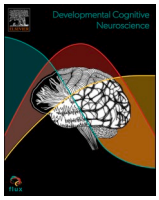
Developmental Cognitive Neuroscience 79 (2026) 101724

Contents lists available at ScienceDirect

Developmental Cognitive Neuroscience

journal homepage: www.elsevier.com/locate/dcn



Facial expression processing is modulated by face gender and anxiety levels in developing youth

Hua Bai [a,b], Yasra Arif [a,b], Jake J. Son [a,b,c], Nathan M. Petro [a,b], Grace C. Ende [a,b], Danielle L. Rice [a,b], Jason A. John [a,b], Anna T. Coutant [a,b], Erica L. Steiner [a,b], Ryan J. Glesinger [a,b], Hannah J. Okelberry [a,b], Brittany K. Taylor [a,b,d], Giorgia Picci [a,b,d], Tony W. Wilson [a,b,d,*]

[a] Institute for Human Neuroscience, Boys Town National Research Hospital, Boys Town, NE, USA
[b] Center for Pediatric Brain Health, Boys Town National Research Hospital, Boys Town, NE, USA
[c] College of Medicine, University of Nebraska Medical Center, Omaha, NE, USA
[d] Department of Pharmacology & Neuroscience, Creighton University School of Medicine, Omaha, NE, USA

ARTICLE INFO

Keywords:
Emotional expression
Happy
Angry
Magnetoencephalography
Sex Characteristics

ABSTRACT

Facial expressions are essential to social interactions, enabling individuals to infer emotional states and intentions of others. Although emotional face processing has been widely studied, the impact of face-gender on expression processing in children and adolescents remains underexplored. The current study quantified age-related changes in the neural oscillatory dynamics serving the processing of faces that vary in gender (female, male) and emotion (angry, happy, neutral) in 186 typically developing youths. Participants completed a gender identification task while viewing emotional faces during magnetoencephalographic imaging. Whole-brain, voxel-wise ANCOVAs were conducted to assess age × face-gender × expression interactions. Behaviorally, reaction times showed age-dependent differences for angry and neutral expressions, with the fastest responses to angry male faces and the slowest to angry female faces. Alpha/beta oscillatory responses differed by face gender in angry and happy conditions, with greater responses to expectancy-violating gender–emotion associations (angry female and happy male faces). Notably, age-related alpha/beta increases within the pre-supplementary motor area were linked to slower behavioral responses to angry male faces, suggesting enhanced inhibitory control over potentially threatening cues. In parallel, changes in gamma oscillations within social-cognitive hubs like the superior temporal gyrus, temporoparietal junction, and supramarginal gyrus supported integrative processing of complex or expectancy-violating expressions. Early alpha/beta responses were further modulated by self-reported anxiety, with higher-anxiety youth showing attentional avoidance to angry male faces. These findings demonstrate distinct functional roles of alpha/beta and gamma oscillations in the developmental tuning of social-cognitive processing and point to how anxiety may alter normative trajectories of face perception.

1. Introduction

Emotional face processing plays a vital role in children's social development, enabling them to decode intentions, infer mental states, and respond appropriately to others in dynamic environments (Burgoon, 1993; Tottenham et al., 2011). These abilities emerge early and are refined over time, supported by the maturation of specialized core and extended face processing networks through childhood and adolescence, allowing for increasingly nuanced interpretation of facial cues (Bayet et al., 2015; Duchaine and Yovel, 2015). Despite substantial evidence on the development of facial expression recognition, less is known about how facial gender interacts with emotional expression to shape these developmental trajectories.

Gender serves as a salient social cue that children quickly learn to interpret through both direct experience and cultural norms (Bem, 1981). By preschool, children prioritize gender over other facial attributes in face perception, with a female face preference evident in infancy, which may reflect a reliance on females as primary caregivers (Quinn et al., 2002). By late childhood, own-gender recognition advantages emerge, especially among girls, suggesting that social

* Corresponding author at: Institute for Human Neuroscience, Boys Town National Research Hospital, Boys Town, NE, USA.
E-mail address: tony.wilson@boystown.org (T.W. Wilson).

https://doi.org/10.1016/j.dcn.2026.101724
Received 9 October 2025; Received in revised form 23 February 2026; Accepted 7 April 2026
Available online 8 April 2026

identification, attentional biases, and/or greater exposure to female faces influence face perception during development (Ge et al., 2008; Rehnman and Herlitz, 2006). Longitudinal and cross-sectional work in older children and adolescents indicates that these patterns continue to be refined with age, and extend to adulthood, where women consistently exhibit own-gender biases in face recognition, while men show more variability (Herlitz and Lovén, 2013). These findings highlight that sex differences in face gender processing emerge early and are linked to differential processing strategies and developmental experience.

Emotion perception is similarly shaped by culturally reinforced gender-emotion associations, which children learn and apply over development. Anger is frequently associated with male faces and interpreted as signaling dominance or threat, while happiness is more commonly associated with female faces and emotional warmth (Harris and Ciaramitaro, 2016; Hess et al., 2009; Plant et al., 2004). Neutral expressions, although often used as control stimuli, are themselves socially ambiguous and may be perceived differently based on face gender, with male neutral faces being rated as more threatening or dominant and female neutral faces being interpreted more positively (Lee et al., 2008). When facial expressions violate these gender-based expectations (e.g., angry female, happy male), the resulting incongruency may be perceived as more socially complex or ambiguous, and prompt greater attentional resources (Burgoon, 1993; Hugenberg and Sczesny, 2006), particularly in children with maturing social-cognitive systems (Bayet et al., 2015). Theories of attention prioritization and motivational relevance support this and suggest that emotionally salient cues are prioritized when they signal potential threat, uncertainty, or social conflict (Maratos and Pessoa, 2019; Vuilleumier, 2005). Developmental neuroimaging and event-related potential (ERP) studies indicate that these violations may amplify early neural responses, with enhanced P1 and N170 ERP components observed for expectancy-violating faces in school-aged children, reflecting heightened perceptual and attentional processing (Liu et al., 2017; Valdés-Conroy et al., 2014). Alpha and beta responses are thought to index attentional gating and top-down control, with decreased alpha/beta oscillations reflecting a potential attentional suppression mechanism when processing task-irrelevant or socially salient cues, while gamma-band oscillations may reflect higher-order integration of social and contextual information (Bacigalupo and Luck, 2022; Foxe and Snyder, 2011; Fries, 2009). This spectrally-specific functional organization provides a mechanistic framework for understanding how developing brains allocate neural resources to expectancy-violating or norm-relevant stimuli, likely to facilitate learning and adaptive social behaviors.

These effects may be particularly pronounced in individuals with elevated anxiety, who exhibit attentional biases to threat and enhanced neural responses to socially complex stimuli, particularly angry faces (Bar-Haim et al., 2007). The hypervigilance–avoidance model proposes that anxious individuals initially over-attend to threat, followed by disengagement to reduce distress (Mogg and Bradley, 1999; Puliafico and Kendall, 2006). These effects may interact with gendered facial expressions, such that angry male faces, perceived as socially dominant or threatening, elicit stronger avoidance or attentional modulation in anxious youth, whereas angry female faces may demand more cognitive processing and evaluation due to expectancy violation. This aligns with pediatric behavioral and ERP evidence that anxiety amplifies the salience of socially ambiguous cues and biases interpretations toward threat (Mobach et al., 2022; Stuijfzand et al., 2018; Waters et al., 2014).

In the present study, we aim to address critical gaps in the field's understanding of emotional face processing in childhood by examining age-related changes in the neural processing of gendered emotional faces using magnetoencephalography (MEG), which offers the high spatiotemporal precision needed to detect and map neural oscillatory dynamics. Specifically, we hypothesized that expectancy-violating faces (e.g., angry female, happy male) would elicit slower and less accurate behavioral responses and that neural oscillatory responses would increase with age, reflecting enhanced attentional allocation and higher-order socio-cognitive processing. We also expected anxiety symptoms to modulate these developmental trajectories, particularly for socially salient or norm-violating gender–expression combinations.

2. Methods

2.1. Participants

A total of 186 healthy children and adolescents ($range_{age}$: 6–17 years; $M_{age} = 10.46$ years, $SD_{age} = 2.77$ years; 102 males) were enrolled in this study. All were recruited from the greater Omaha metropolitan area as part of the Developmental Multimodal Imaging of Neurocognitive Dynamics (Dev-MIND) study (R01-MH121101). Of the 186 participants, 155 identified as White, 24 as multiracial, five as Black/African American, one as Asian, and one did not report their race. This distribution corresponds closely to the racial demographics of the greater Omaha metropolitan area. Exclusion criteria included neurological or psychiatric disorders, history of head trauma, current substance use, and standard MEG/MRI exclusion criteria. Written assent and consent were obtained from the participants and their guardians. The Institutional Review Board approved the study.

2.2. MEG experimental paradigm and data acquisition

The task paradigm, MEG acquisition, and preprocessing procedures are identical to those reported in Bai et al. (2025). Briefly, participants completed a facial expression viewing task in the MEG, with three different expressions from 40 unique actors (aged 18–30 years), balanced by sex and race/ethnicity (White, Black/African American, Asian, and Hispanic), all derived from the RADIATE face dataset (Conley et al., 2018). The task consisted of 240 trials, divided into six conditions: two face-genders (male, female) × three expressions (neutral, angry, happy), with 40 trials per condition. Each trial began with a 1600 ± 100 ms fixation cross followed by a 1500 ms face display. Participants were instructed to classify the face as male or female using a button press, regardless of the facial expression. The task duration was approximately 13 minutes and was programmed using the Psychophysics Toolbox (Brainard, 1997) and presented using a PROPixx DLP projector (VPixx Technologies, Saint Bruno, Canada).

MEG data were recorded throughout the task using a two-layer VACOSHIELD magnetically shielded room and a 306-sensor MEGIN Neo MEG system (Helsinki, Finland) with 204 planar gradiometers and 102 magnetometers. Data were sampled at 1 kHz with an acquisition bandwidth of 0.1–330 Hz. Head movement and noise were removed using the signal space separation method with a temporal extension (Taulu et al., 2005; Taulu and Simola, 2006). Only data from the 204 planar gradiometers were used in analyses.

2.3. MRI acquisition and MEG-MRI coregistration

Head-position indicator (HPI) coils were attached to each participant's head and localized with a 3D FASTRAK digitizer (Polhemus, Colchester, VT, USA). Coil locations were measured with respect to three fiducial points and the scalp surface, allowing for co-registration of MEG data with structural MRI. High-resolution structural MRI data were acquired using a 3 T Siemens Prisma magnet with a 32-channel head coil. Imaging parameters included a TR of 2400 ms, TE of 2.05 ms, slice thickness of 1 mm, and voxel size of 1.0 × 1.0 × 1.0 mm. After co-registration, functional MEG data were transformed into standardized space using the transform that was previously applied to the structural MRI.

2.4. MEG data preprocessing

The continuous MEG data were epoched into 3000 ms segments (−1500 to 1500 ms) with a −400 to 0 ms baseline. Artifacts from cardiac

and ocular activity were removed using signal-space projection (SSP; Uusitalo and Ilmoniemi, 1997), and a 60 Hz notch filter minimized line noise. Remaining artifacts were removed using a fixed threshold method tailored to each participant, based on amplitude and gradient distributions across trials. This approach accounted for individual differences in head size, sensor distance, and other factors influencing signal amplitude. Based on individual distributions, thresholds were set to reject trials with the highest amplitude and/or gradient values per participant. Following artifact rejection, participants with technical issues or lower than 60% accepted trials were excluded, and an average of 220.96 trials (SD = 13.76, min = 171, max = 240) per participant were available for subsequent analyses. Across participants, the average number of accepted trials per condition was as follows: angry female face: M = 33.83, SD = 3.26; angry male face: M = 35.36, SD = 2.67; happy female face: M = 34.36, SD = 2.80; happy male face: M = 35.45, SD = 2.50; neutral female face: M = 34.38, SD = 2.69; neutral male face: M = 35.09, SD = 2.61.

To test for equal trial distribution, a repeated-measures ANCOVA (age × face gender × expression) was conducted. Results showed significant effects of age ($F(1, 149) = 22.09$, $p < .001$, $\eta p^2 = 0.13$) and face gender ($F(1, 149) = 8.63$, $p = .004$, $\eta p^2 = 0.06$). Older participants had more accepted trials overall, and male faces yielded more accepted trials than female faces. Since the number of trials can affect the signal-to-noise ratio (SNR) and thus bias developmental effects, we covaried out the square root of the number of trials per person in all functional mapping analyses (Pulliam et al., 2024). The residual maps of neural activity were used for subsequent whole-brain analysis.

2.5. Sensor level statistics

The remaining artifact-free epochs were transformed into the time-frequency domain using complex demodulation with a time-frequency resolution of 1 Hz by 50 ms (Kovach and Gander, 2016). These spectral power estimates were normalized to the baseline power per frequency bin using the −400 to 0 ms window and then averaged across trials. A data-driven approach was used to identify the time-frequency windows for beamforming, with paired-sample t-tests across all participants and conditions performed on the spectrogram pixels across the array. Significant pixels were clustered and corrected for multiple comparisons using a nonparametric permutation testing approach with 10,000 iterations (Ernst, 2004; Maris and Oostenveld, 2007; Wiesman and Wilson, 2020).

2.6. MEG source imaging and statistics

For each significant time-frequency window, cortical oscillatory responses were imaged using the dynamic imaging of coherent sources (DICS) beamformer (Gross et al., 2001; Van Veen et al., 1997). The cross-spectral densities of MEG gradiometers were averaged over the time-frequency range of interest and used to generate voxel-wise estimates of neural power by isolating signals from specific brain regions while suppressing noise from other areas. The resulting source power images were normalized using a pre-stimulus baseline (Hillebrand et al., 2005). Images were generated for each face-gender × expression condition (angry female, angry male, happy female, happy male, neutral female, neutral male) and included in subsequent statistical analyses.

2.7. Anxiety assessment

Participants' anxiety symptoms were assessed using the Behavioral Assessment System for Children (BASC-3; Reynolds and Kamphaus, 2015), a standardized measure for evaluating behavioral and emotional functioning in children (ages 8–11 years) and adolescents (ages 12–21 years). Participants rated items on a 4-point scale (0 = never, 1 = sometimes, 2 = often, 3 = almost always), with higher scores indicating greater levels of anxiety. The BASC-3 demonstrates strong psychometric properties, including internal consistency ranging from 0.92 to 0.97, test-retest reliability from r = .87–.94, and strong concurrent validity with well-established assessments (Reynolds and Kamphaus, 2015). Given the developmental focus of the present study, raw scores from the anxiety subscale were used in all statistical models.

2.8. Statistical analyses

2.8.1. Whole-brain analysis

To examine developmental differences in neural oscillatory power during the processing of gendered facial expressions, a whole-brain repeated-measures ANCOVA was conducted in MATLAB (R2018b) using a [2 (face gender) × 3 (expression) × age] model, with participant sex included as a covariate to control for potential own-gender biases or female advantages in face perception. To further check the statistical assumptions for including participant sex as a covariate of no interest, we examined whether age differed between sexes and whether the association between age and the primary behavioral and neural outcome measures differed by sex (i.e., homogeneity of regression). Results showed no significant sex difference in age distribution and no significant age-by-sex interactions for any outcome measure (all ps >.05), indicating unbiased age distributions and parallel age slopes across sexes.

To correct for multiple comparisons, we applied a stringent significance threshold of $p < .005$, with a minimum cluster size of 8 contiguous voxels to ensure robust findings. To further probe significant three-way interactions (face gender × expression × age), pseudo-t values were extracted from significant cluster peaks (all ps <.005), and post hoc tests were performed using SPSS (Version 29) to clarify which gendered expressions showed robust age-related changes and how these developmental patterns differed by face gender. Finally, we conducted sensitivity analyses using the whole-brain models described above with the original pseudo-t maps, without covarying out SNR, to test whether including the square root of the number of trials as a covariate meaningfully altered the functional neural patterns (see "*MEG data preprocessing*").

2.8.2. Neurobehavioral moderation and mediation

Moderation and mediation models were conducted in R Studio (Version 4.4.2) using the *lavaan* package to test whether neural oscillatory responses modulated age-related changes in reaction time. Only face-gender × expression conditions (e.g., angry male faces) showing significant age effects in post-hoc analyses were tested. Moderation models examined whether neural oscillatory activity modified the strength or direction of the age–reaction time relationship, while mediation models assessed whether task-related neural activity explained the age-related improvement in response times. All models included participant sex as a covariate and used bias-corrected 95% confidence intervals with 10,000 bootstrapping iterations. A multiple comparison correction was applied within each frequency band of the identified conditions using the false discovery rate (FDR).

2.8.3. Moderation effects of self-reported anxiety

To examine whether anxiety symptoms modulate developmental changes in neural responses to gendered emotional faces, we extended post hoc models that had identified significant age × face-gender interactions. Specifically, for expressions showing a significant age × face-gender effect, we added an age × face-gender × anxiety term in a linear mixed-effects model using R Studio (Version 4.4.2), controlling for participant sex. This approach allowed us to test whether anxiety altered age-related trajectories of neural responses to female versus male faces within specific emotional conditions. For expressions with significant three-way interactions, simple slopes were probed at low (−1 SD), mean, and high (+1 SD) anxiety levels to visualize how age-related changes in neural activity varied across anxiety. Anxiety symptoms, assessed using the BASC-3, were approximately normally distributed

(skewness = 0.59, kurtosis = 2.96) and were mean-centered prior to inclusion in all models. Multiple comparisons within each expression (angry, happy, neutral) were FDR-corrected.

3. Results

3.1. Demographic and behavioral analyses

Following initial preprocessing, 149 participants remained (M_{age} = 10.06 years, SD_{age} = 2.65 years; 80 males). Thirty-seven participants were excluded due to poor task performance, excessive MEG noise, and/or technical issues. Demographics and descriptive statistics for measures of interest in the final sample after exclusions are detailed in Table 1. Repeated-measures ANCOVAs were conducted using SPSS (Version 29) on reaction time (RT) and accuracy, with face gender (male, female) and expression (angry, happy, neutral) as within-subjects factors, age as a continuous covariate, and participant sex as a covariate of no interest. A significant three-way interaction was found for RT ($F(2, 290) = 10.64$, $p < .001$, $\eta_p^2 = 0.07$), with age-dependent differences in responses to gendered facial expressions in the angry ($F(1, 145) = 11.06$, $p = .001$, $\eta_p^2 = 0.07$) and neutral ($F(1, 145) = 5.46$, $p = .021$, $\eta_p^2 = 0.04$) conditions, but not the happy condition **(**Fig. 1**B).** Post-hoc comparisons indicated that participants, irrespective of age, responded significantly faster to male than female faces in the angry condition ($F(1, 145) = 21.14$, $p < .001$, $\eta_p^2 = 0.13$), with angry male faces being processed the quickest and angry female faces being the slowest across all conditions. No significant three-way interaction was observed for accuracy, but the two-way age-by-face-gender interaction was present ($F(1, 137) = 8.06$, $p = .005$, $\eta_p^2 = 0.06$), with higher accuracy for male faces and a steeper age-related increase for female faces (Fig. 1**C).**

Table 1
Demographic and Descriptive Statistics of the Final and Subset Samples.

	Final Sample	Anxiety Subset
	n (%)	**n (%)**
n	149	107
sex, males	80 (53.69)	57 (53.27)
Race		
Caucasian/White	123 (82.55)	89 (83.18)
African American/Black	4 (2.68)	3 (2.80)
Asian	1 (0.67)	1 (0.93)
More than one race	20 (13.42)	14 (13.08)
Not reported	1 (0.67)	0
Ethnicity		
Hispanic	7 (4.70)	5 (4.67)
Non-Hispanic	142 (95.30)	102 (95.33)
	Mean (SD), range	**Mean (SD), range**
Age (years)	10.06 (2.65), 6.02–15.29	11.33 (2.10), 8.01–15.29
Reaction Time (ms)		
Angry female faces	880.71 (165.52), 539.14–1315.41	-
Angry male faces	836.86 (143.28), 397.34–1179.03	-
Happy female faces	859.48 (147.05), 491.62–1190.86	-
Happy male faces	840.71 (143.75), 555.15–1228.61	-
Neutral female faces	854.58 (147.09), 520.65–1215.28	-
Neutral male faces	853.92 (157.99), 410.24–1252.27	-
Self-reported Anxiety	-	11.24 (6.79), 0.00–34.00

Note. The final sample (n = 149) includes the remaining participants after MEG preprocessing exclusions. The anxiety subset sample (n = 107) includes participants with available self-reported anxiety data. Values are presented as *n* (%) for categorical variables and mean (SD), range for continuous variables. Reported values for anxiety are based on raw scores from the self-report Behavioral Assessment System for Children (BASC-3), which was completed by those eight years-old and older.

3.2. MEG sensor-level analysis

Statistical analysis of time-frequency spectrograms revealed significant alpha/beta (11–20 Hz) and gamma (64–84 Hz) activity in sensors near occipital and parietal regions across all conditions ($ps < .001$, corrected; Fig. 2). Specifically, we observed a strong decrease in oscillatory power relative to the baseline in the alpha/beta frequency range from 150 to 750 ms, which was imaged as two non-overlapping time-frequency windows of interest (i.e., early: 150–450 ms, late: 450–750 ms). Within the gamma frequency band, there was a strong increase in oscillatory power relative to baseline between 500 and 800 ms.

3.3. Dynamic functional mapping analyses

3.3.1. Age × face gender × expression interactions in alpha/beta oscillations

Whole-brain ANCOVAs of early alpha/beta oscillations revealed significant three-way interactions in the left pre-supplementary motor area (Fig. 3**A**; pre-SMA; $F(2, 248) = 7.60$, $p < .001$, $\eta_p^2 = 0.06$), left lateral occipital cortex (LOC; $F(2, 248) = 7.62$, $p < .001$, $\eta_p^2 = 0.06$), left inferior occipital cortex (IOC; $F(2, 248) = 7.60$, $p < .001$, $\eta_p^2 = 0.06$), and the left cerebellum ($F(2, 248) = 7.54$, $p < .001$, $\eta_p^2 = 0.06$). To unpack these interactions, we examined age-related slopes for each gender–expression pair (e.g., angry male faces) and decomposed the three-way interactions into two-way age-by-face-gender interactions within each expression condition (e.g., age × face gender in the angry condition).

In the left pre-SMA, early alpha/beta oscillations became stronger (i.e., more negative relative to baseline) with age to angry male faces (b = –0.49, t = –2.37, p = .019) and this differed from age-related changes in responses to female faces (for both angry ($F(1, 124) = 6.41$, $p = .013$, $\eta_p^2 = 0.05$) and neutral ($F(1, 124) = 4.40$, $p = .038$, $\eta_p^2 = 0.04$) expressions. In the left LOC, early alpha/beta responses became stronger with increasing age for angry female (b = –0.72, t = –2.30, p = .023), happy male (b = –0.87, t = –3.09, p = .002), and neutral male faces (b = –0.74, t = –2.52, p = .013), with significant age × face-gender interactions in angry ($F(1, 124) = 8.34$, $p = .005$, $\eta_p^2 = 0.06$) and happy ($F(1, 124) = 6.69$, $p = .011$, $\eta_p^2 = 0.05$) conditions. Similar patterns were observed in the left IOC, where early alpha/beta responses became stronger with age to angry female (b = –0.70, t = –2.04, p = .043) and happy male faces (b = –0.79, t = –2.65, p = .009), with significant age × face-gender interactions in angry ($F(1, 124) = 9.78$, $p = .002$, $\eta_p^2 = 0.07$) and happy ($F(1, 124) = 5.94$, $p = .016$, $\eta_p^2 = 0.05$) conditions. In the left cerebellum, early alpha/beta oscillatory responses increased with age to happy male faces (b = –0.85, t = –3.66, $p < .001$) and significantly differed from happy female faces ($F(1, 124) = 17.57$, $p < .001$, $\eta_p^2 = 0.12$).

During the late alpha/beta window, a sustained three-way interaction was identified in the left pre-SMA (Fig. 3**B**; $F(2, 242) = 6.23$, $p = .002$, $\eta_p^2 = 0.05$). Alpha/beta responses became stronger with age for angry male faces (b = –1.74, t = –3.32, p = .001) and significantly differed from angry female faces ($F(1, 121) = 6.31$, $p = .013$, $\eta_p^2 = 0.05$). In contrast, responses to neutral male faces weakened with age (b = 0.68, t = 2.00, p = .047).

Finally, our sensitivity analyses using the raw MEG images (i.e., those without SNR regressed out) showed that, across early and late alpha/beta windows, the same regions remained significant at the original threshold ($p < .005$, $k \geq 8$). These analyses support that the reported developmental effects are not driven by systematic differences in trial numbers, nor dependent on the inclusion of SNR as a covariate in our primary analyses.

3.3.2. Age × face gender × expression interactions in gamma oscillations

Whole-brain ANCOVAs on gamma activity revealed significant

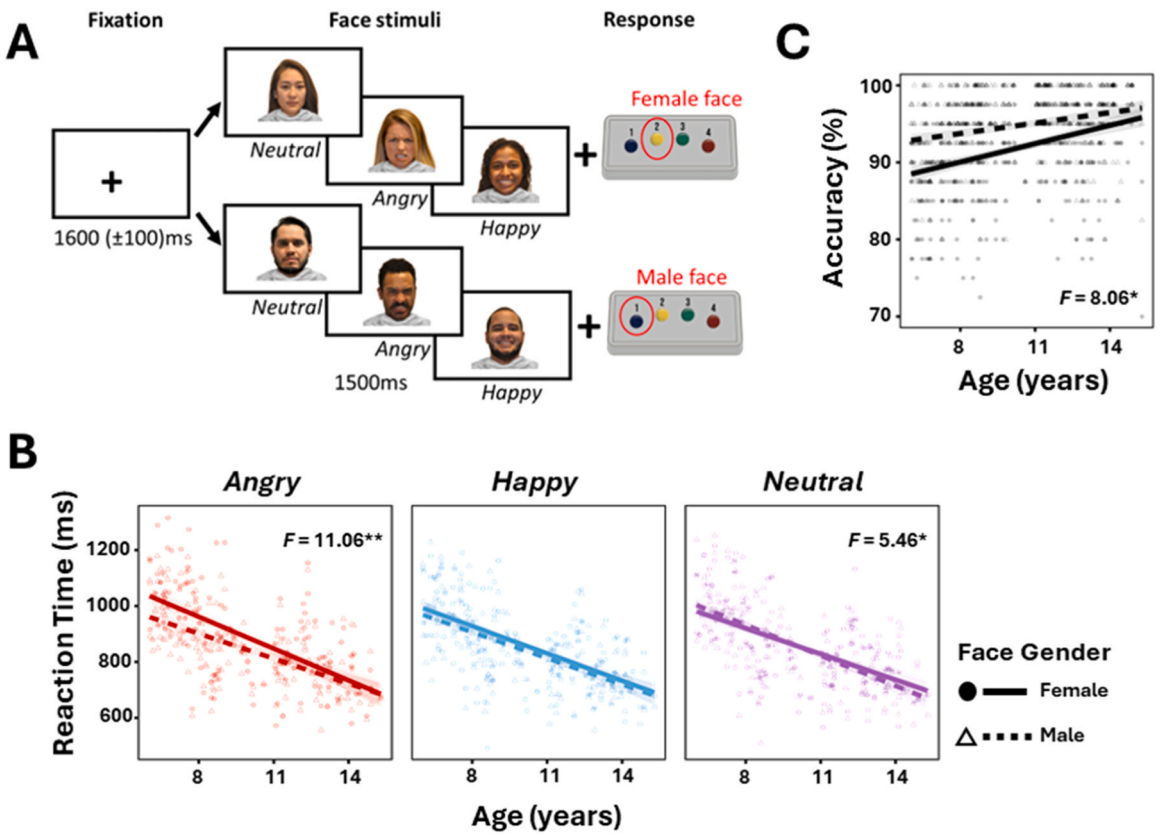


Fig. 1. Task paradigm and behavioral performance. A: MEG facial expression viewing task. The final sample consisted of 149 healthy youth (M_{age} = 10.06 years, SD_{age} = 2.65 years; 80 males) who viewed emotional expressions (i.e., angry, happy, neutral) presented on a screen. Participants were instructed to respond to the gender of the stimulus. All face stimuli were taken from the RADIATE dataset, with consent from all actors to use their photographs for research and scientific purposes (Conley et al., 2018). **B:** Reaction time as a function of age across gendered emotional expressions. Scatterplots with regression lines illustrate significant age-by-face-gender interactions for angry (red) and neutral (purple) but not happy expressions (blue). Reaction time (ms) is displayed on the y-axis and age (years) on the x-axis. **C:** Accuracy as a function of age on face gender. Scatterplots with regression lines illustrate a significant interaction between age and face gender. Accuracy (%) is plotted on the y-axis and age (years) on the x-axis. Solid lines represent female faces, while dashed lines represent male faces. *$p < .05$, **$p < .005$.

three-way interactions in the left supramarginal gyrus (Fig. 4; SMG; $F(2, 254) = 7.59$, $p < .001$, $\eta_p^2 = 0.06$), left temporoparietal junction (TPJ; $F(2, 254) = 6.21$, $p = .002$, $\eta_p^2 = 0.05$), left superior temporal gyrus (STG; $F(2, 254) = 6.32$, $p = .002$, $\eta_p^2 = 0.05$), and right inferior occipital cortex (IOC; $F(2, 254) = 8.40$, $p < .001$, $\eta_p^2 = 0.06$).

In the left SMG, gamma power increased with age for angry female ($b = 0.49$, $t = 2.67$, $p = .009$) and happy male faces ($b = 0.48$, $t = 3.49$, $p < .001$), with significant age × face-gender interactions in the happy condition ($F(1, 127) = 12.75$, $p < .001$, $\eta_p^2 = 0.09$). In the left TPJ, age was associated with increased gamma responses for angry female ($b = 0.47$, $t = 3.61$, $p < .001$) and neutral male faces ($b = 0.35$, $t = 3.24$, $p = .002$), with significant age × face-gender differences in the angry condition ($F(1, 127) = 9.83$, $p = .002$, $\eta_p^2 = 0.07$). In the left STG, gamma oscillations became stronger with age in response to angry female ($b = 0.38$, $t = 2.27$, $p = .025$) and neutral female faces ($b = 0.49$, $t = 2.80$, $p = .006$), with significant age × face-gender differences in happy ($F(1, 127) = 4.46$, $p = .037$, $\eta_p^2 = 0.03$) and neutral ($F(1, 127) = 7.35$, $p = .008$, $\eta_p^2 = 0.06$) conditions. In theright IOC, gamma power increased with age for happy female faces ($b = 0.31$, $t = 2.30$, $p = .023$) and neutral male faces ($b = 0.31$, $t = 2.67$, $p = .025$), but decreased for happy male faces ($b = –0.42$, $t = –2.47$, $p = .015$), with significant age-related face-gender differences only for happy faces ($F(1, 127) = 10.71$, $p = .001$, $\eta_p^2 = 0.08$).

Again, we conducted sensitivity analyses using the original pseudo-t functional maps without covarying out SNR. The results indicated that the left SMG, TPJ, and right IOC remained significant at the original threshold ($p < .005$, $k \geq 8$), while the left STG remained significant at the same p-threshold but its cluster size shrank ($k = 4$). These findings suggest that these gamma findings were not driven by systematic differences in trial numbers or inclusion of SNR as a covariate.

3.3.3. *Brain–behavior relationships*

Alpha/beta oscillations in the left pre-SMA significantly moderated the relationship between age and behavioral performance during angry male face processing in both the early ($b = −1.63$, $SE = 0.57$, 95% CI [−2.87, −0.62], $p_{uncorrect} = .004$, $p_{FDR} = .028$) and late ($b = −1.98$, $SE = 0.61$, 95% CI [−3.37, −0.94], $p_{uncorrect} = .001$, $p_{FDR} = .002$) alpha/beta windows. Because the moderation effects were consistently observed across windows, alpha/beta response power was averaged across early and late windows to simplify interpretation and visualization. The averaged alpha/beta response strength significantly moderated the association between age and RT to angry male faces ($b = −0.92$, $SE = 0.34$, 95% CI [−1.58, −0.25], $p = .006$). Simple slope analysis revealed that age was significantly associated with RT for angry male faces at stronger (−1 SD; $b = −20.07$, $SE = 5.75$, $p < .001$), mean ($b = −31.58$, $SE = 3.92$, $p < .001$), and weaker (+1 SD; $b = −43.08$, $SE = 5.75$, $p < .001$) levels of averaged left pre-SMA alpha/beta oscillatory activity. Faster response times with increasing age were observed across all levels, but the effect was strongest for participants with weaker alpha/beta responses in the pre-SMA, as indicated by the steepest slope in the + 1 SD group (Fig. 5**A**).

Exploratory mediation analyses revealed that gamma responses in the left TPJ significantly mediated the relationship between age and RT on angry female face processing (Fig. 5**B**; ab = −0.07, SE = 0.04, 95% CI

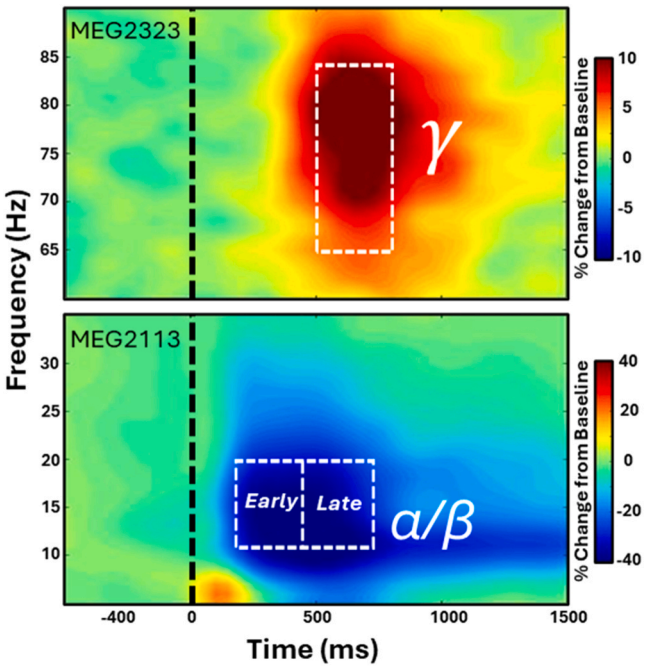


Fig. 2. Sensor-level neural responses. Time-frequency spectrograms from near the posterior parietal cortex revealed robust changes in alpha/beta (11–20 Hz; early: 150–450 ms, late: 450–750 ms) and gamma (64–84 Hz, 500–800 ms) power relative to the baseline period. Time (ms) is shown on the x-axis and frequency (Hz) on the y-axis. The vertical black dotted line represents the onset of the face stimuli at 0 ms. The spectrogram is scaled as a percentage change from the baseline, with the color scale bar per spectrogram to the right.

[−0.15, −0.01], $p_{uncorrect}$ =.038, p_{FDR} =.26). The direct effect of age on RT remained robust (c' = −0.50, SE = 0.07, 95% CI [−0.64, −0.36], $p < .001$), with a total effect of −0.57 (SE = 0.06, 95% CI [−0.69, −0.44], $p < .001$). However, the indirect effect did not survive correction for multiple comparisons and was reported here for transparency.

3.3.4. Age-related alpha/beta responses to gendered expressions vary by anxiety level

Among the 149 participants included in the whole-brain analysis, 107 youth aged eight years and above had BASC-3 anxiety scores and were included in these follow-up anxiety analyses, which were restricted to expressions showing a significant age × face-gender interaction in the whole-brain post-hoc tests. Note that the self-report version of BASC-3 was designed to assess those eight years old and older. In the early alpha/beta window, a significant age × face-gender × anxiety interaction emerged in the LOC during angry face processing (b = 0.17, SE = 0.06, 95% CI [0.05, 0.29], $t(88)$ = 2.67, $p_{uncorrect}$ = .009, p_{FDR} = .024). Simple slope analyses revealed that alpha/beta oscillatory responses to angry female faces increased across anxiety levels, whereas youth with high anxiety showed weaker alpha/beta oscillatory responses to angry male faces with age (Fig. 5C; b = 1.44, SE = 0.66, p = .03). An additional three-way interaction in the left cerebellum during happy face processing did not survive FDR correction (b = –0.14, SE = 0.06, 95% CI [0.05, 0.29], $t(88)$ = –2.03, $p_{uncorrect}$ = .046, p_{FDR} = .14) and was reported for transparency only.

4. Discussion

The present study examined developmental changes in the neural oscillatory dynamics underlying the processing of gendered emotional faces, including angry, happy, and neutral expressions. Our findings reveal a two-stage, distinct functional pattern of alpha/beta and gamma oscillations. Alpha/beta activity appears to support attentional engagement and sensory prioritization, whereas gamma activity may index higher-order social-cognitive integration. Importantly, the alpha/beta dynamics in visual attention processing were influenced not only by age but also by individual differences in anxiety symptoms, highlighting potential divergence from normative developmental trajectories in children with heightened threat sensitivity. At the behavioral level, children showed age-related differentiation in reaction times for angry and neutral expressions, with angry male faces being processed most quickly and angry female faces most slowly. This pattern suggests enhanced sensitivity to socially salient or expectancy-violating expressions across development, aligning with prior evidence that culturally shaped gender–emotion associations may guide attentional allocation and influence behavioral responses (Bayet et al., 2015; Plant et al., 2004).

Whole-brain oscillatory analyses revealed spectral- and region-specific developmental effects. In the alpha/beta range, the strength of neural oscillations increased with age in visual-perceptual (LOC, IOC) and sensorimotor-control regions (cerebellum, pre-SMA), consistent with early attentional engagement and preparation for adaptive responses. In LOC and IOC, these stronger early responses to angry female and happy male faces likely reflect greater perceptual sensitivity to gender-norm incongruence, enabling children to allocate attentional resources efficiently to socially salient cues (Freeman et al., 2010; Maratos and Pessoa, 2019). Within sensorimotor-control regions, the cerebellum exhibited stronger early alpha/beta responses to happy male faces, while in the pre-SMA, such activity was sustained in response to angry male faces across early and late windows. The cerebellum has traditionally been linked to motor coordination, but is increasingly implicated in social cognition and emotional evaluation, particularly in timing and error prediction (Schmahmann, 2019; Van Overwalle, 2009). The pre-SMA, through its anatomic and functional links to limbic cortex and prefrontal areas, potentially serves as the neural pathway by which emotions engage and influence the process of motor planning during face processing (Nachev et al., 2008). Experimental evidence from repetitive transcranial magnetic stimulation further demonstrates that inhibition of the pre-SMA enhances the perceived emotional valence of threatening visual stimuli, supporting its role in top-down inhibitory control (Rodigari and Oliveri, 2014). Thus, the observed relationship between stronger alpha/beta oscillatory activity in the pre-SMA and slower reaction time to angry male faces with age suggests that older children may increasingly recruit inhibitory control circuitry to regulate responses to threatening cues. These patterns are consistent with alpha/beta responses supporting context-dependent top-down gating of sensory and motor systems during socially relevant processing (Foxe et al., 1998; Mazaheri and Jensen, 2010).

Complementing these alpha/beta patterns, gamma oscillations exhibited age-related increases in higher-order regions crucial for integrating social-affective information, including the TPJ, STG, and SMG, particularly for angry female faces. These regions are key nodes of the social brain implicated broadly in affective processing, including theory of mind, perspective-taking, and conflict resolution (Van Overwalle, 2009). Age-related gamma increases suggest that resolving norm-violating expressions or complex social signals requires integrative processing in these networks, which may help explain why children responded more slowly to angry female faces compared with angry male faces. These findings converge with ventral attention network models, where unexpected or incongruent social cues recruit the TPJ and STG to support stimulus-driven reorienting (Corbetta and Shulman, 2002). Preliminary mediation analyses provided tentative evidence that gamma activity in the TPJ may facilitate more efficient behavioral responses to angry female face processing, though this effect did not survive our stringent correction for multiple comparisons. We also observed stronger gamma oscillations in the TPJ for neutral male faces and in the STG for neutral female faces. The absence of a consistent gender-specific pattern for neutral faces may reflect the inherently ambiguous nature of

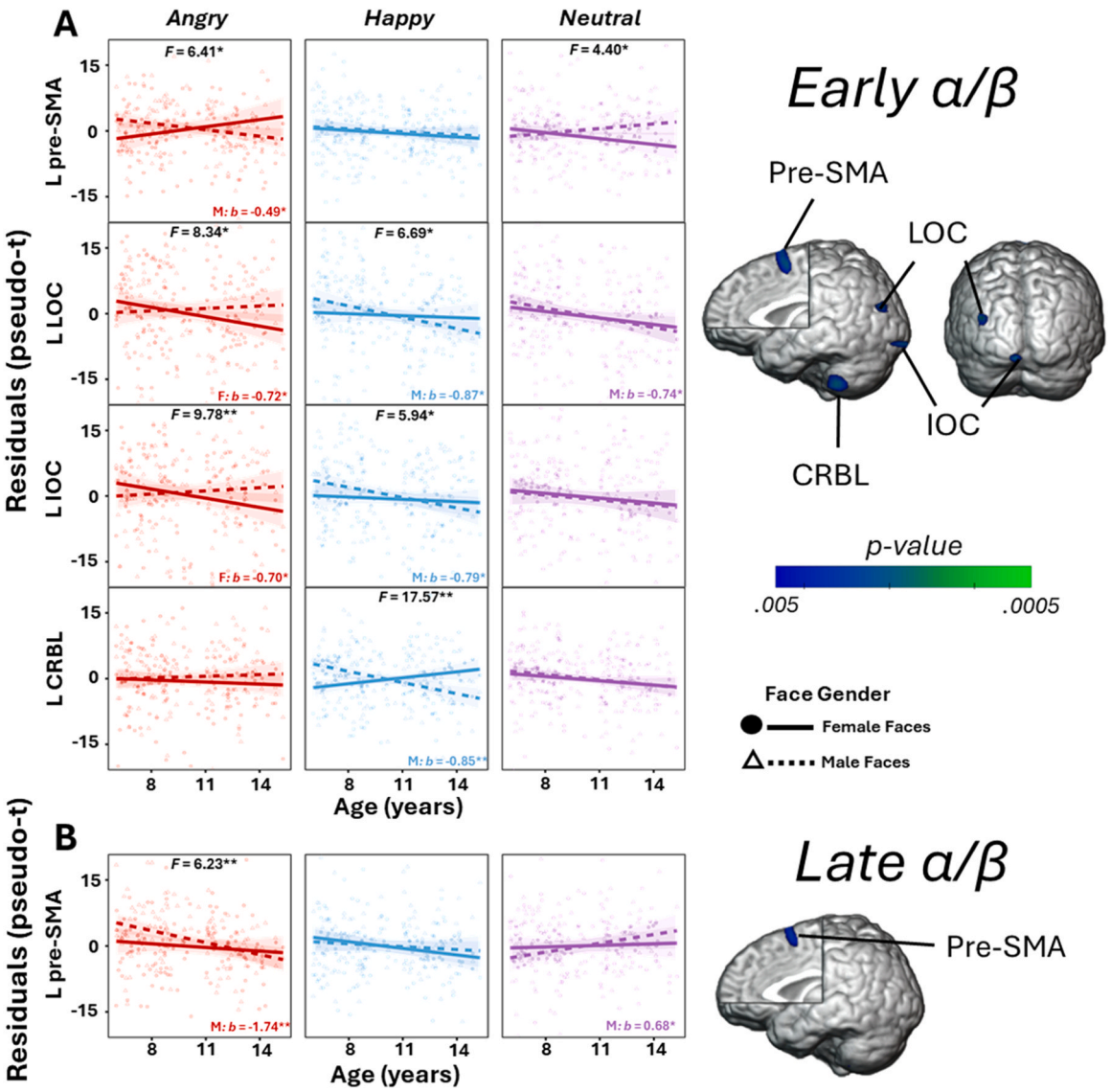


Fig. 3. Age × Face Gender × Expression interactions in early and late alpha/beta oscillatory dynamics. Whole-brain statistical maps display significant clusters showing three-way interactions between age, face gender, and expression during the early (A) and late (B) alpha/beta time windows. Scatterplots illustrate age-related changes in early alpha oscillatory activity for each facial expression (angry: red, happy: blue, neutral: purple), differing by facial gender (female: solid lines; male: dashed lines) across regions including the left pre-supplementary motor area (pre-SMA), lateral occipital cortex (LOC), inferior occipital cortex (IOC), and cerebellum (CRBL). Post hoc analyses are annotated with F values for significant two-way age × face gender interactions and unstandardized beta coefficients for significant age-related slopes. Shaded areas represent standard errors. Pseudo-t values with the number of trials per condition regressed out are displayed on the y-axis and age (years) on the x-axis. A common y-axis scale was applied across regions for visualization; all data were included in the statistical models, and plotted slopes accurately represent the tested interactions. F = female faces; M = male faces. *$p < .05$, **$p < .005$.

these expressions, which is not strongly modulated by facial gender. Overall, these findings are consistent with predictive coding frameworks, in which gamma activity facilitates bottom-up integration and prediction error signaling, complementing alpha/beta-mediated top--down attentional control (Bastos et al., 2012; Fries, 2009).

We also found that anxiety modulated early alpha/beta responses to gendered facial expressions in the left LOC, consistent with hypervigilance-avoidance models (Bar-Haim et al., 2007; Puliafico and Kendall, 2006). Youth with higher anxiety showed weaker alpha/beta oscillations to angry male faces, suggesting attentional suppression or avoidance of potentially threatening cues, while responses to angry female faces increased consistently across anxiety levels (Bacigalupo and Luck, 2022; Hess et al., 2009). These patterns indicate that anxious youth may diverge from normative trajectories by showing exaggerated early-stage attentional responses to potentially threatening cues. Such biases may influence subsequent social interpretation and regulation and contribute to the interpersonal difficulties and emotional dysregulation commonly observed in pediatric anxiety (Brotman et al., 2017).

Taken together, our findings of two-stage, complementary neural processing of gendered emotional faces align with prior work on the functional specialization of neural oscillations. Early alpha/beta activity supports perceptual prioritization and attentional gating, allowing children to detect and evaluate socially salient or expectancy-incongruent expressions, while gamma oscillations reflect integrative processes in higher-order social-cognitive hubs, supporting interpretation and evaluation of complex social signals. Developmental increases in the strength of these oscillatory responses correspond to more efficient behavioral responses, particularly for expectancy-incongruent expressions. Further, anxiety appears to modulate early-stage processing, potentially influencing the amplification and trajectory of downstream higher-order processing of social-affective information, which has implications for social-emotional development.

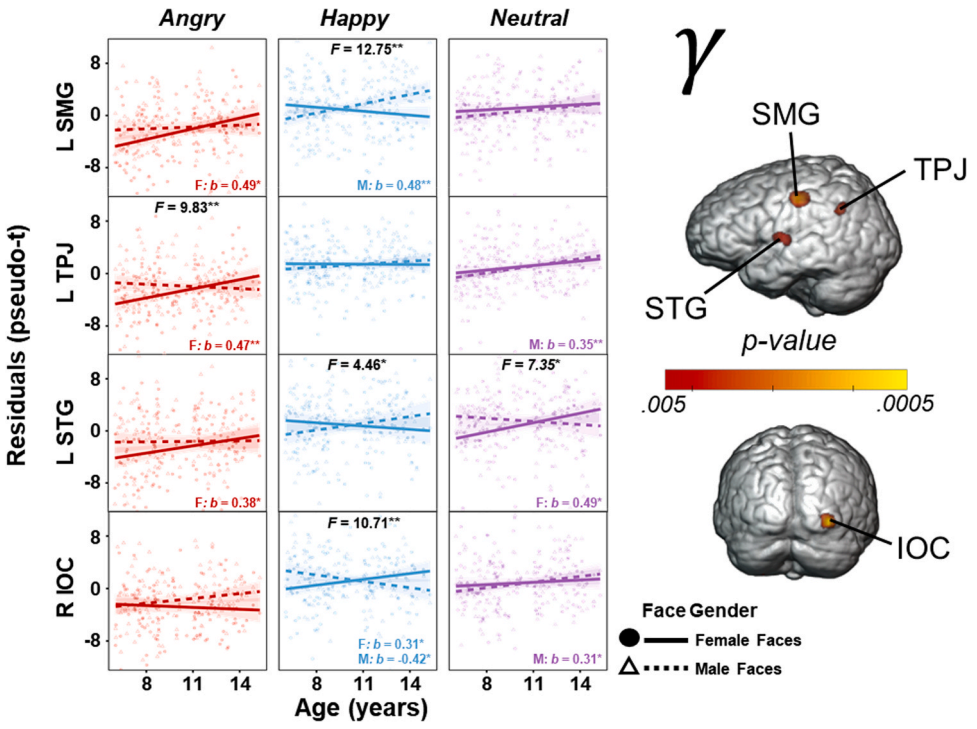


Fig. 4. Age × Face Gender × Expression interactions in gamma oscillatory dynamics. Whole-brain statistical maps display significant clusters showing three-way interactions among age, face gender, and expression in the gamma frequency window. Scatterplots illustrate age-related changes in gamma oscillatory power for each facial expression (angry: red; happy: blue; neutral: purple), differing by face gender (female: solid lines; male: dashed lines) across the left supramarginal gyrus (SMG), left temporoparietal junction (TPJ), left superior temporal gyrus (STG), and right inferior occipital cortex (IOC). Post hoc analyses are annotated with F values for significant two-way age × face gender interactions and unstandardized beta coefficients for significant age-related slopes. Shaded areas represent standard errors. Pseudo-t values with the number of trials per condition regressed out are displayed on the y-axis and age (years) on the x-axis. A common y-axis scale was applied across regions for visualization; all data were included in the statistical models, and plotted slopes accurately represent the tested interactions. F = female faces; M = male faces. $^{*}p < .05$, $^{**}p < .005$.

Before closing, several limitations should be acknowledged. First, our sample included only typically developing children. Future work should examine whether these patterns generalize to clinical populations with anxiety or social-affective disorders, such as social anxiety disorder or autism spectrum disorder. Second, contextual moderators, including cultural expectations, parenting style, and socioeconomic status, were not assessed but may affect gendered-emotion processing. Third, the cross-sectional design limits our ability to track within-individual developmental changes. Longitudinal studies are necessary to clarify how oscillatory markers of early sensory gating and later socio-emotional integration support trajectories of social cognition and psychopathology risk. Fourth, although face stimuli were racially balanced, the predominantly White sample raises the possibility of own-race familiarity effects (Meissner and Brigham, 2001). Also, because all stimuli depicted adults, future work would benefit from paradigms that include stimuli from similar developmental stages (e.g., children, teens) for participants (Picci and Scherf, 2016). Future work should test whether these patterns generalize across more diverse samples and age-matched stimuli. Fifth, although MEG provides excellent spatiotemporal precision, our focus on gradiometer type sensors, while beneficial for noise cancellation and cortical source detection, may have limited sensitivity to deeper limbic structures (e.g., amygdala), leaving the contributions of pertinent subcortical circuits potentially incomplete. However, any such effects were likely limited, as there is now a growing collection of studies demonstrating hippocampal and amygdala responses using gradiometer type sensors (Badura-Brack et al., 2018; Hall et al., 2025, 2026), as well as at least two studies showing nearly identical hippocampal responses using gradiometer and magnetometer type sensors independently in the same cohort using the same MEG instrument and cognitive task (Meehan et al., 2021; Rempe et al., 2025). Finally, while it is not a limitation of MEG, the beamformer source imaging method chosen to reconstruct the MEG data in this study has the weakness that neural sources that are highly temporally-correlated (i.e., synchronous) are often attenuated, and this can lead to reduced sensitivity toward slow wave delta and theta responses, as well as deep activity (e.g., amygdala). While this is an important consideration, in practice, the correlation among source time series must remain quite high (e.g., $r > .6$) over at least 50% of the entire imaging window for this weakness to have a noticeable effect (Hadjipapas et al., 2005). The classic example of such a scenario is the bilateral primary auditory responses when sustained tones are presented binaurally (Hillebrand et al., 2005). Since our imaging windows were 300 ms duration and our task would not be expected to elicit temporally-sustained, synchronous, bilateral responses, this limitation of beamforming likely had a negligible effect on our results.

In summary, this study demonstrates that neural processing of gendered emotional faces may emerge through distinct functional patterns, with early attentional engagement in the alpha/beta range and later social-cognitive integration in the faster gamma bands. These processes interact with age and anxiety symptoms, showing how perceptual and social-cognitive systems jointly facilitate children's interpretation of faces within culturally shaped gender–emotion contexts. These findings advance our understanding of the neural mechanisms underlying emotion perception and face processing and point to potential targets for early interventions in youth with elevated anxiety.

CRediT authorship contribution statement

Nathan M. Petro: Writing – review & editing, Software, Methodology. **Grace C. Ende:** Writing – review & editing, Data curation. **Danielle L. Rice:** Writing – review & editing, Data curation. **Jason A. John:** Writing – review & editing, Data curation. **Brittany K. Taylor:** Writing – review & editing, Software, Methodology, Funding acquisition,

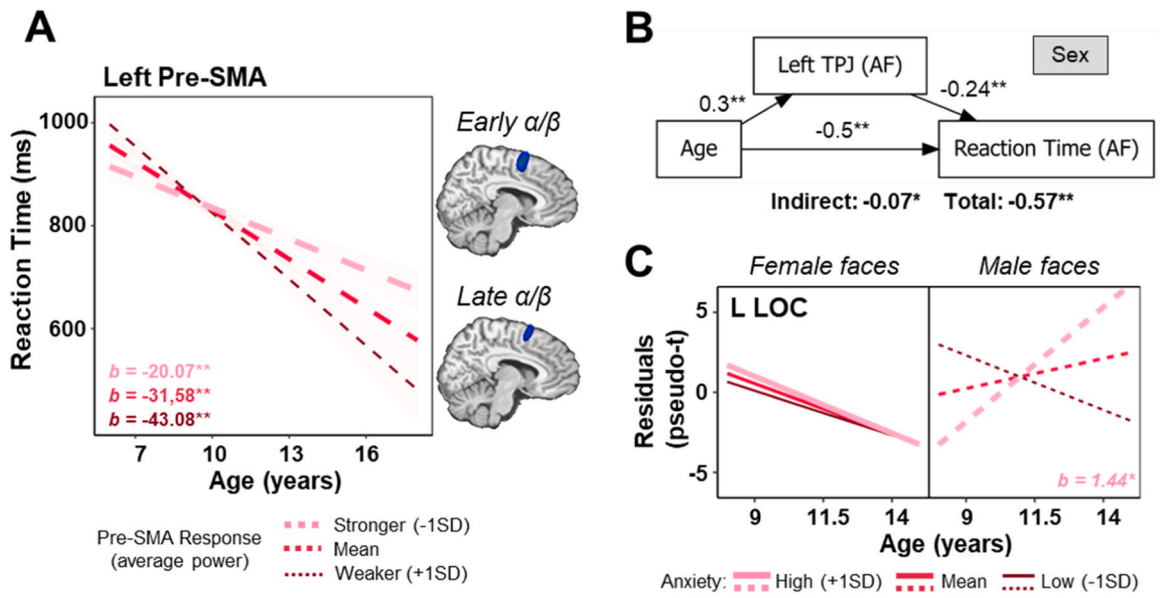


Fig. 5. Neurobehavioral Associations and Moderation Effect of Anxiety on Gendered Angry Faces. A: The line plot illustrates the moderation of the age–-reaction time relationship for angry male faces by average alpha/beta oscillatory activity in the left pre-supplementary motor area (pre-SMA; collapsed across early and late windows). Simple slope analyses were conducted at three levels of alpha/beta response strength: stronger (−1 SD; thicker pink line), mean (red line), and weaker (+1 SD; thinner dark red line), with slope coefficients and asterisks indicating significance displayed. Shaded areas represent standard errors. Faster reaction times with age were observed across all participants, with the effect being attenuated in those showing stronger alpha/beta responses (more negative from baseline) and amplified in those with weaker alpha/beta responses. Sagittal views of the left pre-SMA in both early and late windows are displayed to the right. Reaction time (ms) is displayed on the y-axis and age (years) on the x-axis. **B:** The path plot illustrates that gamma responses in the left temporoparietal junction (TPJ) mediated the relationship between age and reaction time to angry female (AF) faces, while controlling for participant sex. Coefficients of path regressions and defined parameters (indirect and total effects) are noted on the plot. The indirect effect in this mediation model did not survive false discovery rate correction, so it is reported as exploratory. **C:** Line plots depict the relationship between age and the left lateral occipital cortex (LOC) alpha/beta responses to angry faces at high (+1 SD; thicker pink line), mean (red line), and low (−1 SD; thinner dark red line) anxiety levels, separated by face gender (female: left; male: right). Simple slope coefficient and asterisk indicate significance. Youths with higher anxiety showed weaker LOC responses to angry male faces, whereas responses to angry female faces remained elevated across all anxiety levels. Pseudo-t values with the number of trials per condition regressed out are shown on the y-axis, and age (years) is on the x-axis. $^{*}p < .05$, $^{**}p < .005$.

Conceptualization. **Hua Bai:** Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Methodology, Formal analysis. **Giorgia Picci:** Writing – review & editing, Supervision, Software, Methodology, Funding acquisition, Conceptualization. **Yasra Arif:** Writing – review & editing, Writing – original draft, Software, Methodology. **Tony W. Wilson:** Writing – review & editing, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Jake J. Son:** Writing – review & editing, Software, Methodology, Funding acquisition, Formal analysis. **Anna T. Coutant:** Writing – review & editing, Data curation. **Erica L. Steiner:** Writing – review & editing, Data curation. **Ryan J. Glesinger:** Writing – review & editing, Data curation. **Hannah J. Okelberry:** Writing – review & editing, Data curation.

Declaration of Competing Interest

The authors declare no competing interests.

Acknowledgment

This research was supported by grants R01-MH121101 (TWW), P20-GM144641 (TWW, BKT, and GP), F30-MH134713 (JJS), and S10-OD028751 (TWW) from the National Institutes of Health. The funders had no role in study design, data collection, analysis, decision to publish, or preparation of the manuscript. The data presented in this manuscript have not been published elsewhere, but an early version of this work was presented at the 2025 meeting of the Association for Psychological Science (APS).

Data availability

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/).

References

Bacigalupo, F., Luck, S.J., 2022. Alpha-band EEG suppression as a neural marker of sustained attentional engagement to conditioned threat stimuli. Soc. Cogn. Affect. Neurosci. 17 (12), 1101–1117. https://doi.org/10.1093/scan/nsac029.

Badura-Brack, A., McDermott, T.J., Heinrichs-Graham, E., Ryan, T.J., Khanna, M.M., Pine, D.S., Bar-Haim, Y., Wilson, T.W., 2018. Veterans with PTSD demonstrate amygdala hyperactivity while viewing threatening faces: a MEG study. Biol. Psychol. 132, 228–232. https://doi.org/10.1016/j.biopsycho.2018.01.005.

Bai, H., Son, J.J., Petro, N.M., Rice, D.L., Ende, G.C., Glesinger, R.J., Okelberry, H.J., John, J.A., Coutant, A.T., Steiner, E.L., Calhoun, V.D., Wang, Y.-P., Stephen, J.M., Taylor, B.K., Picci, G., Wilson, T.W., 2025. Dynamic developmental signatures of facial expression processing differ by emotion. Commun. Biol. 8 (1), 1395. https://doi.org/10.1038/s42003-025-08808-z.

Bar-Haim, Y., Lamy, D., Pergamin, L., Bakermans-Kranenburg, M.J., van IJzendoorn, M. H., 2007. Threat-related attentional bias in anxious and nonanxious individuals: a meta-analytic study. Psychol. Bull. 133 (1), 1–24. https://doi.org/10.1037/0033-2909.133.1.1.

Bastos, A.M., Usrey, W.M., Adams, R.A., Mangun, G.R., Fries, P., Friston, K.J., 2012. Canonical microcircuits for predictive coding. Neuron 76 (4), 695–711. https://doi.org/10.1016/j.neuron.2012.10.038.

Bayet, L., Pascalis, O., Quinn, P.C., Lee, K., Gentaz, É., Tanaka, J.W., 2015. Angry facial expressions bias gender categorization in children and adults: behavioral and computational evidence. Front. Psychol. 6. https://doi.org/10.3389/fpsyg.2015.00346.

Bem, S.L., 1981. Gender schema theory: a cognitive account of sex typing. Psychol. Rev. 88 (4), 354–364. https://doi.org/10.1037/0033-295X.88.4.354.

Brainard, D.H., 1997. The psychophysics toolbox. Spat. Vis. 10 (4), 433–436.

Brotman, M.A., Kircanski, K., Stringaris, A., Pine, D.S., Leibenluft, E., 2017. Irritability in youths: a translational model. Am. J. Psychiatry 174 (6), 520–532. https://doi.org/10.1176/appi.ajp.2016.16070839.

Burgoon, J.K., 1993. Interpersonal expectations, expectancy violations, and emotional communication. J. Lang. Soc. Psychol. 12 (1–2), 30–48. https://doi.org/10.1177/0261927X93121003.
Conley, M.I., Dellarco, D.V., Rubien-Thomas, E., Cohen, A.O., Cervera, A., Tottenham, N., Casey, B., 2018. The racially diverse affective expression (RADIATE) face stimulus set. Psychiatry Res. 270, 1059–1067. https://doi.org/10.1016/j.psychres.2018.04.066.
Corbetta, M., Shulman, G.L., 2002. Control of goal-directed and stimulus-driven attention in the brain. Nat. Rev. Neurosci. 3 (3), 201–215. https://doi.org/10.1038/nrn755.
Duchaine, B., Yovel, G., 2015. A revised neural framework for face processing. Annu. Rev. Vis. Sci. 1 (1), 393–416. https://doi.org/10.1146/annurev-vision-082114-035518.
Ernst, M.D., 2004. Permutation methods: a basis for exact inference. Stat. Sci. 19 (4), 676–685. https://doi.org/10.1214/088342304000000396.
Foxe, J.J., Simpson, G.V., Ahlfors, S.P., 1998. Parieto-occipital ~1 0Hz activity reflects anticipatory state of visual attention mechanisms. NeuroReport 9 (17), 3929.
Foxe, J.J., Snyder, A.C., 2011. The role of alpha-band brain oscillations as a sensory suppression mechanism during selective attention. Front. Psychol. 2. https://doi.org/10.3389/fpsyg.2011.00154.
Freeman, J.B., Rule, N.O., Adams, R.B., Ambady, N., 2010. The neural basis of categorical face perception: graded representations of face gender in fusiform and orbitofrontal cortices. Cereb. Cortex 20 (6), 1314–1322. https://doi.org/10.1093/cercor/bhp195.
Fries, P., 2009. Neuronal gamma-band synchronization as a fundamental process in cortical computation. Annu. Rev. Neurosci. 32 (32, 2009), 209–224. https://doi.org/10.1146/annurev.neuro.051508.135603.
Ge, L., Anzures, G., Wang, Z., Kelly, D.J., Pascalis, O., Quinn, P.C., Slater, A.M., Yang, Z., Lee, K., 2008. An inner-face advantage in children's recognition of familiar peers. J. Exp. Child Psychol. 101 (2), 124–136. https://doi.org/10.1016/j.jecp.2008.05.006.
Gross, J., Kujala, J., Hämäläinen, M., Timmermann, L., Schnitzler, A., Salmelin, R., 2001. Dynamic imaging of coherent sources: studying neural interactions in the human brain. Proc. Natl. Acad. Sci. 98 (2), 694–699. https://doi.org/10.1073/pnas.98.2.694.
Hadjipapas, A., Hillebrand, A., Holliday, I.E., Singh, K.D., Barnes, G.R., 2005. Assessing interactions of linear and nonlinear neuronal sources using MEG beamformers: a proof of concept. Clin. Neurophysiol. Off. J. Int. Fed. Clin. Neurophysiol. 116 (6), 1300–1313. https://doi.org/10.1016/j.clinph.2005.01.014.
Hall, M.C., Rempe, M.P., Casagrande, C.C., Glesinger, R.J., Petro, N.M., Garrison, G.M., John, J.A., Dietz, S.M., Schantell, M., Bai, H., Arif, Y., Embury, C.M., Bashford, S., Okelberry, H.J., Petts, A.J., Keifer, E.L., May-Weeks, P.E., Picci, G., Heinrichs-Graham, E., Wilson, T.W., 2025. Age-related alterations in alpha and beta oscillations support preservation of semantic processing in healthy aging. Npj Aging 11 (1), 73. https://doi.org/10.1038/s41514-025-00263-8.
Hall, M.C., Rempe, M.P., John, J.A., Garrison, G.M., Glesinger, R., Casagrande, C.C., Petro, N.M., Okelberry, H.J., Petts, A.J., Bai, H., Bashford, S., Dietz, S.M., May-Weeks, P.E., Taylor, B.K., Arif, Y., Heinrichs-Graham, E., Picci, G., Spooner, R.K., Wilson, T.W., 2026. Hippocampal and cortical oscillatory dynamics support semantic processing and performance. Commun. Biol. https://doi.org/10.1038/s42003-026-09718-4.
Harris, D.A., Ciaramitaro, V.M., 2016. Interdependent mechanisms for processing gender and emotion: the special status of angry male faces. Front. Psychol. 7. https://doi.org/10.3389/fpsyg.2016.01046.
Herlitz, A., Lovén, J., 2013. Sex differences and the own-gender bias in face recognition: a meta-analytic review. Vis. Cogn. 21 (9–10), 1306–1336. https://doi.org/10.1080/13506285.2013.823140.
Hess, U., Adams Jr., R.B., Grammer, K., Kleck, R.E., 2009. Face gender and emotion expression: are angry women more like men? J. Vis. 9 (12), 19. https://doi.org/10.1167/9.12.19.
Hillebrand, A., Singh, K.D., Holliday, I.E., Furlong, P.L., Barnes, G.R., 2005. A new approach to neuroimaging with magnetoencephalography. Hum. Brain Mapp. 25 (2), 199–211. https://doi.org/10.1002/hbm.20102.
Hugenberg, K., Sczesny, S., 2006. On wonderful women and seeing smiles: social categorization moderates the happy face response latency advantage. Soc. Cogn. 24 (5), 516–539. https://doi.org/10.1521/soco.2006.24.5.516.
Kovach, C.K., Gander, P.E., 2016. The demodulated band transform. J. Neurosci. Methods 261, 135–154. https://doi.org/10.1016/j.jneumeth.2015.12.004.
Lee, E., Kang, J.I., Park, I.H., Kim, J.-J., An, S.K., 2008. Is a neutral face really evaluated as being emotionally neutral? Psychiatry Res. 157 (1–3), 77–85. https://doi.org/10.1016/j.psychres.2007.02.005.
Liu, C., Liu, Y., Iqbal, Z., Li, W., Lv, B., Jiang, Z., 2017. Symmetrical and asymmetrical interactions between facial expressions and gender information in face perception. Front. Psychol. 8, 1383. https://doi.org/10.3389/fpsyg.2017.01383.
Maratos, F.A., Pessoa, L., 2019. What drives prioritized visual processing? A motivational relevance account. Prog. Brain Res. 247, 111–148. https://doi.org/10.1016/bs.pbr.2019.03.028.
Maris, E., Oostenveld, R., 2007. Nonparametric statistical testing of EEG- and MEG-data. J. Neurosci. Methods 164 (1), 177–190. https://doi.org/10.1016/j.jneumeth.2007.03.024.
Mazaheri, A., Jensen, O., 2010. Rhythmic pulsing: linking ongoing brain activity with evoked responses. Front. Hum. Neurosci. 4. https://doi.org/10.3389/fnhum.2010.00177.
Meehan, C.E., Wiesman, A.I., Spooner, R.K., Schantell, M., Eastman, J.A., Wilson, T.W., 2021. Differences in rhythmic neural activity supporting the temporal and spatial cueing of attention. Cereb. Cortex 31 (11), 4933–4944. https://doi.org/10.1093/cercor/bhab132.
Meissner, C.A., Brigham, J.C., 2001. Thirty years of investigating the own-race bias in memory for faces: a meta-analytic review. Psychol. Public Policy Law 7 (1), 3–35. https://doi.org/10.1037/1076-8971.7.1.3.
Mobach, L., Rinck, M., Becker, E.S., Carl, T., Klein, A.M., Rapee, R.M., Hudson, J.L., 2022. Facing uncertainty: interpretation of ambiguous emotional faces in childhood social anxiety disorder. J. Clin. Child Adolesc. Psychol. 51 (6), 955–969. https://doi.org/10.1080/15374416.2022.2070850.
Mogg, K., Bradley, B.P., 1999. Orienting of attention to threatening facial expressions presented under conditions of restricted awareness. Cogn. Emot. 13 (6), 713–740. https://doi.org/10.1080/026999399379050.
Nachev, P., Kennard, C., Husain, M., 2008. Functional role of the supplementary and pre-supplementary motor areas. Nat. Rev. Neurosci. 9 (11), 856–869. https://doi.org/10.1038/nrn2478.
Picci, G., Scherf, K.S., 2016. From caregivers to peers: puberty shapes human face perception. Psychol. Sci. 27 (11), 1461–1473. https://doi.org/10.1177/0956797616663142.
Plant, E.A., Kling, K.C., Smith, G.L., 2004. The influence of gender and social role on the interpretation of facial expressions. Sex. Roles A J. Res. 51 (3–4), 187–196. https://doi.org/10.1023/B:SERS.0000037762.10349.13.
Puliafico, A.C., Kendall, P.C., 2006. Threat-related attentional bias in anxious youth: a review. Clin. Child Fam. Psychol. Rev. 9 (3–4), 162–180. https://doi.org/10.1007/s10567-006-0009-x.
Pulliam, H.R., Springer, S.D., Rice, D.L., Ende, G.C., Johnson, H.J., Willett, M.P., Wilson, T.W., Taylor, B.K., 2024. Neurotoxic effects of home radon exposure on oscillatory dynamics serving attentional orienting in children and adolescents. NeuroImage 292, 120606. https://doi.org/10.1016/j.neuroimage.2024.120606.
Quinn, P.C., Yahr, J., Kuhn, A., Slater, A.M., Pascalis, O., 2002. Representation of the gender of human faces by infants: a preference for female. Perception 31 (9), 1109–1121. https://doi.org/10.1068/p3331.
Rehnman, J., Herlitz, A., 2006. Higher face recognition ability in girls: magnified by own-sex and own-ethnicity bias. Memory 14 (3), 289–296. https://doi.org/10.1080/09658210500233581.
Rempe, M.P., Casagrande, C.C., Embury, C.M., Arif, Y., Bashford, S., Garrison, G.M., Glesinger, R.J., Okelberry, H.J., Keifer, E.L., Picci, G., Heinrichs-Graham, E., Wilson, T.W., 2025. Hippocampal and cortical oscillatory dynamics reflect semantic processing and predict behavioural performance. J. Physiol. 603 (10), 3089–3106. https://doi.org/10.1113/JP287373.
Reynolds, C.R., Kamphaus, R.W., 2015. Behavior Assessment System for Children. 3rd (BASC–3) edn. NCS Pearson, Inc, Bloomington.
Rodigari, A., Oliveri, M., 2014. Disrupting SMA activity modulates explicit and implicit emotional responses: an rTMS study. Neurosci. Lett. 579, 30–34. https://doi.org/10.1016/j.neulet.2014.07.012.
Schmahmann, J.D., 2019. The cerebellum and cognition. Neurosci. Lett. Cerebellum Health Dis. 688, 62–75. https://doi.org/10.1016/j.neulet.2018.07.005.
Stuijfzand, S., Creswell, C., Field, A.P., Pearcey, S., Dodd, H., 2018. Research Review: Is anxiety associated with negative interpretations of ambiguity in children and adolescents? A systematic review and meta-analysis. J. Child Psychol. Psychiatry 59 (11), 1127–1142. https://doi.org/10.1111/jcpp.12822.
Taulu, S., Simola, J., Kajola, M., 2005. Applications of the signal space separation method. IEEE Trans. Signal Process. 53 (9), 3359–3372. https://doi.org/10.1109/TSP.2005.853302.
Taulu, S., Simola, J., 2006. Spatiotemporal signal space separation method for rejecting nearby interference in MEG measurements. Phys. Med. Biol. 51 (7), 1759–1768. https://doi.org/10.1088/0031-9155/51/7/008.
Tottenham, N., Hare, T.A., Casey, B.J., 2011. Behavioral assessment of emotion discrimination, emotion regulation, and cognitive control in childhood, adolescence, and adulthood. Front. Psychol. 2. https://doi.org/10.3389/fpsyg.2011.00039.
Uusitalo, M.A., Ilmoniemi, R.J., 1997. Signal-space projection method for separating MEG or EEG into components. Med. Biol. Eng. Comput. 35 (2), 135–140. https://doi.org/10.1007/BF02534144.
Valdés-Conroy, B., Aguado, L., Fernández-Cahill, M., Romero-Ferreiro, V., Diéguez-Risco, T., 2014. Following the time course of face gender and expression processing: a task-dependent ERP study. Int. J. Psychophysiol. 92 (2), 59–66. https://doi.org/10.1016/j.ijpsycho.2014.02.005.
Van Overwalle, F., 2009. Social cognition and the brain: a meta-analysis. Hum. Brain Mapp. 30 (3), 829–858. https://doi.org/10.1002/hbm.20547.
Van Veen, B.D., Van Drongelen, W., Yuchtman, M., Suzuki, A., 1997. Localization of brain electrical activity via linearly constrained minimum variance spatial filtering. IEEE Trans. Biomed. Eng. 44 (9), 867–880. https://doi.org/10.1109/10.623056.
Vuilleumier, P., 2005. How brains beware: neural mechanisms of emotional attention. Trends Cogn. Sci. 9 (12), 585–594. https://doi.org/10.1016/j.tics.2005.10.011.
Waters, A.M., Bradley, B.P., Mogg, K., 2014. Biased attention to threat in paediatric anxiety disorders (generalized anxiety disorder, social phobia, specific phobia, separation anxiety disorder) as a function of 'distress' versus 'fear' diagnostic categorization. Psychol. Med. 44 (3), 607–616. https://doi.org/10.1017/S0033291713000779.
Wiesman, A.I., Wilson, T.W., 2020. Attention modulates the gating of primary somatosensory oscillations. NeuroImage 211, 116610. https://doi.org/10.1016/j.neuroimage.2020.116610.