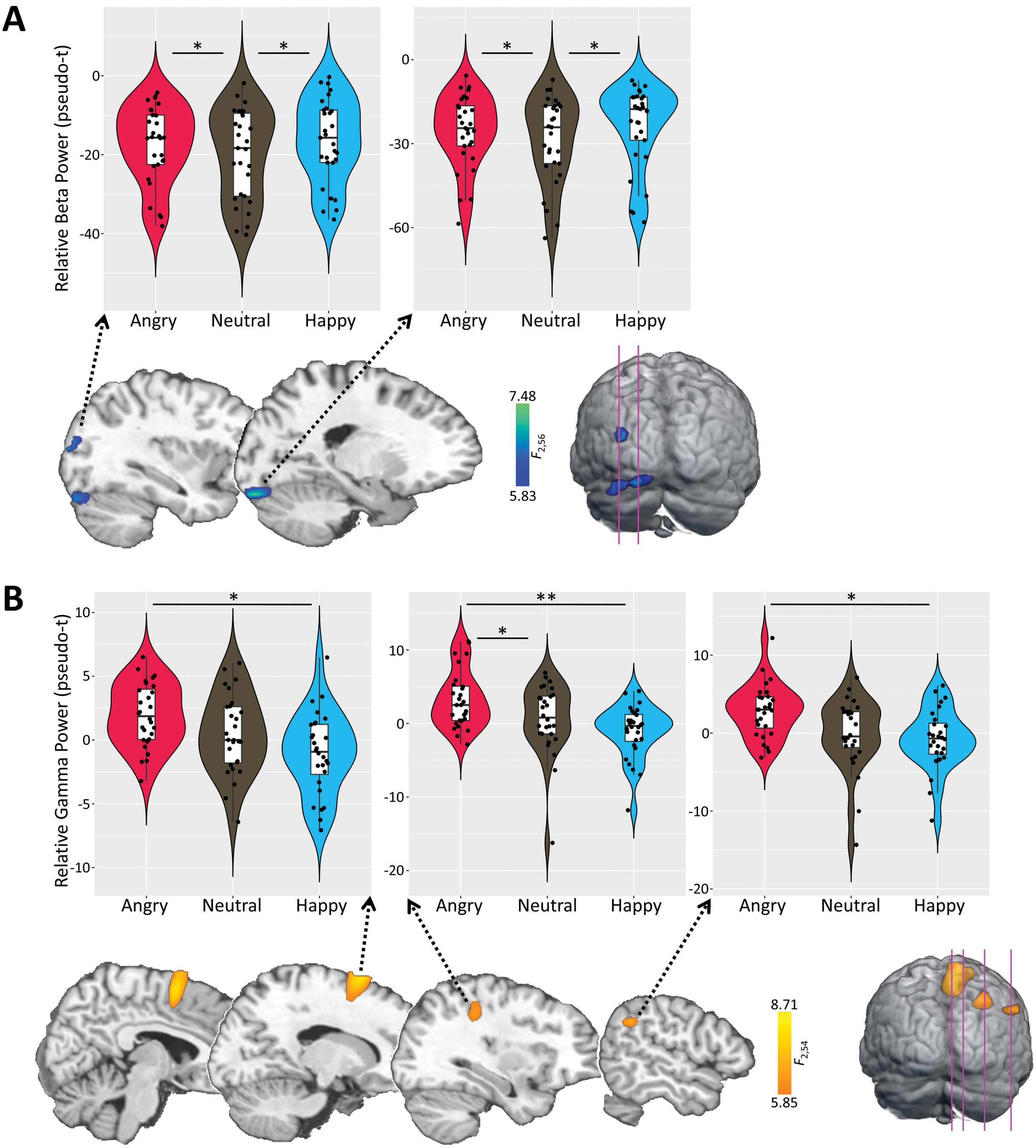

Figure 5. Differences in oscillatory activity between angry, neutral, and happy faces for (A) beta and (B) gamma responses. The brain images illustrate the *F*-values for facial affect differences thresholded at $P < .005$, corrected. In the data plots, the dots represent the relative oscillatory power for each participant, taken from the peak-voxel in the corresponding clusters. The box plots illustrate the mean, first, and third quartiles, and the whiskers indicate the minima and maxima. The violin plots illustrate the probability density. Horizontal bars depict the significant pairwise differences (** $P < .001$, * $P < .01$, all Bonferroni corrected).

The theta differences were located in superior parietal, inferior temporal cortices, and precuneus, which guide attention (Cavanna and Trimble 2006) and extract meaning from visual information (Kiani et al. 2007, Margulies et al. 2009). Taken together, theta differences likely reflect the swift activation of visual and attention systems in response to affective expressions.

In addition to these visual attention regions, neural activity in this early theta window differed by affect in the anterior hippocampus. Interestingly, this region has been widely reported during face processing tasks (Apps et al. 2012, Mundy et al. 2013). Broadly, this region is thought to serve in the integration of complex perceptual information with mentalizing and memory processes (Zeidman et al. 2015, Zeidman and Maguire 2016) to derive emotional meaning (Satpute et al. 2012, Takahashi et al. 2015), which perhaps influences the biological processes underlying affective states (Fanselow and Dong 2010, Lau et al. 2010). While the precuneus is involved in visual attention, as discussed earlier, this region has also been suggested to integrate visual information with internal memory processes and visual imagery (Fletcher et al. 1995, Cavanna and Trimble 2006, Takahashi et al. 2015) to serve cognition broadly (Spreng et al. 2010, Yeager et al. 2022). In the context of this literature, the stronger theta responses in the hippocampus, and perhaps precuneus, for angry faces may reflect the linking of faces' perceptual information with internal memory to rapidly determine the expression's emotional relevance.

Stronger beta oscillations were observed for neutral relative to affective expressions in the middle occipital and fusiform gyri. The fusiform has been robustly related to face processing (Haxby et al. 2002, Kanwisher and Yovel 2006, Fusar-Poli et al. 2009), while the middle occipital gyrus has also been related to face processing (Frühholz et al. 2010, Jehna et al. 2011, Kimura et al. 2012, Heckendorf et al. 2016), particularly their low-level visual features (Rotshtein et al. 2007). Beta oscillations (i.e. desynchronizations or decreases relative to baseline) have long been associated with active cortical engagement (Pfurtscheller and Klimesch 1992), especially during active working memory (Hanslmayr et al. 2012, Heinrichs-Graham and Wilson 2015, Proskovec et al. 2016, 2019, Pavlov and Kotchoubey 2022, Springer et al. 2023). Interestingly, stronger responses (i.e. desynchronizations) for neutral compared to affective expressions in the current study suggest that emotional content diminishes activation of these cortical regions. This effect could reflect the interference of emotional content on performing the task of identifying the sex of each face, involving the processing of specific facial features along ventral visual regions (Duchaine and Yovel 2015), thus leading to stronger beta oscillations for neutral relative to affective expressions.

Gamma oscillatory responses were strongest for angry faces and weakest for happy faces in the TPJ extending into a more medial area of the inferior parietal. This finding is consistent with previous work where angry faces elicited stronger gamma activity relative to neutral and/or positive expressions (Luo et al. 2007, 2009, Sato et al. 2011, Balconi and Bortolotti 2013), and other works which showed stronger gamma for arousing emotional relative to neutral images of scenes (Keil et al. 2001, 2007, Martini et al. 2012; Müller et al. 1999). In general, gamma-band activity during visual processing has long been seen as a signature of efficient neural computations (Uhlhaas et al. 2009, Wilson et al. 2018), where visual information is bound into coherent percepts (Keil et al. 1999, Tallon-Baudry and Bertrand 1999, Fries et al. 2001). Along these lines, the inferior parietal cortex and TPJ are known to serve domain-general cognitive functions (Igelström and Graziano 2017). Moreover, the TPJ is thought serve social cognition by guiding attention toward emotional content (Kastner et al. 2017, Kim et al. 2018), including angry faces (Inuggi et al. 2014), and attributing social meaning to other's behaviours (Schurz et al. 2014, Krall et al. 2015, Patel et al. 2019). Stronger gamma oscillations toward angry faces in these regions thus may reflect the facilitation of emotional content in visual perception, and in determining their emotional relevance.

In addition to these temporo-parietal effects, gamma activity was strongest for angry faces in the pre-SMA. Meta-analyses have shown this pre-SMA region to be consistently active during face processing (Fusar-Poli et al. 2009) and more strongly for affective faces (Sabatinelli et al. 2011, Müller et al. 2018). The involvement of this region may reflect the impact of emotion on motor responses, given that pre-SMA gamma tends to increase immediately preceding target-directed motor movement (Gunduz et al. 2016), and is stronger in the presence of distracting information (Gaetz et al. 2013). Alternatively, this region has also been tied to the generation of certain facial expressions (Krolak-Salmon et al. 2006, Kircher et al. 2013), suggesting that it may be involved in identifying emotionality in the expression (Müller et al. 2018) perhaps by 'mirroring' facial muscle activity (Niedenthal 2007). Broadly, the impact of emotional content on motor systems shown here is consistent with notions that the activation of motor systems in the brain is fundamental to emotion processing (Frijda 2000, Lang and Bradley 2010).

Strong alpha oscillations were observed following stimulus onset, but these neural responses did not differ across emotion conditions. This is at odds with many studies finding stronger alpha oscillations for affective compared to neutral faces (Güntekin and Basar 2007, Balconi et al. 2009a, 2009b, Sollfrank et al. 2021) and scenes (Schubring and Schupp 2019, 2021), indicative of stronger activation of visual attention systems (Klimesch 2012, Wiesman et al. 2017). However, this effect is often not observed (Aftanas et al. 2002, Uusberg et al. 2013, Güntekin and Başar 2014). Interestingly, a recent review concluded that stronger alpha oscillations are reliably observed only during the most highly arousing and motivationally relevant emotional images [i.e. injury or erotic scenes; (Codispoti et al. 2023)]. Thus, the relatively low-arousing expressions in the current study may not produce emotion-related alpha effects. These findings may suggest an apparent dissociation between alpha and beta oscillatory responses, which could be a focus of future investigations.

Before closing, it is important to acknowledge limitations of this study. Brain activity was not compared between faces and non-face objects. Thus, it is unclear if the regions uncovered in the comparison of expressions are generally involved in face processing *per se* or instead in detecting and interpreting their emotional relevance. Similarly, it is unclear if these regions may be involved in processing other forms of emotional content (e.g. emotional scenes) or are specific to affective faces. Future work should expand on the current findings to determine if these regions and/or frequency bands are broadly involved in face and/or emotion processing. In addition, the current sample consisted of healthy adults; future studies should test if these findings extend to younger and older populations, or within those with mental illness, where changes in affective face processing are known to occur (Marwick and Hall 2008, Gentili et al. 2016, MacNamara et al. 2017, Pei et al. 2023). Lastly, per our lack of findings in the exploratory analysis of the magnetometer signals, it should be noted that while magnetometers are more sensitive than gradiometers to deep sources, many studies have shown that planar gradiometers are sensitive enough to detect neural activity in the hippocampal area, amygdala, and neighbouring regions (Badura-Brack et al. 2017, 2018a, 2018b, Lew et al. 2021, Ott et al. 2021, Petro et al. 2022, Picci et al. 2023, Rempe et al. 2025), including the current work which showed stronger hippocampal theta responses for angry relative to happy and neutral faces. There was also a recent study that showed comparable sensitivity to hippocampal sources in both planar gradiometer and magnetometer data collected simultaneously (Meehan et al. 2021). Future work may continue to explore magnetometer data using different analytical pipelines.

The current study found enhanced theta and gamma oscillatory activity for angry (and happy) compared to neutral expressions across ventral visual, parietal, and pre-SMA cortices, which are generally consistent with the distributed brain networks discussed in the literature. In addition, beta oscillations were stronger for neutral compared to angry and happy expressions in the fusiform and middle occipital cortices, likely reflecting the impact of emotional content on task-directed attention toward the sex of the face. These results are consistent with the notion that affective face processing involves a distributed brain network, which communicates low-level perceptual information with high-level memory, mentalizing, and motor planning systems to strategically guide attention and behavioural programmes (Adolphs 2003). These results highlight the utility of multispectral dynamic imaging to study the multifaceted components of affective face processing, which may pay dividends to understanding mental health disorders where social cognition is impaired.

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Data availability statement

The data used in this article will be made publicly available through the COINS framework at the completion of the study (https://coins.trendscenter.org/).

Conflict of interest. None declared.

References

Adolphs R. Cognitive neuroscience of human social behaviour. *Nat Rev Neurosci* 2003;**4**:165–178. https://doi.org/10.1038/nrn1056

Aftanas LI, Varlamov AA, Pavlov SV *et al.* Time-dependent cortical asymmetries induced by emotional arousal: EEG analysis of event-related synchronization and desynchronization in individually defined frequency bands. *Int J Psychophysiol* 2002;**44**:67–82. https://doi.org/10.1016/S0167-8760(01)00194-5

Allison T, Puce A, McCarthy G *et al.* Social perception from visual cues: Role of the STS region. *Trends Cogn Sci* 2000;**4**:267–78. https://doi.org/10.1016/S1364-6613(00)01501-1

Amaral DG. The amygdala and social behavior: what's fear got to do with it?. In: Gorman JM (ed.), *Fear and Anxiety: the Benefits of Translational Research*. Arlington, VA, US: American Psychiatric Publishing Inc, 2004;251–63.

Apps MAJ, Tajadura-Jiménez A, Turley G *et al.* The different faces of one's self: an fMRI study into the recognition of current and past self-facial appearances. *NeuroImage* 2012;**63**:1720–29. https://doi.org/10.1016/j.neuroimage.2012.08.053

Badura-Brack A, Heinrichs-Graham E, McDermott TJ *et al.* Resting-state neurophysiological abnormalities in posttraumatic stress disorder: a magnetoencephalography study. *Front Human Neurosci* 2017;**11**:205. https://doi.org/10.3389/fnhum.2017.00205

Badura-Brack A, McDermott TJ, Becker KM *et al.* Attention training modulates resting-state neurophysiological abnormalities in posttraumatic stress disorder. *Psychiatry Res Neuroim* 2018a;**271**:135–41. https://doi.org/10.1016/j.pscychresns.2017.11.008

Badura-Brack A, McDermott TJ, Heinrichs-Graham E *et al.* Veterans with PTSD demonstrate amygdala hyperactivity while viewing threatening faces: a MEG study. *Biol Psychol* 2018b;**132**:228–32. https://doi.org/10.1016/j.biopsycho.2018.01.005

Balconi M, Bortolotti A. Conscious and unconscious face recognition is improved by high-frequency rTMS on pre-motor cortex. *Consciousness and Cognition* 2013;**22**:771–78. https://doi.org/10.1016/j.concog.2013.04.013

Balconi M, Brambilla E, Falbo L. BIS/BAS, cortical oscillations and coherence in response to emotional cues. *Brain Res Bull* 2009a;**80**:151–57. https://doi.org/10.1016/j.brainresbull.2009.07.001

Balconi M, Falbo L, Brambilla E. BIS/BAS responses to emotional cues: self report, autonomic measure and alpha band modulation. *Pers Individ Dif* 2009b;**47**:858–63. https://doi.org/10.1016/j.paid.2009.07.004

Balconi M, Lucchiari C. EEG correlates (event-related desynchronization) of emotional face elaboration: A temporal analysis. *Neurosci Lett* 2006;**392**:118–23. https://doi.org/10.1016/j.neulet.2005.09.004

Blauch NM, Behrmann M, Plaut DC. A connectivity-constrained computational account of topographic organization in primate high-level visual cortex. *Proc Natl Acad Sci* 2022;**119**:e2112566119. https://doi.org/10.1073/pnas.2112566119

Bocharov A, Knyazev G. Interaction of anger with anxiety and responses to emotional facial expressions. *Pers Individ Dif* 2010;**50**:398–403. https://doi.org/10.1016/j.paid.2010.11.003

Bruce V, Young A. Understanding face recognition. *Br J Psychol* 1986;**77**:305–27. https://doi.org/10.1111/j.2044-8295.1986.tb02199.x

Calder AJ, Jansen J. Configural coding of facial expressions: the impact of inversion and photographic negative. *Visual Cognition* 2005;**12**:495–518. https://doi.org/10.1080/13506280444000418

Campagnoli RR, Wieser MJ, Gruss LF *et al.* How the visual brain detects emotional changes in facial expressions: evidence from driven and intrinsic brain oscillations. *Cortex; a Journal Devoted to the Study of the Nervous System and Behavior* 2019;**111**:35–50. https://doi.org/10.1016/j.cortex.2018.10.006

Cavanagh JF, Frank MJ. Frontal theta as a mechanism for cognitive control. *Trends Cogn Sci* 2014;**18**:414–21. https://doi.org/10.1016/j.tics.2014.04.012

Cavanna AE, Trimble MR. The precuneus: a review of its functional anatomy and behavioural correlates. *Brain* 2006;**129**:564–83. https://doi.org/10.1093/brain/awl004

Codispoti M, de Cesarei A, Ferrari V. Alpha-band oscillations and emotion: a review of studies on picture perception. *Psychophysiology* 2023;**60**:e14438. https://doi.org/10.1111/psyp.14438

Conley MI, Dellarco DV, Rubien-Thomas E *et al.* The racially diverse affective expression (RADIATE) face stimulus set. *Psychiatry Res* 2018;**270**:1059–67. https://doi.org/10.1016/j.psychres.2018.04.066

Dalal SS, Sekihara K, Nagarajan SS. Modified beamformers for coherent source region suppression. *IEEE Trans Bio-Med Eng* 2006;**53**:1357–63. https://doi.org/10.1109/TBME.2006.873752

Doucet GE, Kruse JA, Keefe A *et al.* Anxiety symptoms are differentially associated with facial expression processing in boys and girls. *Soc Cognit Affective Neurosci* 2024;**19**:nsae085. https://doi.org/10.1093/scan/nsae085

Duchaine B, Yovel G. A revised neural framework for face processing. *Annu Rev Vision Sci.* 2015;**1**:393–416. https://doi.org/10.1146/annurev-vision-082114-035518

Ekman P, Friesen WV. Constants across cultures in the face and emotion. *J Pers Soc Psychol* 1971;**17**:124–29. https://doi.org/10.1037/h0030377

Ernst MD. Permutation methods: a basis for exact inference. *Stat Sci* 2004;**19**:676–85. https://doi.org/10.1214/088342304000000396

Ertl M, Hildebrandt M, Ourina K *et al.* Emotion regulation by cognitive reappraisal—the role of frontal theta oscillations. *NeuroImage*

2013;**81**:412–21. https://doi.org/10.1016/j.neuroimage.2013.05.044

Fanselow MS, Dong H-W. Are the dorsal and ventral hippocampus functionally distinct structures?. *Neuron* 2010;**65**:7–19. https://doi.org/10.1016/j.neuron.2009.11.031

Fletcher PC, Frith CD, Baker SC *et al.* The mind's eye—precuneus activation in memory-related imagery. *NeuroImage* 1995;**2**:195–200. https://doi.org/10.1006/nimg.1995.1025

Fries P, Reynolds JH, Rorie AE *et al.* Modulation of oscillatory neuronal synchronization by selective visual attention. *Science* 2001;**291**:1560–63. https://doi.org/10.1126/science.1055465

Frijda NH. Emotions. In: Pawlik K and Rosenzweig M (eds), *International Handbook of Psychology*. London: Sage Publications Ltd, 2000, 207–22. https://doi.org/10.4135/9781848608399.n12

Frith C. Role of facial expressions in social interactions. *Philos Trans R Soc B* 2009;**364**:3453–58. https://doi.org/10.1098/rstb.2009.0142

Frühholz S, Godde B, Lewicki P *et al.* Face recognition under ambiguous visual stimulation: fMRI correlates of "encoding styles. *Human Brain Mapp* 2010;**32**:1750–61. https://doi.org/10.1002/hbm.21144

Fusar-Poli P, Placentino A, Carletti F *et al.* Functional atlas of emotional faces processing: a voxel-based meta-analysis of 105 functional magnetic resonance imaging studies. *J Psychiatry Neurosci* 2009;**34**:418–32.

Gaetz W, Liu C, Zhu H *et al.* Evidence for a motor gamma-band network governing response interference. *NeuroImage* 2013;**74**:245–53. https://doi.org/10.1016/j.neuroimage.2013.02.013

Gentili C, Cristea IA, Angstadt M *et al.* Beyond emotions: a meta-analysis of neural response within face processing system in social anxiety. *Exp Biol Med*. 2016;**241**:225–37. https://doi.org/10.1177/1535370215603514

Gobbini MI, Haxby JV. Neural systems for recognition of familiar faces. *Neuropsychologia* 2007;**45**:32–41. https://doi.org/10.1016/j.neuropsychologia.2006.04.015

Gregory E, Tanaka JW, Liu X. Emotional gist: the rapid perception of facial expressions. *Cogn Emot* 2021;**35**:385–92. https://doi.org/10.1080/02699931.2020.1823322

Grill-Spector K, Weiner KS, Kay K *et al.* The functional neuroanatomy of human face perception. *Annu Rev Vision Sci*. 2017;**3**:167–96. https://doi.org/10.1146/annurev-vision-102016-061214

Gross J, Kujala J, Hämäläinen M *et al.* Dynamic imaging of coherent sources: studying neural interactions in the human brain. *Proc Natl Acad Sci* 2001;**98**:694–99. https://doi.org/10.1073/pnas.98.2.694

Gunduz A, Brunner P, Sharma M *et al.* Differential roles of high gamma and local motor potentials for movement preparation and execution. *Brain-Comput Interfaces* 2016;**3**:88–102. https://doi.org/10.1080/2326263X.2016.1179087

Güntekin B, Basar E. Emotional face expressions are differentiated with brain oscillations. *Int J Psychophysiol* 2007;**64**:91–100. https://doi.org/10.1016/j.ijpsycho.2006.07.003

Güntekin B, Başar E. A review of brain oscillations in perception of faces and emotional pictures. *Neuropsychologia* 2014;**58**:33–51. https://doi.org/10.1016/j.neuropsychologia.2014.03.014

Hanslmayr S, Staudigl T, Fellner M-C. Oscillatory power decreases and long-term memory: the information via desynchronization hypothesis. *Front Human Neurosci* 2012;**6**:74. https://www.frontiersin.org/articles/10.3389/fnhum.2012.00074

Haxby JV, Hoffman EA, Gobbini MI. The distributed human neural system for face perception. *Trends in Cognitive Sciences* 2000;**4**:223–33. https://doi.org/10.1016/s1364-6613(00)01482-0

Haxby JV, Hoffman EA, Gobbini MI. Human neural systems for face recognition and social communication. *Biol Psychiatry* 2002;**51**:59–67. https://doi.org/10.1016/S0006-3223(01)01330-0

Heckendorf E, Huffmeijer R, Bakermans-Kranenburg MJ *et al.* Neural processing of familiar and unfamiliar children's faces: effects of experienced love withdrawal, but no effects of neutral and threatening priming. *Front Human Neurosci* 2016;**10**:231. https://doi.org/10.3389/fnhum.2016.00231

Heinrichs-Graham E, Wilson TW. Spatiotemporal oscillatory dynamics during the encoding and maintenance phases of a visual working memory task. *Cortex* 2015;**69**:121–30. https://doi.org/10.1016/j.cortex.2015.04.022

Hillebrand A, Singh KD, Holliday IE *et al.* A new approach to neuroimaging with magnetoencephalography. *Human Brain Mapp* 2005;**25**:199–211. https://doi.org/10.1002/hbm.20102

Hinojosa JA, Mercado F, Carretié L. N170 sensitivity to facial expression: A meta-analysis. *Neurosci Biobehav Rev* 2015;**55**:498–509. https://doi.org/10.1016/j.neubiorev.2015.06.002

Hoechstetter K, Bornfleth H, Weckesser D *et al.* BESA source coherence: a new method to study cortical oscillatory coupling. *Brain Topogr* 2004;**16**:233–38. https://doi.org/10.1023/b:brat.0000032857.55223.5d

Igelström KM, Graziano MSA. The inferior parietal lobule and temporoparietal junction: a network perspective. *Neuropsychologia* 2017;**105**:70–83. https://doi.org/10.1016/j.neuropsychologia.2017.01.001

Ilyka D, Johnson MH, Lloyd-Fox S. Infant social interactions and brain development: a systematic review. *Neurosci Biobehav Rev* 2021;**130**:448–69. https://doi.org/10.1016/j.neubiorev.2021.09.001

Inuggi A, Sassi F, Castillo A *et al.* Cortical response of the ventral attention network to unattended angry facial expressions: an EEG source analysis study. *Frontiers in Psychology* 2014;**5**:1498. https://www.frontiersin.org/articles/10.3389/fpsyg.2014.01498

Itier RJ, Taylor MJ. N170 or N1? Spatiotemporal differences between object and face processing using ERPs. *Cereb Cortex* 2004;**14**:132–42. https://doi.org/10.1093/cercor/bhg111

Itthipuripat S, Wessel JR, Aron AR. Frontal theta is a signature of successful working memory manipulation. *Exp Brain Res* 2013;**224**:255–62. https://doi.org/10.1007/s00221-012-3305-3

Jehna M, Neuper C, Ischebeck A *et al.* The functional correlates of face perception and recognition of emotional facial expressions as evidenced by fMRI. *Brain Res* 2011;**1393**:73–83. https://doi.org/10.1016/j.brainres.2011.04.007

Kanwisher N, Yovel G. The fusiform face area: a cortical region specialized for the perception of faces. *Philos Trans R Soc B* 2006;**361**:2109–28. https://doi.org/10.1098/rstb.2006.1934

Kastner S, Chen Q, Jeong SK *et al.* A brief comparative review of primate posterior parietal cortex: A novel hypothesis on the human toolmaker. *Neuropsychologia* 2017;**105**:123–34. https://doi.org/10.1016/j.neuropsychologia.2017.01.034

Keil A, Müller MM, Gruber T *et al.* Effects of emotional arousal in the cerebral hemispheres: a study of oscillatory brain activity and event-related potentials. *Clin Neurophysiol* 2001;**112**:2057–68. https://doi.org/10.1016/s1388-2457(01)00654-x

Keil A, Müller MM, Ray WJ *et al.* Human gamma band activity and perception of a gestalt. *J Neurosci* 1999;**19**:7152–61. https://doi.org/10.1523/JNEUROSCI.19-16-07152.1999

Keil A, Stolarova M, Moratti S *et al.* Adaptation in human visual cortex as a mechanism for rapid discrimination of aversive stimuli. *NeuroImage* 2007;**36**:472. https://doi.org/10.1016/j.neuroimage.2007.02.048

Kiani R, Esteky H, Mirpour K *et al.* Object category structure in response patterns of neuronal population in monkey inferior temporal cortex. *J Neurophysiol* 2007;**97**:4296–309. https://doi.org/10.1152/jn.00024.2007

Kim S-Y, Shin JE, Lee YI *et al*. Neural evidence for persistent attentional bias to threats in patients with social anxiety disorder. *Soc Cognit Affective Neurosci* 2018;**13**:1327–36. https://doi.org/10.1093/scan/nsy101

Kimura M, Kondo H, Ohira H *et al*. Unintentional temporal context-based prediction of emotional faces: an electrophysiological study. *Cerebral Cortex 1991* 2012;**22**:1774–85. https://doi.org/10.1093/cercor/bhr244

Kircher T, Pohl A, Krach S *et al*. Affect-specific activation of shared networks for perception and execution of facial expressions. *Soc Cognit Affective Neurosci* 2013;**8**:370–77. https://doi.org/10.1093/scan/nss008

Kleiner M, Brainard D, Pelli D *et al*. What's new in psychtoolbox-3. *Perception* 2007;**36**:1–16.

Klimesch W. Alpha-band oscillations, attention, and controlled access to stored information. *Trends Cognit Sci* 2012;**16**:606–617. https://doi.org/10.1016/j.tics.2012.10.007

Knyazev GG, Slobodskoj-Plusnin JY, Bocharov AV. Event-related delta and theta synchronization during explicit and implicit emotion processing. *Neuroscience* 2009;**164**:1588–600. https://doi.org/10.1016/j.neuroscience.2009.09.057

Knyazev GG, Slobodskoj-Plusnin JY, Bocharov AV. Gender differences in implicit and explicit processing of emotional facial expressions as revealed by event-related theta synchronization. *Emotion* 2010;**10**:678–87. https://doi.org/10.1037/a0019175

Kovach CK, Gander PE. The demodulated band transform. *J Neurosci Methods* 2016;**261**:135–54. https://doi.org/10.1016/j.jneumeth.2015.12.004

Krall SC, Rottschy C, Oberwelland E *et al*. The role of the right temporoparietal junction in attention and social interaction as revealed by ALE meta-analysis. *Brain Struct Funct* 2015;**220**:587. https://doi.org/10.1007/s00429-014-0803-z

Krolak-Salmon P, Hénaff M-A, Vighetto A *et al*. Experiencing and detecting happiness in humans: The role of the supplementary motor area. *Ann Neurol* 2006;**59**:196–99. https://doi.org/10.1002/ana.20706

Lang PJ, Bradley MM. Emotion and the motivational brain. *Biol. Psychol* 2010;**84**:437–50. https://doi.org/10.1016/j.biopsycho.2009.10.007

Lau JYF, Goldman D, Buzas B *et al*. BDNF gene polymorphism (val66met) predicts amygdala and anterior hippocampus responses to emotional faces in anxious and depressed adolescents. *NeuroImage* 2010;**53**:952–61. https://doi.org/10.1016/j.neuroimage.2009.11.026

LeDoux JE. Emotion circuits in the brain. *Annu Rev Neurosci* 2000;**23**:155–84. https://doi.org/10.1146/annurev.neuro.23.1.155

Lew BJ, Fitzgerald EE, Ott LR *et al*. Three-year reliability of MEG resting-state oscillatory power. *NeuroImage* 2021;**243**:118516. https://doi.org/10.1016/j.neuroimage.2021.118516

Lukito S, Fortea L, Groppi F *et al*. Should perception of emotions be classified according to threat detection rather than emotional valence? An updated meta-analysis for a whole-brain atlas of emotional faces processing. *J Psychiatry Neurosci* 2023;**48**:E376–E389. https://doi.org/10.1503/jpn.230065

Luo Q, Holroyd T, Jones M *et al*. Neural dynamics for facial threat processing as revealed by gamma band synchronization using MEG. *NeuroImage* 2007;**34**:839–47. https://doi.org/10.1016/j.neuroimage.2006.09.023

Luo Q, Mitchell D, Cheng X *et al*. Visual awareness, emotion, and gamma band synchronization. *Cereb Cortex* 2009;**19**:1896–904. https://doi.org/10.1093/cercor/bhn216

MacNamara A, Klumpp H, Kennedy AE *et al*. Transdiagnostic neural correlates of affective face processing in anxiety and depression. *Depress Anxiety* 2017;**34**:621–31. https://doi.org/10.1002/da.22631

Margulies DS, Vincent JL, Kelly C *et al*. Precuneus shares intrinsic functional architecture in humans and monkeys. *Proc Natl Acad Sci* 2009;**106**:20069–74. https://doi.org/10.1073/pnas.0905314106

Maris E, Oostenveld R. Nonparametric statistical testing of EEG- and MEG-data. *Journal of Neurosci Methods* 2007;**164**:177–90. https://doi.org/10.1016/j.jneumeth.2007.03.024

Martini N, Menicucci D, Sebastiani L *et al*. The dynamics of EEG gamma responses to unpleasant visual stimuli: from local activity to functional connectivity. *NeuroImage* 2012;**60**:922–32. https://doi.org/10.1016/j.neuroimage.2012.01.060

Marwick K, Hall J. Social cognition in schizophrenia: a review of face processing. *Br Med Bul* 2008;**88**:43–58. https://doi.org/10.1093/bmb/ldn035

Matsumoto D, Keltner D, Shiota MN *et al*. Facial expressions of emotion. In: Lewis M, Haviland-Jones JM and Barrett LF (eds), *Handbook of Emotions 3rd Ed*. New York, NY, US: The Guilford Press, 2008, 211–34.

Meehan CE, Wiesman AI, Spooner RK *et al*. Differences in rhythmic neural activity supporting the temporal and spatial cueing of attention. *Cereb Cortex* 2021;**31**:4933–44. https://doi.org/10.1093/cercor/bhab132

Müller MM, Keil A, Gruber T *et al*. Processing of affective pictures modulates right-hemispheric gamma band EEG activity. *Clin Neurophysiol* 1999;**110**:1913–20. https://doi.org/10.1016/S1388-2457(99)00151-0

Müller VI, Höhner Y, Eickhoff SB. Influence of task instructions and stimuli on the neural network of face processing: an ALE meta-analysis. *Cortex* 2018;**103**:240–55. https://doi.org/10.1016/j.cortex.2018.03.011

Mundy ME, Downing PE, Dwyer DM *et al*. A critical role for the hippocampus and perirhinal cortex in perceptual learning of scenes and faces: complementary findings from amnesia and FMRI. *J Neurosci* 2013;**33**:10490–502. https://doi.org/10.1523/JNEUROSCI.2958-12.2013

Nachson I. On the modularity of face recognition: the riddle of domain specificity. *Journal of Clinical and Experimental Neuropsychology* 1995;**17**:256–75. https://doi.org/10.1080/01688639508405122

Niedenthal PM. Embodying emotion. *Science* 2007;**316**:1002–05. https://doi.org/10.1126/science.1136930

Nummenmaa L, Calvo MG. Dissociation between recognition and detection advantage for facial expressions: a meta-analysis. *Emotion* 2015;**15**:243–56. https://doi.org/10.1037/emo0000042

Öhman A. Face the beast and fear the face: animal and social fears as prototypes for evolutionary analyses of emotion. *Psychophysiology* 1986;**23**:123–45. https://doi.org/10.1111/j.1469-8986.1986.tb00608.x

Öhman A, Lundqvist D, Esteves F. The face in the crowd revisited: a threat advantage with schematic stimuli. *J Pers Soc Psychol* 2001;**80**:381–96. https://doi.org/10.1037/0022-3514.80.3.381

Ott LR, Penhale SH, Taylor BK *et al*. Spontaneous cortical MEG activity undergoes unique age- and sex-related changes during the transition to adolescence. *NeuroImage* 2021;**244**:118552. https://doi.org/10.1016/j.neuroimage.2021.118552

Palomero-Gallagher N, Amunts K. A short review on emotion processing: a lateralized network of neuronal networks. *Brain Struct Funct* 2022;**227**:673–84. https://doi.org/10.1007/s00429-021-02331-7

Papp N, Ktonas P. Critical evaluation of complex demodulation techniques for the quantification of bioelectrical activity. *Biomed Sci Instrum*. 1977;**13**:135–45.

Patel GH, Sestieri C, Corbetta M. The evolution of the temporoparietal junction and posterior superior temporal sulcus. *Cortex* 2019;**118**:38–50. https://doi.org/10.1016/j.cortex.2019.01.026

Pavlov YG, Kotchoubey B. Oscillatory brain activity and maintenance of verbal and visual working memory: a systematic review. *Psychophysiology* 2022;**59**:e13735. https://doi.org/10.1111/psyp.13735

Pei G, Xiao Q, Pan Y *et al.* Neural evidence of face processing in social anxiety disorder: a systematic review with meta-analysis. *Neurosci Biobehav Rev* 2023;**152**:105283. https://doi.org/10.1016/j.neubiorev.2023.105283

Petro NM, Ott LR, Penhale SH *et al.* Eyes-closed versus eyes-open differences in spontaneous neural dynamics during development. *NeuroImage* 2022;**258**:119337. https://doi.org/10.1016/j.neuroimage.2022.119337

Petro NM, Tong TT, Henley DJ *et al.* Individual differences in valence bias: fMRI evidence of the initial negativity hypothesis. *Soc Cognit Affective Neurosci* 2018;**13**:687–98. https://doi.org/10.1093/scan/nsy049

Petro NM, Tottenham N, Neta M. Exploring valence bias as a metric for frontoamygdalar connectivity and depressive symptoms in childhood. *Dev. Psychobiol* **63**:2021;1–16. https://doi.org/10.1002/dev.22084

Pfurtscheller G, Klimesch W. Event-related synchronization and desynchronization of alpha and beta waves in a cognitive task. In: Başar E and Bullock TH (eds) *Induced Rhythms in the Brain*. Boston, MA: Birkhäuser, 1992, 117–28. https://doi.org/10.1007/978-1-4757-1281-0_6

Phelps EA, Ling S, Carrasco M. Emotion facilitates perception and potentiates the perceptual benefits of attention. *Psychol Sci* 2006;**17**:292–99. https://doi.org/10.1111/j.1467-9280.2006.01701.x

Picci G, Ott LR, Penhale SH *et al.* Developmental changes in endogenous testosterone have sexually-dimorphic effects on spontaneous cortical dynamics. *Human Brain Mapp* 2023;**44**:6043–54. https://doi.org/10.1002/hbm.26496

Pierce JE, Clancy E, Petro NM *et al.* Task-irrelevant emotional faces impact BOLD responses more for prosaccades than antisaccades in a mixed saccade fMRI task. *Neuropsychologia* 2022;**177**:108428. https://doi.org/10.1016/j.neuropsychologia.2022.108428

Pierce JE, Petro NM, Clancy E *et al.* Specialized late cingulo-opercular network activation elucidates the mechanisms underlying decisions about ambiguity. *NeuroImage* 2023;**279**:120314. https://doi.org/10.1016/j.neuroimage.2023.120314

Pitcher D, Garrido L, Walsh V *et al.* Transcranial magnetic stimulation disrupts the perception and embodiment of facial expressions. *J Neurosci* 2008;**28**:8929–33. https://doi.org/10.1523/JNEUROSCI.1450-08.2008

Poline J-B, Worsley KJ, Holmes AP *et al.* Estimating smoothness in statistical parametric maps: variability of p values. *J Comput Assist Tomogr* 1995;**19**:788. https://doi.org/10.1097/00004728-199509000-00017

Proskovec AL, Heinrichs-Graham E, Wilson TW. Aging modulates the oscillatory dynamics underlying successful working memory encoding and maintenance. *Human Brain Mapp* 2016;**37**:2348–61. https://doi.org/10.1002/hbm.23178

Proskovec AL, Heinrichs-Graham E, Wilson TW. Load modulates the alpha and beta oscillatory dynamics serving verbal working memory. *NeuroImage* 2019;**184**:256–65. https://doi.org/10.1016/j.neuroimage.2018.09.022

Puce A, Allison T, Bentin S *et al.* Temporal cortex activation in humans viewing eye and mouth movements. *J Neurosci* 1998;**18**:2188–99. https://doi.org/10.1523/JNEUROSCI.18-06-02188.1998

Rempe MP, Casagrande CC, Embury CM *et al.* Hippocampal and cortical oscillatory dynamics reflect semantic processing and predict behavioral performance. *J Physiol* 2025. https://doi.org/10.1113/JP287373

Rossion B, Caldara R, Seghier M *et al.* A network of occipito-temporal face-sensitive areas besides the right middle fusiform gyrus is necessary for normal face processing. *Brain* 2003;**126**:2381–95. https://doi.org/10.1093/brain/awg241

Rotshtein P, Vuilleumier P, Winston J *et al.* Distinct and convergent visual processing of high and low spatial-frequency information in faces. *Cerebral Cortex* 2007;**17**:2713–24. https://doi.org/10.1093/cercor/bhl180

Sabatinelli D, Fortune EE, Li Q *et al.* Emotional perception: meta-analyses of face and natural scene processing. *NeuroImage* 2011;**54**:2524–33. https://doi.org/10.1016/j.neuroimage.2010.10.011

Sato W, Kochiyama T, Uono S *et al.* Rapid amygdala gamma oscillations in response to fearful facial expressions. *Neuropsychologia* 2011;**49**:612–17. https://doi.org/10.1016/j.neuropsychologia.2010.12.025

Satpute AB, Mumford JA, Naliboff BD *et al.* Human anterior and posterior hippocampus respond distinctly to state and trait anxiety. *Emotion* 2012;**12**:58–68. https://doi.org/10.1037/a0026517

Schindler S, Bublatzky F. Attention and emotion: an integrative review of emotional face processing as a function of attention. *Cortex* 2020;**130**:362–86. https://doi.org/10.1016/j.cortex.2020.06.010

Schubring D, Schupp HT. Affective picture processing: alpha- and lower beta-band desynchronization reflects emotional arousal. *Psychophysiology* 2019;**56**:e13386. https://doi.org/10.1111/psyp.13386

Schubring D, Schupp HT. Emotion and brain oscillations: high arousal is associated with decreases in alpha- and lower beta-band power. *Cereb Cortex* 2021;**31**:1597–608. https://doi.org/10.1093/cercor/bhaa312

Schurz M, Radua J, Aichhorn M *et al.* Fractionating theory of mind: A meta-analysis of functional brain imaging studies. *Neurosci Biobehav Rev* 2014;**42**:9–34. https://doi.org/10.1016/j.neubiorev.2014.01.009

Scott LS, Arcaro MJ. A domain-relevant framework for the development of face processing. *Nature Reviews Psychology* 2023;**2**:183–95. https://doi.org/10.1038/s44159-023-00152-5

Sollfrank T, Kohnen O, Hilfiker P *et al.* The effects of dynamic and static emotional facial expressions of humans and their avatars on the EEG: an ERP And ERD/ERS study. *Front Neurosci* 2021;**15**. https://www.frontiersin.org/journals/neuroscience/articles/10.3389/fnins.2021.651044

Spreng RN, Stevens WD, Chamberlain JP *et al.* Default network activity, coupled with the frontoparietal control network, supports goal-directed cognition. *NeuroImage* 2010;**53**:303–17. https://doi.org/10.1016/j.neuroimage.2010.06.016

Springer SD, Okelberry HJ, Willett MP *et al.* Age-related alterations in the oscillatory dynamics serving verbal working memory processing. *Aging* 2023;**15**:14574–90. https://doi.org/10.18632/aging.205403

Sweeny TD, Suzuki S, Grabowecky M *et al.* Detecting and categorizing fleeting emotions in faces. *Emotion* 2013;**13**:76–91. https://doi.org/10.1037/a0029193

Takahashi HK, Kitada R, Sasaki AT *et al.* Brain networks of affective mentalizing revealed by the tear effect: the integrative role of the medial prefrontal cortex and precuneus. *Neurosci. Res* 2015;**101**:32–43. https://doi.org/10.1016/j.neures.2015.07.005

Tallon-Baudry C, Bertrand O. Oscillatory gamma activity in humans and its role in object representation. *Trends Cognit Sci* 1999;**3**:151–62. https://doi.org/10.1016/S1364-6613(99)01299-1

Tanaka JW, Farah MJ. Parts and wholes in face recognition. *Q J Exp Psychol-A* 1993;**46**:225–45. https://doi.org/10.1080/14640749308401045

Tanaka JW, Kaiser MD, Butler S *et al.* Mixed emotions: holistic and analytic perception of facial expressions. *Cognition & Emotion* 2012;**26**:961–77. https://doi.org/10.1080/02699931.2011.630933

Taulu S, Simola J. Spatiotemporal signal space separation method for rejecting nearby interference in MEG measurements. *Phys Med Biol* 2006;**51**:1759–68. https://doi.org/10.1088/0031-9155/51/7/008

Uhlhaas PJ, Pipa G, Lima B *et al.* Neural synchrony in cortical networks: history, concept and current status. *Front Integr Neurosci* 2009;**3**:17. https://doi.org/10.3389/neuro.07.017.2009

Uusberg A, Uibo H, Kreegipuu K *et al.* EEG alpha and cortical inhibition in affective attention. *Int J Psychophysiol* 2013;**89**:26–36. https://doi.org/10.1016/j.ijpsycho.2013.04.020

Uusitalo MA, Ilmoniemi RJ. Signal-space projection method for separating MEG or EEG into components. *Med Biol Eng Comput* 1997;**35**:135–40. https://doi.org/10.1007/BF02534144

Van Veen BD, van Drongelen W, Yuchtman M *et al.* Localization of brain electrical activity via linearly constrained minimum variance spatial filtering. *IEEE Trans Bio-Med Eng* 1997;**44**:867–80. https://doi.org/10.1109/10.623056

Vuilleumier P, Armony JL, Driver J *et al.* Effects of attention and emotion on face processing in the human brain: an event-related fMRI study. *Neuron* 2001;**30**:829–41. https://doi.org/10.1016/S0896-6273(01)00328-2

Weidner EM, Moratti S, Schindler S *et al.* Amygdala and cortical gamma-band responses to emotional faces are modulated by attention to valence. *Psychophysiology* 2024;**61**:e14512. https://doi.org/10.1111/psyp.14512

Wiesman AI, Heinrichs-Graham E, Proskovec AL *et al.* Oscillations during observations: dynamic oscillatory networks serving visuospatial attention. *Human Brain Mapp* 2017;**38**:5128–40. https://doi.org/10.1002/hbm.23720

Wiesman AI, O'Neill J, Mills MS *et al.* Aberrant occipital dynamics differentiate HIV-infected patients with and without cognitive impairment. *Brain* 2018;**141**:1678–1690. https://doi.org/10.1093/brain/awy097

Wiesman AI, Wilson TW. The impact of age and sex on the oscillatory dynamics of visuospatial processing. *NeuroImage* 2019;**185**:513–20. https://doi.org/10.1016/j.neuroimage.2018.10.036

Wilson TW. Noninvasive Neurophysiological Imaging with Magnetoencephalography. In: Xiong H and Gendelman HE (eds), *Current Laboratory Methods in Neuroscience Research*. New York, NY: Springer, 2014, 293–311. https://doi.org/10.1007/978-1-4614-8794-4_21

Wilson TW, Heinrichs-Graham E, Proskovec AL *et al.* Neuroimaging with magnetoencephalography: a dynamic view of brain pathophysiology. *Transl Res* 2016;**175**:17–36. https://doi.org/10.1016/j.trsl.2016.01.007

Wilson TW, McDermott TJ, Mills MS *et al.* tDCS modulates visual gamma oscillations and basal alpha activity in occipital cortices: evidence from MEG. *Cerebral Cortex* 2018;**28**:1597–609. https://doi.org/10.1093/cercor/bhx055

Worsley KJ, Marrett S, Neelin P *et al.* A unified statistical approach for determining significant signals in images of cerebral activation. *Human Brain Mapp* 1996;**4**:58–73. https://doi.org/10.1002/(SICI)1097-0193(1996)4:1<58::AID-HBM4>3.0.CO;2-O

Yeager BE, Bruss J, Duffau H *et al.* Central precuneus lesions are associated with impaired executive function. *Brain Struct Funct* 2022;**227**:3099–108. https://doi.org/10.1007/s00429-022-02556-0

Yordanova YN, Duffau H, Herbet G. Neural pathways subserving face-based mentalizing. *Brain Struct Funct* 2017;**222**:3087–105. https://doi.org/10.1007/s00429-017-1388-0

Zeidman P, Maguire EA. Anterior hippocampus: the anatomy of perception, imagination and episodic memory. *Nat Rev Neurosci* 2016;**17**:173–182 https://doi.org/10.1038/nrn.2015.24

Zeidman P, Mullally SL, Maguire EA. Constructing, perceiving, and maintaining scenes: hippocampal activity and connectivity. *Cereb Cortex* 2015;**25**:3836–55. https://doi.org/10.1093/cercor/bhu266

Zhang D, Wang L, Luo Y *et al.* Individual differences in detecting rapidly presented fearful faces. *PLOS ONE* 2012;**7**:e49517. https://doi.org/10.1371/journal.pone.0049517

Zouaoui I, Zellag M, Hernout J *et al.* Alpha and theta oscillations during the cognitive reappraisal of aversive pictures: a spatio-temporal qEEG investigation. *Int J Psychophysiol* 2023;**192**:13–25. https://doi.org/10.1016/j.ijpsycho.2023.07.001

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