

Research paper

Generalization of familiarity-related neural patterns to emotional facial expressions

Madeline Molly Ely , Géza Gergely Ambrus ^{*} 

School of Psychology, Bournemouth University, Poole House P319, Talbot Campus, Fern Barrow, Poole, Dorset BH12 5BB, United Kingdom

ARTICLE INFO

Keywords:

MVPA
EEG
Face perception
Facial expression
Face familiarity

ABSTRACT

Emotional facial expressions are known to bias face processing, yet it remains unclear whether such effects extend to neural signals associated with face familiarity. In this secondary analysis of openly available EEG data, we used cross-dataset multivariate pattern analysis (MVPA) to test whether established neural signatures of face familiarity generalize across emotional expressions. Participants viewed faces in two independent experiments: one involving explicit emotion categorization (happy, angry, sad, neutral) and another involving personally familiar and unfamiliar identities. Classifiers trained to distinguish familiar from unfamiliar faces were cross-applied to emotional expressions, and vice versa, using complementary relabeling strategies. Across analyses, neural patterns for angry expressions showed the strongest and most sustained generalization to familiarity-related neural signals, emerging around 200 ms post-stimulus and persisting throughout the trial (peak Cohen's $d = 1.35$ over posterior regions). Neural patterns for happy and sad expressions showed weaker and more transient generalization (200–400 ms), while neutral expressions consistently aligned with patterns for unfamiliarity. These findings demonstrate that threat-related facial expressions exhibit neural dynamics that show convergence in pattern structure with established familiarity signals, extending prior evidence that emotional expressions, particularly anger, systematically modulate face representations beyond identity.

1. Introduction

Facial expressions are central to human social interaction, shaping how we perceive, interpret, and remember others. Emotional signals in faces capture attention rapidly and modulate subsequent processing, reflecting their adaptive role in detecting opportunities and threats in the environment. Clarifying the workings of this processing advantage has significant implications for our understanding of the interaction between emotion, attention, and memory. In this study, we investigate the neural underpinnings of emotion processing in faces using cross-dataset multivariate pattern analysis, with a focus on the modulation of face-familiarity signals by facial expressions.

In our previous work (Ely & Ambrus, 2025), we showed that facial expressions modulate neural representations of face identity for previously unfamiliar individuals, with the strongest effects observed for angry faces. This effect suggests that emotional expressions, and threat-related expressions in particular, can amplify representational dimensions that are normally strengthened through learning and repeated exposure. Identity and familiarity represent distinct, yet

related, aspects of face perception that both contribute to the stability and distinctiveness of face representations. While identity concerns the specific, unique features of an individual, familiarity relates to the accumulated experience and knowledge of that individual. Both constructs are supported by underlying face representations that become more stable and distinct as familiarity increases (Kok et al., 2017; Popova & Wiese, 2022, 2023). An open question, therefore, is whether the enhancement of identity representations observed for emotional expressions extends to neural signals associated with face familiarity. The present study was designed to test this hypothesis by examining whether emotional expressions show systematic overlap with established neural signatures of familiarity.

Familiarity is typically conceptualized as a rapid, automatic signal of prior encounter. This “feeling of knowing” serves as a mechanism for identifying previously seen stimuli and is often distinguished from more effortful, detail-oriented memory processes (Addante et al., 2024; Bowles et al., 2007; Rugg & Yonelinas, 2003; Yonelinas & Jacoby, 1996). In the domain of social perception, face familiarity represents the immediate sense of recognition experienced when encountering a

* Corresponding author.

E-mail address: g.ambrus@gmail.com (G.G. Ambrus).

<https://doi.org/10.1016/j.brainres.2026.150355>

Received 17 March 2026; Received in revised form 20 April 2026; Accepted 28 April 2026

Available online 29 April 2026

0006-8993/© 2026 The Author(s). Published by Elsevier B.V. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

known individual (Burton et al., 2011; Hancock et al., 2000; Kramer et al., 2018; Popova & Wiese, 2022, 2023; Wiese et al., 2022; Wiese & Schweinberger, 2011). This process operates as a graded neural signal influenced by behavioral relevance and social importance, rather than requiring the explicit retrieval of specific biographical or contextual memories (Dalski et al., 2023; Karimi-Rouzbahani et al., 2021; Li et al., 2022). At the neural level, this “feeling of knowing” is characterized by temporally sustained and spatially distributed EEG patterns, typically occurring between 200–600 ms post-stimulus (Dalski, Kovács, & Ambrus, 2022). These neural signatures represent a robust, functionally broad representation that generalizes across diverse identities and modes of familiarization, as well as varying task contexts (Dalski, Kovács, Wiese, et al., 2022; Wiese et al., 2021).

Research on emotional face perception has extensively examined how facial expressions modulate attention and memory, providing important context for understanding how emotional significance biases face processing, even in the absence of familiarity per se. One long-standing debate concerns whether happy or angry faces hold priority in visual processing. The angry face superiority effect proposes that threatening expressions are detected most efficiently, supported by findings that angry faces capture and hold attention even under restricted awareness (Fox et al., 2000; Mogg & Bradley, 1999; Öhman et al., 2001). In contrast, the happy face superiority effect suggests that smiles are detected more efficiently, possibly due to their social distinctiveness and cooperative value (Becker et al., 2011; Švegar et al., 2013). Together, these perspectives illustrate that emotional expressions, positive or negative, reliably bias attentional systems.

Beyond attention, emotional expressions also modulate memory for faces. Early behavioral studies showed improved recognition for smiling faces compared to neutral or pouting expressions (Kotzoor, 1989), and more recent work demonstrated superior recall and recognition for happy faces over neutral or angry ones (D’Argembeau et al., 2003; Foa et al., 2000). Other studies, however, point to an advantage for negative expressions: angry faces are more resistant to forgetting (Tay & Yang, 2017) and can be stored in greater numbers in visual short-term memory (Jackson et al., 2009). This mixed evidence has motivated the view that happy and angry faces may confer processing advantages at different stages, or through different mechanisms.

Electrophysiological studies support the idea that emotional expressions shape not only attention but also memory encoding and retrieval. Emotional expressions during learning modulate early perceptual components (P1, N170) as well as later recognition-related ERPs (Langeslag et al., 2009; Righi et al., 2012). Negative expressions, in particular, have been linked to enhanced recollection and liberal response criteria in recognition memory tasks (Johansson et al., 2004). However, many of these studies rely on identical images across study and test phases, raising concerns about contributions of low-level image similarity to apparent memory benefits (Ambrus et al., 2017; Collin et al., 2022). Indeed, some interpretations suggest that the impact of emotional expressions on behavior can be attributed to basic visual properties of the stimulus images (Coelho et al., 2011; Collin et al., 2022; Savage et al., 2013).

The literature demonstrates that emotional expressions systematically modulate the neural processing of faces across attentional and memory-related dimensions. The present study builds on this foundation by asking whether these emotion-driven neural dynamics show systematic similarity to distributed patterns described for familiarity.

Despite decades of behavioral and ERP research, the neural mechanisms through which emotional expressions influence face familiarity remain poorly characterized. Most EEG studies have focused on isolated components or single-emotion designs, limiting the ability to capture shared and generalizable neural patterns. Recent advances in cross-dataset multivariate pattern analysis (MVPA) offer a way to probe such generalizable neural structure by testing whether distributed spatiotemporal patterns identified in one experimental context can be used to decode data from another (Ambrus, 2024). Here, we extend this

approach to test whether similarity in the spatiotemporal structure of familiarity-related neural patterns supports generalization to emotional expressions, and vice versa.

Based on behavioral findings showing processing advantages for emotional compared to neutral faces, we predicted that emotional expressions (happy, angry, sad) would exhibit stronger overlap with familiarity-associated neural patterns than neutral expressions. Accordingly, our hypotheses concern graded differences in cross-domain neural pattern similarity, and guided by our prior results, we expect that threat-related expressions (i.e., angry faces) would show the strongest and most sustained cross-domain similarity.

2. Methods

We analyzed EEG data from two previously published face-processing experiments (see Fig. 1). In the *Facial Expressions* study (Ely & Ambrus, 2025), participants categorized standardized faces depicting four facial expressions. In the *Personally Familiar and Unfamiliar Faces* study (Wiese et al., 2022), participants viewed grayscale images of personally familiar and unfamiliar identities while performing an incidental task. A multivariate cross-classification approach allowed us to characterize the temporal dynamics of familiarity-emotion overlap while minimizing stimulus- and task-specific confounds.

2.1. Datasets

Data were drawn from two previously published EEG experiments. The emotion dataset included 24 participants who performed a two-alternative forced-choice (2AFC) task on emotional facial expressions (Ely & Ambrus, 2025). The familiarity dataset included 22 participants who viewed personally familiar and unfamiliar faces (Wiese et al., 2022). EEG data were processed further starting from the pre-processed datasets reported in the original studies. No additional preprocessing was applied beyond re-referencing, baseline correction, and resampling to a common sampling rate to ensure compatibility across datasets. Full preprocessing pipelines are described in the original publications. The analysis protocol was approved by the ethics committee of Bournemouth University.

2AFC Facial Expressions (Ely & Ambrus, 2025). The experimental stimuli consisted of frontal color photographs of eight previously unfamiliar individuals selected from the KDEF database (Lundqvist et al., 1998). The four male and four female identities were each depicted in four facial expressions (happy, angry, sad, and neutral). In total, 32 unique images were presented in the study. The presentation order of these images was randomized. Using a 2AFC design, each facial image was displayed for a duration of 1000 ms, preceded by a 200 ms fixation cross. Subsequently, a choice screen appeared, featuring the correct emotion and an incorrect emotion, with an interstimulus interval ranging from 500 to 1000 ms. Participants were instructed to identify the correct emotion portrayed by the face using the left or right key, with no time limit set for the response. Each image was shown 12 times, with the veridical facial expression paired with an incorrect choice four times, with ensuring a balanced distribution of response key assignments. Instances of participants providing incorrect responses resulted in the reintroduction of the corresponding trial into the sequence, to be rescheduled for a later time-point in the experiment. For the purposes of this analysis, incorrect responses were included, but repeated rescheduled trials were excluded to prevent repetition-driven familiarity confounds. Consequently, each participant’s dataset comprised 12 repetitions of an image, totaling 96 presentations of facial expressions and 48 presentations of identities, amounting to a set of 384 trials.

Familiar and Unfamiliar Faces. The experimental stimuli comprised facial photographs featuring individuals who were either highly personally familiar (e.g., close friends, relatives) or unknown to the participants. The 50 images of a familiar identity and the 50 photographs of the unknown identity were trial-unique, luminance adjusted

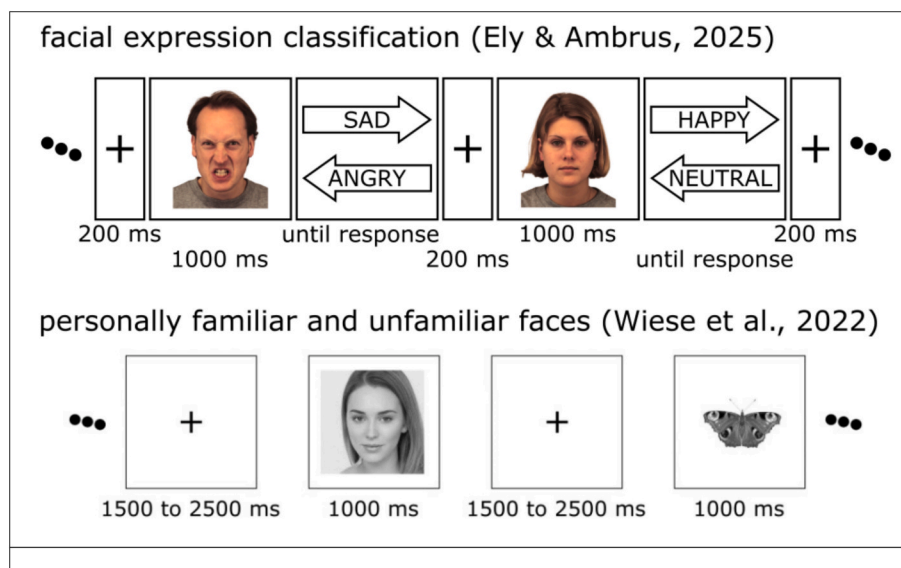


Fig. 1. Experimental designs of the two datasets included in the present study. 2AFC Facial Expressions (Ely & Ambrus, 2025, top): Twenty-four participants completed a two-alternative forced-choice task with 32 color photographs (four identities \times two genders \times four emotions) from the KDEF database. Each image was shown 12 times (384 trials total), with participants identifying the depicted emotion after a 1000 ms presentation. Personally Familiar and Unfamiliar Faces (Wiese et al., 2022, bottom): twenty-two participants viewed 100 trial-unique grayscale images (50 familiar, 50 unfamiliar identities), presented for 1000 ms with variable fixation intervals. Familiar/unfamiliar identities were participant-specific, and a butterfly detection task was included to maintain attention.

and presented in grayscale for a duration of 1000 ms against a gray background. The familiar and unfamiliar identities were distinct for each participant. To sustain participant engagement, participants were instructed to respond to the infrequent appearance of images of butterflies; responses to the face stimuli were not required. Intervals between trials were marked by a fixation cross, with a presentation duration spanning 1500–2500 ms. An extra set of stimuli, consisting of a familiar and an unfamiliar identity, was presented, with each image repeated 50 times. These trials were excluded from the current study's analysis.

2.2. Analysis pipeline

The analytical framework employed in this study was based on those outlined in Dalski, Kovács, & Ambrus (2022), Dalski, Kovács, Wiese, et al. (2022), Ambrus (2024) and Ely et al. (2026). To characterize the temporal evolution of information content associated with personally familiar and unfamiliar stimuli, a within-experiment approach was adopted, using leave-one-subject-out analyses on the test experiment. Multivariate cross-classification analyses were performed across the two experiments, aiming to probe the temporal dynamics of neural patterns linked to memory processes within the face-emotion dataset. The time-resolved analyses were conducted across all electrodes, as well as within regions of interest and through sensor-space spatio-temporal searchlight procedures.

Linear discriminant analysis (LDA) classifiers were trained on combined data from all participants at each time point. These trained classifiers were subsequently applied to predict stimulus familiarity in the test dataset for every trial within each participant. In all analyses, classifiers trained at a given timepoint in the training dataset were tested on activity at the corresponding timepoint in the test dataset (see Fig. 2. and below).

2.3. Cross-classification logic

Relabeling. This approach leverages the inherent flexibility of Multivariate Pattern Analysis, wherein the labels in a dataset can be systematically altered to align with the labels in another dataset intended for cross-classification. This relabeling enables the exploration of

generalizable patterns shared between processes in both experiments. This approach has proven successful in prior studies. For instance, in Dalski, Wiese, Kovács & Ambrus (2022), it was employed to investigate face-familiarity signals in the context of deception, while in Ambrus (2024), it was utilized to probe the contributions of familiarity and recollection to face-familiarity signals. Here, we used this approach to test whether neural patterns associated with emotional expressions modulate these shared familiarity signals.

In the present study, classifiers trained to distinguish personally familiar from unfamiliar faces were applied to the emotion dataset using alternative label mappings that aligned emotional expressions with familiarity categories. Specifically, emotional expressions were assigned the label 'familiar' and neutral expressions the label 'unfamiliar', or, in complementary analyses, each emotional expression was evaluated separately with respect to its likelihood of being classified as 'familiar' by a familiarity-trained classifier.

Crucially, this relabeling does not imply that emotional expressions possess intrinsic familiarity, or that neutral expressions are inherently unfamiliar at a perceptual or experiential level. All faces in the emotion dataset were experimentally unfamiliar to participants. It constitutes an analytical analogy that allows us to assess whether the neural activity elicited by emotional faces (compared to neutral faces) shares systematic structure with previously characterized familiarity-related patterns. Successful cross-classification under this framework indicates similarity in spatiotemporal neural patterns sufficient to support generalization, without assuming functional equivalence between emotion and familiarity processing.

Familiarity to Emotion (Each Emotion Separately). Data from all participants in the face-familiarity experiment were merged into a training dataset. Classifiers were trained at each time point to distinguish between trials with familiar versus unfamiliar faces. These classifiers were employed to classify trials in the face-emotion dataset for each facial expression. Data from each participant were tested individually, and the classification performance, denoting the proportion of trials classified as 'familiar', was aggregated for statistical testing for each facial expression at every time point.

Familiarity to Emotion (With Neutral as Unfamiliar). Similar to the previous scenario, data from all participants in the face-familiarity experiment were merged into a training dataset. Classifiers were

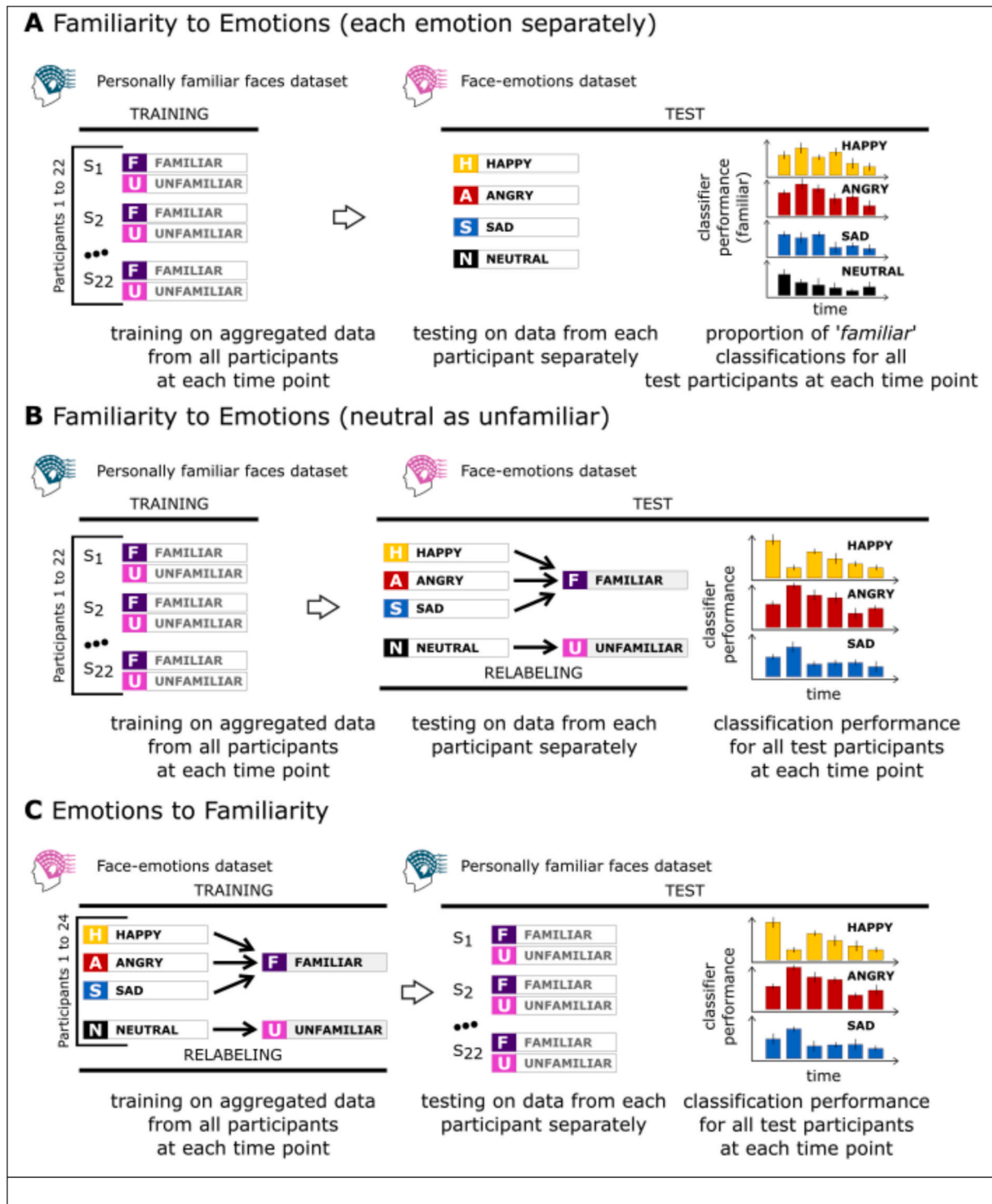


Fig. 2. Analysis pipeline. (A) Familiarity to Emotion, each emotion separately. Here, the data from all participants in the face-familiarity experiment were merged into a training dataset. Classifiers were trained at each time point to classify trials with familiar vs. unfamiliar faces. These classifiers were then used to classify trials in the face-emotion dataset for each facial expression. Here, data from each participant was tested separately, then classification performance, i.e., the proportion of trials classified as 'familiar', were then aggregated for statistical testing for each facial expression at each time point. (B) Familiarity to Emotion, with neutral as unfamiliar. Again, data from all participants in the face-familiarity experiment were merged into a training dataset, and classifiers were trained at each time point to classify trials with familiar vs. unfamiliar faces. These classifiers were then applied to the face-emotion dataset, where trials for the neutral expression were relabeled as 'unfamiliar' and trials for emotional expressions were relabeled as 'familiar'. Data from each participant was tested separately, then the classification accuracy scores were then aggregated for statistical testing for each emotional expression at each time point. (C) Emotions to Familiarity. Data from participants in the face-emotion experiment was merged into one dataset, with trials for each emotional expression (happy, angry, sad) relabeled as 'familiar', and trials for the neutral expression relabeled as 'unfamiliar'. Then, for each emotional expression separately (neutral – happy, neutral – angry, neutral – sad), classifiers were trained at each time-point, with the new familiar/unfamiliar labels. These classifiers were then tested on the face-familiarity dataset containing data for familiar and unfamiliar faces. Here, each participant's data was tested separately, and the classification accuracy scores were then aggregated for statistical testing for each training emotion at each time point.

trained at each time point to classify trials with familiar versus unfamiliar faces. These classifiers were then applied to the face-emotion dataset, where trials for the neutral expression were relabeled as ‘*unfamiliar*’, and trials for emotional expressions were relabeled as ‘*familiar*’. Data from each participant were tested independently, and the resulting classification accuracy scores were aggregated for statistical testing for each emotional expression at each time point.

Emotions to Familiarity. The data from participants in the face-emotion experiment were consolidated into a unified dataset. Trials for each emotional expression (happy, angry, sad) were relabeled as ‘*familiar*’, while trials for the neutral expression were relabeled as ‘*unfamiliar*’. Separate classifiers were trained at each time-point for each emotional expression (neutral – happy, neutral – angry, neutral – sad) using the new *familiar/unfamiliar* labels. These classifiers were subsequently tested on the face-familiarity dataset, which contained data for familiar and unfamiliar faces. Each participant's data was tested independently, and the resulting classification accuracy scores were aggregated for statistical testing. This process was conducted for each training emotion at every time point.

2.4. Multivariate pattern analysis

Time-resolved multivariate pattern analysis involved conducting cross-classification on data from all channels and pre-defined regions of interest. These regions of interest were based on Ambrus et al. (2019, 2021); Ambrus, 2024 and Dalski et al. (2022a, 2022b, 2023); Wiese et al., 2022 and were defined as bilaterally symmetric anterior, central, and posterior electrode clusters, each comprising approximately 10–12 neighboring electrodes with overlapping midline electrodes. Cross-classification was executed on shared channels within the training and test datasets (Ambrus, 2024; Li et al., 2022). The exact region-of-interest composition scheme is available in Supplementary Information Fig. 1.

Spatio-temporal searchlight analysis involved the systematic examination of individual sensors. The approach entailed separate training and testing on data derived from the specific channel and its neighboring electrodes. This procedure was repeated for each channel and its adjacent sensors.

Statistical testing procedures were applied to common-average-referenced, baseline-corrected (–200 to 0 ms) data spanning from –200 to 1000 ms, re-sampled to 200 Hz. To ensure balanced trial counts during both training and testing, under-sampling was implemented to match the minimum trial count within the classes of interest for each participant. A participant-level moving average of 35 ms (covering 7 consecutive time points) was employed on all decoding accuracy data (Ely & Ambrus, 2025). For region-of-interest-based time-resolved analyses, classification accuracies underwent two-tailed, one-sample cluster permutation tests (10,000 iterations) against the chance level (50%). Additional one-sample, two-sided Bayesian *t*-tests (Teichmann et al., 2022) were also performed. In these analyses, a non-directional whole-Cauchy prior with a moderate width ($r = 0.707$) was used, and an interval from $\delta = -0.5$ to $+0.5$ was excluded. The resulting Bayes factors were subjected to thresholding, with values surpassing 10 taken as indicative of strong evidence (Moerel et al., 2022; Wetzels et al., 2011). Spatio-temporal one-sample cluster permutation tests were used to evaluate the searchlight results (against the 50% chance level, with 10,000 iterations). All analyses were implemented in Python using MNE-Python (Gramfort et al., 2014), scikit-learn (Pedregosa et al., 2011), and SciPy (Virtanen et al., 2020), with Bayesian statistics computed in R (Morey et al., 2015).

3. Results

3.1. Familiarity to Emotion cross-classification (each facial expression separately)

When classifiers trained on personally familiar versus unfamiliar

faces were applied to the emotion dataset (Fig. 3.), only angry expressions showed reliable cross-classification with familiarity signals. Happy, sad, and neutral expressions did not yield significant effects in any of the analyses.

For angry faces, a robust overlap in neural patterns was observed from ~200 ms onwards. Significant clusters emerged across central and posterior regions, with the largest and most sustained effects over posterior sites (200–995 ms, peak Cohen's $d > 1$). A searchlight analysis confirmed this finding, revealing a widespread spatio-temporal cluster from 135–995 ms, peaking at 420 ms over PO4 (cluster $p = 0.002$, Cohen's $d = 1.35$). In contrast, Bayesian analyses of neutral expressions provided evidence in the opposite direction (i.e., alignment with “unfamiliar”), especially around 250 ms.

Bayesian analyses on time-resolved cross-classification were consistent with the cluster permutation test results. Additional effects for the neutral expression were observed in the ca. 240–280 ms peak in bilateral central and posterior electrode clusters, evidencing ‘unfamiliar’ classification (Bayes factors between 10 and 30). For a complete report on statistics, see Supplementary Table 1A-D.

3.2. Familiarity to Emotion cross-classification (neutral relabeled as unfamiliar)

Next, we asked whether emotional expressions in general align with familiarity signals by re-labeling neutral faces as “unfamiliar” and emotional faces as “familiar.” Under this scheme, angry expressions again produced the strongest generalization effect, with reliable decoding across early (200–400 ms) and late (>400 ms) windows.

Specifically, two significant clusters were observed across all electrodes (205–290 ms and 330–485 ms), both with large effect sizes (peak Cohen's $d > 1$). Searchlight analysis revealed an extended posterior cluster spanning nearly the entire epoch (130–1000 ms, cluster $p = 0.0002$). Happy expressions showed weaker and more transient overlap, with a single posterior cluster between 145–340 ms (peak at 260 ms, Cohen's $d = 1.33$). Sad expressions showed a localized effect in the left posterior ROI (185–295 ms, Cohen's $d = 0.80$), but no consistent clusters elsewhere. Results of the Bayesian analyses on time-resolved cross-classification were consistent with those of the cluster permutation tests. For a complete statistical report, see Supplementary Table 2A-C.

Thus, when neutral was treated as ‘unfamiliar’, all three emotional expressions showed some evidence of pattern-overlap with familiarity, but angry faces again dominated the effect in both strength and temporal extent.

3.3. Emotion to Familiarity cross-classification

Finally, we reversed the analysis; classifiers trained to distinguish emotional (vs. neutral) expressions were tested on the familiarity dataset. This revealed that angry, happy, and sad expressions all generalized to familiarity, though with important differences in timing and strength.

Angry faces produced the most reliable effects, with a large and sustained cluster starting at ~200 ms and lasting through the epoch (cluster $p < 0.0001$, peak Cohen's $d = 1.71$). Searchlight analysis confirmed a widespread posterior cluster peaking at 430 ms (Cohen's $d > 2.0$).

Happy faces yielded two significant clusters across all electrodes (180–335 ms and 415–650 ms, Cohen's $d \sim 1.25$). A searchlight analysis revealed a sustained effect beginning at 170 ms, peaking over FCz (Cohen's $d > 2.1$).

Sad faces showed three significant clusters (200–350 ms, 385–645 ms, and 700–995 ms), with peaks around 260, 445, and 825 ms (Cohen's $d \sim 1.1$ – 1.2). Searchlight analyses also identified extended effects, though notably one late cluster shifted toward the “unfamiliar” direction (325–990 ms over C4).

Bayesian analyses on time-resolved cross-classification largely

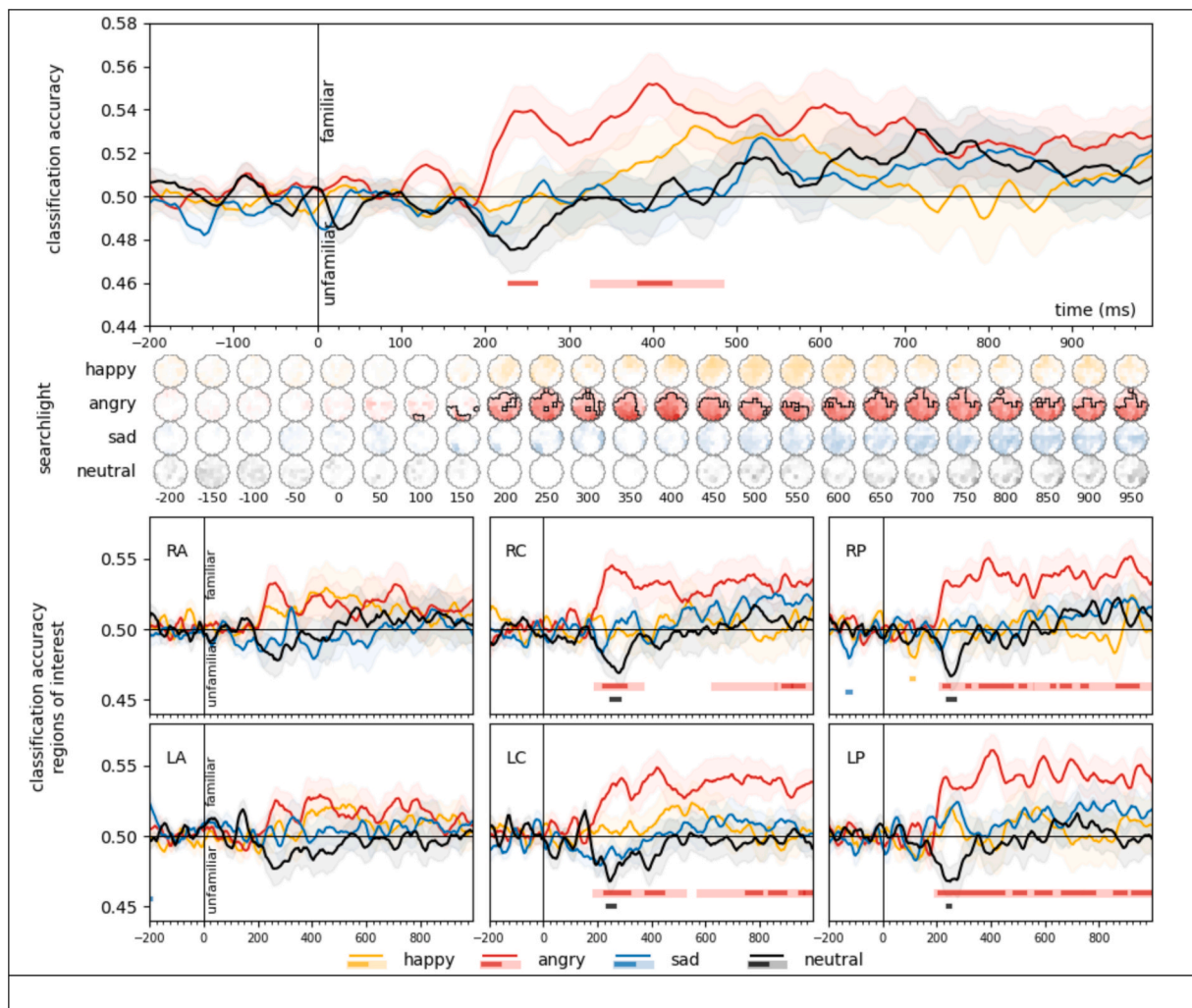


Fig. 3. Familiarity to Emotion cross-classification, for each facial expression separately. Classifiers were trained on the face-familiarity dataset to classify trials with familiar vs. unfamiliar faces. These classifiers were then used to classify trials in the face-emotion dataset for each facial expression. The y-axis denotes the proportion of trials in each facial expression classified as ‘familiar’. *Top panel:* classification performance over all electrodes. *Middle Panels:* spatio-temporal searchlight results are shown as scalp maps, with classification accuracy scores averaged in 50 ms steps. Sensors and time points forming parts of significant clusters are marked. Two-sided spatio-temporal cluster permutation tests, $p < 0.05$. *Bottom panels:* ROI analyses. The same analysis as in the top panel but repeated for six pre-defined electrode clusters separately. RA/LA: right/left anterior, RC/LC: right/left central, RP/LP: right/left posterior. Light lines denote significant clusters revealed by the two-sided cluster permutation tests, $p < 0.05$; dark lines denote results of the Bayesian statistical analyses, two-sided one-sample Bayesian t -tests, $bf > 10$. Error ranges denote \pm SEM. For detailed statistics, see Supplementary Table 1A-D.

mirrored the cluster permutation test results. For a complete statistical report, see Supplementary Table 2D-F. Together, these results indicate that when emotion is used as a training signal, all three expressions generalize to familiarity, but angry expressions again produce the clearest and most consistent overlap.

Across all three analysis strategies, patterns for angry expressions showed the strongest and most sustained overlap with familiarity signals, beginning around 200 ms and persisting throughout the trial. Happy and sad expressions produced weaker and more transient effects, largely confined to early time windows (200–400 ms). Neutral expressions consistently aligned with unfamiliarity.

4. Discussion

The present study examined how neural signals of face familiarity generalize across emotional expressions, using cross-dataset multivariate pattern analysis. We found that neural patterns for emotional expressions are more likely to be classified as resembling familiarity, and that angry faces in particular produced robust, sustained overlap with

familiarity signals across multiple analyses.

4.1. Methodological note

Results of cross-dataset multivariate pattern analysis require careful interpretation regarding what generalization across experiments can and cannot imply. As all faces in the facial expression dataset were experimentally unfamiliar, classifications of emotional faces as ‘familiar’ reflect similarity to familiarity-associated neural patterns, not veridical familiarity. Furthermore, successful cross-classification here indicates that the distributed patterns of scalp-recorded neural activity elicited by these processes share sufficiently similar structure for a classifier trained on one domain to perform above chance in the other and is not evidence for identical neuronal populations encoding both emotion and familiarity. This similarity may emerge either because the underlying representations overlap in content, or because the temporal dynamics of the processes rely on common stages of information processing. As others have noted (Carlson et al., 2020; Grootswagers et al., 2017; Hebart & Baker, 2018), MVPA generalization is best understood

as evidence for shared representational geometry or shared computational stages, rather than evidence for strict neural identity between processes.

Importantly, the relabeling strategy used here shapes the analytical contrast by specifying which dimensions of the data are tested for generalization, i.e., it determines the hypothesis being evaluated (here: whether emotional expressions align with familiarity-associated neural patterns under the imposed mapping). Alternative relabeling schemes would test different representational correspondences, and their evaluation lies beyond the scope of the present study. Accordingly, the present findings should be interpreted as evidence that the observed pattern of generalization is consistent with this specific representational hypothesis, rather than as an exhaustive characterization of emotion-familiarity relationships.

Several mechanisms may account for the overlap observed here. One possibility is that emotional expressions modulate attentional gain during perceptual encoding. Emotional faces, particularly those conveying threat, are known to engage attentional systems more strongly than neutral faces (Schindler & Bublatzky, 2020; Vuilleumier & Pourtois, 2007). This attentional enhancement may indirectly increase the clarity or depth of identity-related processing and thereby increase the similarity between emotional-face responses and those observed for familiar faces. Another possibility is that emotional expressions, especially negative ones, increase the distinctiveness of identity representations. Behavioral and neuroimaging evidence suggests that negative expressions can enhance both perceptual discrimination and memory-related recapitulation of facial identity (Bowen et al., 2018; Jackson & Raymond, 2008), which could result in representational changes that resemble those associated with familiarization.

A related interpretation is that familiarity and emotional significance rely, in part, on shared high-level systems for evaluating social relevance. Both familiarity and emotion confer meaning that extends beyond the physical structure of the face, activating networks in the medial temporal lobe, the temporoparietal junction, and prefrontal cortex (Adolphs et al., 1996; Deen et al., 2024; Gainotti, 2007; Gobbini & Haxby, 2007). Overlap in these higher-order evaluative processes may contribute to the representational similarity observed in the present analysis. Finally, similarities may arise from recurrent feedback mechanisms. Emotional expressions have been shown to amplify top-down modulation from higher-level cortical regions (Barrett & Bar, 2009; Pourtois et al., 2013), and familiarity signals likewise involve feedback from memory-related regions to visual cortex (Landi et al., 2021; McLelland et al., 2014; Ramon et al., 2015). If both emotion and familiarity rely on recurrent refinement during mid-latency processing, this may produce convergent temporal dynamics detectable in MVPAs.

While these accounts are not mutually exclusive, distinguishing between them requires experimental manipulation of attention, memory demands, and emotional relevance within a single design. The present results nonetheless demonstrate that emotional expressions, and angry expressions in particular, engage neural processes that converge with established familiarity-related dynamics around the 200 ms mark and persist thereafter.

4.2. Emotional expressions evoke neural patterns that resemble familiarity-associated signals

When cross-classifying from the face-familiarity to the face-emotion dataset, we observed a numerically higher ‘familiar’ classification rates for emotional expressions (happy, angry, sad) compared to neutral faces, particularly in the 200 to 400 ms time window (Fig. 3). This enhancement is not only in broad alignment with behavioral findings of increased recall for emotional expressions compared to neutral faces (Lee & Cho, 2019; Liu et al., 2014), but it also supports our subsequent analyses. In these analyses, through relabeling, we utilized the neutral condition as an analog for ‘unfamiliar’ stimuli in cross-classification to the face-familiarity dataset. Relabeling the neutral condition as

unfamiliar resulted in consistent and reliable effects observed in both the familiarity-to-emotion (Fig. 4) and the emotion-to-familiarity decoding direction (Fig. 5).

4.3. Angry expressions show robust overlap with familiarity codes

The relationship between identity and expression processing has been extensively debated since Bruce and Young’s (Bruce & Young, 1986) influential work, questioning whether facial identity and expression are processed through independent routes (see also Calder et al., 2001; Calder & Young, 2005). Expression effects on identity recognition support the idea that identity processing is not entirely separate from expression processing.

In our previous study (Ely & Ambrus, 2025) we observed enhanced representations for identity in response to angry facial expressions for previously unknown faces. Based on those results, we expected to see the highest cross-classification accuracies with familiar faces in the angry condition in our present analysis. In line with this prediction, angry expressions produced the clearest and most reliable cross-classification overlap with familiarity-related activity, beginning around 200 ms and extending throughout the epoch. This effect was strongest over central and posterior regions and was observed in both directions of cross-classification. These findings are most consistent with the idea that threat-related signals receive prioritized neural processing (Öhman et al., 2001; Schindler & Bublatzky, 2020). As our study did not involve a test for face memory, however, our results do not allow us to conclude that angry expressions were genuinely remembered better than other expressions. Instead, they demonstrate that angry expressions share neural dynamics with familiarity across multiple analyses.

Various hypotheses suggest that emotional signals are differentially attended to, and are classified based on valence or associated meaning, leading to different predictions regarding the correlation between the valence of face stimuli during training and subsequent recognition performance. D’Argembeau and colleagues (D’Argembeau et al., 2003; D’Argembeau & Van der Linden, 2011) propose an explanation for studies where negative stimuli, particularly angry faces, are associated with worse memory performance. They suggest that negative stimuli, such as anger, narrow attention towards threat indicators, while positive stimuli broaden attentional focus. According to their proposal, angry faces may automatically direct attention toward facial expressions, disrupting the course of elaborative processing and leading to worse memory performance. Proposing an explanation for the heightened attention noted in numerous studies towards happy facial expressions, Becker and colleagues (2011) argue against innate ‘happiness detectors,’ positing instead that smiles evolved greater visual distinctiveness due to their unambiguous social function in fostering cooperation.

In contrast, Bowen et al. (2018) propose that negative events, compared to positive events, result in both increased encoding of sensory detail and a closer resemblance between the sensory encoding signature and the sensory retrieval signature. Additionally, their model suggests that negative valence enhances the reactivation and storage of sensory details over offline periods, leading to a greater divergence between the sensory recapitulation of negative and positive memories over time. In an alternative interpretation, Švegar et al. (2013) suggest that angry expressions are initially prioritized due to the advantage of early threat detection in the environment. According to this account, however, in subsequent cognitive processing stages, happy expressions are given priority as smiling serves as a mechanism for establishing and maintaining cooperative relationships. In the present data, we do not observe a corresponding later-stage advantage for happy expressions relative to angry faces, suggesting that in this representational context and timeframe under study, threat-related prioritization dominates across both early and later phases.

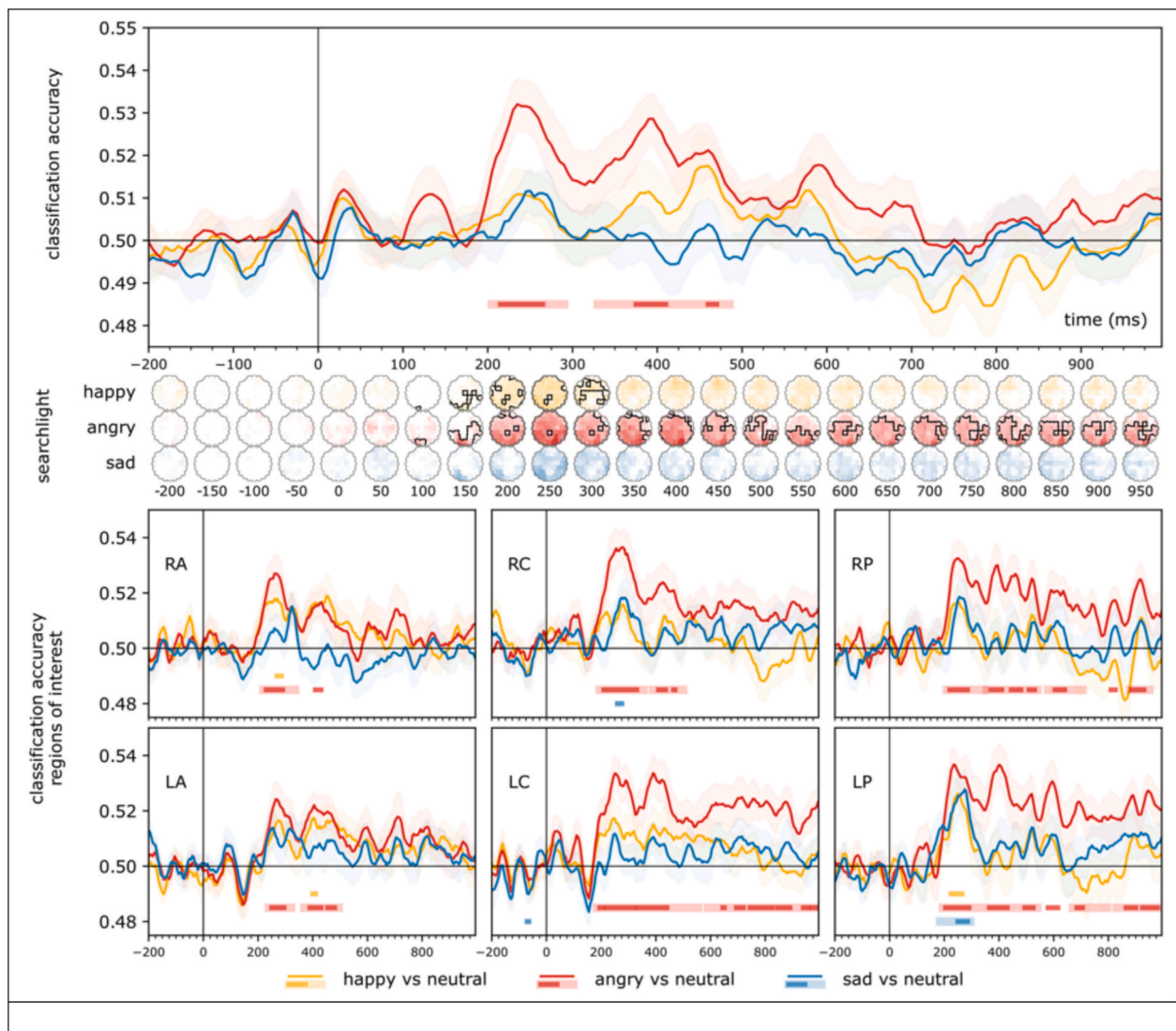


Fig. 4. Familiarity to Emotion cross-classification, with neutral as unfamiliar. Classifiers were trained on the face-familiarity dataset to classify trials with familiar vs. unfamiliar faces. These classifiers were then applied to the face-emotion dataset, where trials for the neutral expression were relabeled as ‘unfamiliar’ and trials for emotional expressions were relabeled as ‘familiar’. *Top panel:* classification performance over all electrodes. *Middle Panels:* spatio-temporal searchlight results are shown as scalp maps, with classification accuracy scores averaged in 50 ms steps. Sensors and time points forming parts of significant clusters are marked. (Two-sided spatio-temporal cluster permutation tests, $p < 0.05$). *Bottom panels:* ROI analyses. The same analysis as in the top panel but repeated for six pre-defined electrode clusters separately. RA/LA: right/left anterior, RC/LC: right/left central, RP/LP: right/left posterior. Light lines denote significant clusters revealed by the two-sided cluster permutation tests, $p < 0.05$; dark lines denote results of the Bayesian statistical analyses, two-sided one-sample Bayesian t -tests, $bf > 10$. Error ranges denote \pm SEM. For detailed statistics, see Supplementary Table 2A-C.

5. Limitations

There are several limitations that should be acknowledged. Most importantly, the absence of a behavioral memory task prevents direct inference about whether the neural overlap between emotion and familiarity corresponds to actual memory enhancement. Although previous work links emotional expressions to improved recognition performance (Liu et al., 2014; Righi et al., 2012), the present study cannot assess such behavioral consequences. The relabeling strategy used here, although effective for cross-classification, imposes interpretive constraints. Relabeling emotional faces as ‘familiar’ constitutes an analytical analogy rather than a statement about their intrinsic properties. Furthermore, the emotional stimulus set was drawn from a posed facial expression database that may not fully capture the variability of expressions encountered in naturalistic settings. The two datasets also differed in task demands, with emotional expressions explicitly task-relevant in one experiment and faces processed incidentally in the

other. Such differences may engage distinct cognitive processes, including decision-making, response preparation, and may modulate attentional engagement. Accordingly, the present findings demonstrate robust cross-domain representational similarity, while mechanistic dissociation will require targeted experimental manipulations in future work. Finally, the present design does not allow us to determine whether the observed overlap reflects face-specific familiarity signals or engagement of more domain-general mechanisms such as attentional prioritization or arousal. Disentangling these possibilities will require control conditions involving non-face stimuli associated with familiarity, differential affective value, or relevance, as demonstrated in recent works (Ambrus, 2024; Klink et al., 2023; Ozdemir & Ambrus, 2025; Wiese et al., 2023).

Despite these limitations, the present findings also highlight the methodological utility of cross-dataset MVPA for identifying neural patterns that generalize across substantial differences in stimulus properties and experimental design. Notably, the two datasets differed

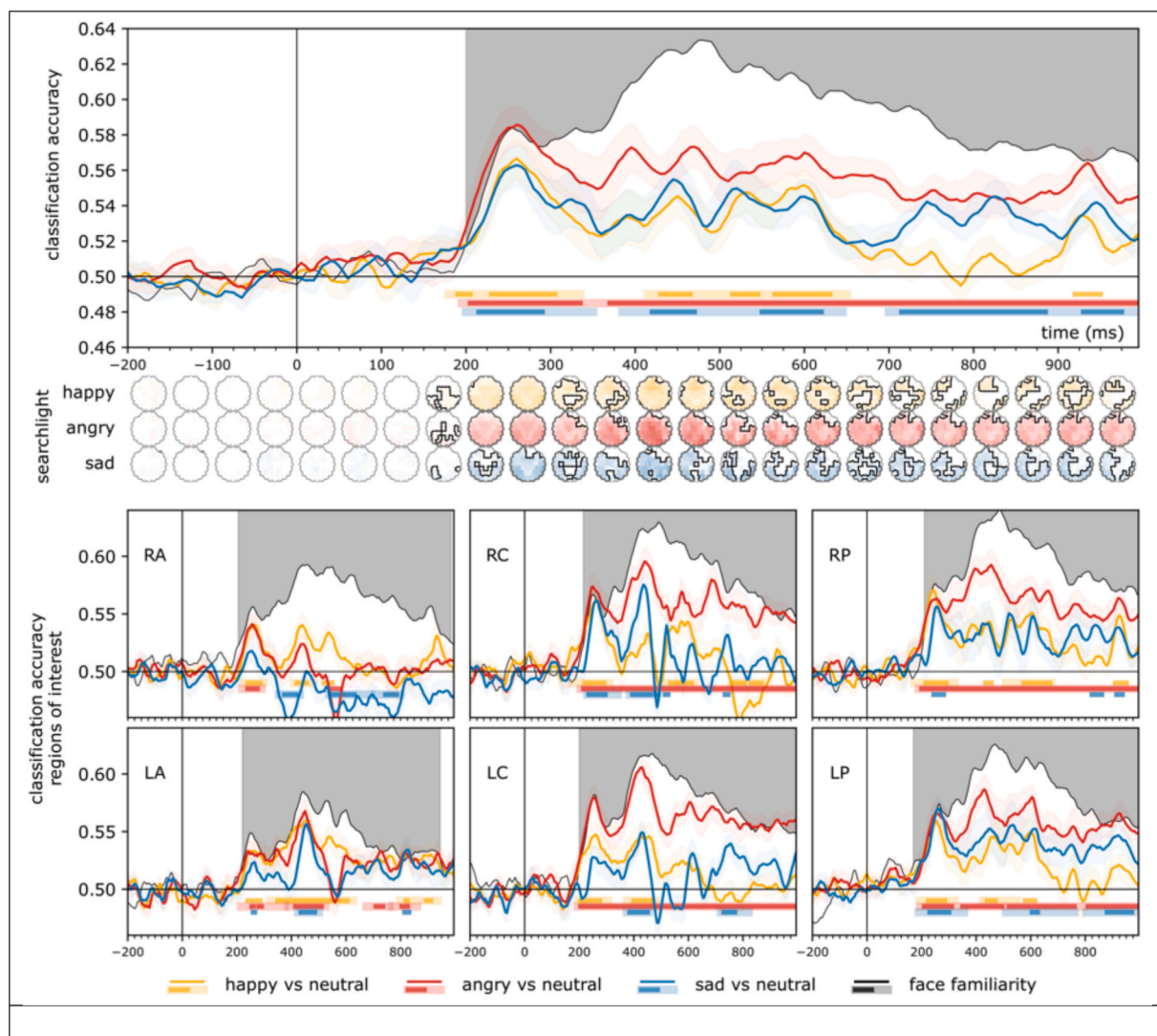


Fig. 5. Emotion to Familiarity cross-classification. In the face-emotion dataset, trials for each emotional expression (happy, angry, sad) were relabeled as ‘familiar’, and trials for the neutral expression relabeled as ‘unfamiliar’. For each emotional expression separately (neutral – happy, neutral – angry, neutral – sad), classifiers were trained at each time-point, which were then tested on the face-familiarity dataset. For comparison, the results of the within-experiment, leave-one-subject-out analysis are shown in grey. *Top panel:* classification performance over all electrodes. *Middle Panels:* spatio-temporal searchlight results are shown as scalp maps, with classification accuracy scores averaged in 50 ms steps. Sensors and time points forming parts of significant clusters are marked. Two-sided spatio-temporal cluster permutation tests, $p < 0.05$. *Bottom panels:* ROI analyses. The same analysis as in the top panel but repeated for six pre-defined electrode clusters separately. RA/LA: right/left anterior, RC/LC: right/left central, RP/LP: right/left posterior. Light lines denote significant clusters revealed by the two-sided cluster permutation tests, $p < 0.05$; dark lines denote results of the Bayesian statistical analyses, two-sided one-sample Bayesian t -tests, $bf > 10$. Error ranges denote \pm SEM. For detailed statistics, see Supplementary Table 2D-F.

in low-level visual characteristics, including the use of color images in the facial expression experiment and grayscale images in the familiarity experiment. Such differences would be expected to reduce decoding performance if classification relied primarily on image-based or early visual features, to which multivariate classifiers are known to be sensitive. The observation of reliable cross-classification despite these differences suggests that the effects reported here are unlikely to be driven by simple low-level visual similarities. Instead, successful generalization across color and grayscale stimuli supports the interpretation that cross-dataset MVPA captured higher-order spatiotemporal neural structure independent of visual attributes. The consistent generalization observed here, especially for angry expressions, therefore suggests that the neural patterns associated with emotional processing share structure with those elicited by familiarity, and that this structure is sufficiently stable to transfer across different experimental contexts.

6. Future directions

The primary contribution of the present work is therefore representational rather than mechanistic: we demonstrate that distributed familiarity-associated EEG patterns generalize systematically to emotional face processing across heterogeneous datasets, without attempting to identify the specific cognitive operations responsible for this similarity. Thus, future research should examine whether emotional expressions facilitate the formation of familiarity by combining emotional exposure with repeated-identity learning paradigms, explicitly testing familiarity and identity acquisition. Representational similarity analysis could be used to map the multidimensional structure of emotional and familiarity representations more explicitly, providing a complementary perspective on how these dimensions interact at the neural level. Additionally, studies employing dynamic or naturalistic stimuli would help determine whether the present findings generalize to

real-world conditions, where expressions unfold over time. Finally, manipulating the task relevance of emotion versus identity could clarify whether the overlap observed here reflects attentional prioritization or deeper representational integration.

7. Conclusion

Taken together, the present findings indicate that emotional expressions, and angry expressions in particular, evoke neural dynamics that share structural similarity with previously characterized familiarity-associated patterns. This convergence emerges around 200 ms and persists across mid- and late-stage processing, suggesting that emotional significance can systematically modulate representational dimensions typically associated with face familiarity. These results contribute to a growing body of work showing that familiarity is supported by temporally extended, generalizable neural patterns. Crucially, the contribution of the present study is representational rather than mechanistic: it demonstrates systematic cross-domain similarity in the spatiotemporal structure of EEG patterns associated with familiarity and emotional expressions, without making claims about the specific cognitive or neural processes that give rise to this similarity. Future research can build on this work by examining the conditions under which such representational convergence arises, and by testing its generality across stimulus domains and task contexts.

8. Data availability statement

The data that support the findings of this study are openly available in OSF at <https://osf.io>, reference number <https://osf.io/7xtdy> (Wiese et al., 2022) and <https://osf.io/zf562> (Ely & Ambrus, 2025).

Funding information

This research received no specific grant from any funding agency in the public, commercial, or not-for-profit sectors.

CRediT authorship contribution statement

Madeline Molly Ely: Writing – review & editing, Writing – original draft, Investigation, Formal analysis, Conceptualization. **Géza Gergely Ambrus:** Writing – review & editing, Writing – original draft, Supervision, Software, Formal analysis, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.brainres.2026.150355>.

References

- Addante, R.J., Clise, E., Waechter, R., Bengson, J., Drane, D.L., Perez-Caban, J., 2024. Context familiarity is a third kind of episodic memory distinct from item familiarity and recollection. *Isience* 27 (12), 111439. <https://doi.org/10.1016/j.isci.2024.111439>.
- Adolphs, R., Damasio, H., Tranel, D., Damasio, A.R., 1996. Cortical Systems for the Recognition of Emotion in Facial Expressions. *J. Neurosci.* 16 (23), 7678–7687. <https://doi.org/10.1523/JNEUROSCI.16-23-07678.1996>.
- Ambrus, G.G., 2024. Shared neural codes of recognition memory. *Sci. Rep.* 14 (1), 15846. <https://doi.org/10.1038/s41598-024-66158-y>.
- Ambrus, G.G., Dotzer, M., Schweinberger, S.R., Kovács, G., 2017. The occipital face area is causally involved in the formation of identity-specific face representations. *Brain Struct. Funct.* 222 (9), 4271–4282. <https://doi.org/10.1007/s00429-017-1467-2>.

- Ambrus, G.G., Eick, C.M., Kaiser, D., Kovács, G., 2021. Getting to know you: Emerging neural representations during face familiarization. *J. Neurosci.* 41 (26), 5687–5698. <https://doi.org/10.1523/JNEUROSCI.2466-20.2021>.
- Ambrus, G.G., Kaiser, D., Cichy, R.M., Kovács, G., 2019. The Neural Dynamics of Familiar Face Recognition. *Cereb. Cortex* 29 (11), 4775–4784. <https://doi.org/10.1093/cercor/bhz010>.
- Becker, D.V., Anderson, U.S., Mortensen, C.R., Neufeld, S.L., Neel, R., 2011. The face in the crowd effect unconfounded: Happy faces, not angry faces, are more efficiently detected in single- and multiple-target visual search tasks. *J. Exp. Psychol. Gen.* 140 (4), 637–659. <https://doi.org/10.1037/a0024060>.
- Bowen, H.J., Kark, S.M., Kensinger, E.A., 2018. NEVER forget: negative emotional valence enhances recapitulation. *Psychon. Bull. Rev.* 25 (3), 870–891. <https://doi.org/10.3758/s13423-017-1313-9>.
- Bowles, B., Crupi, C., Mirsattari, S.M., Pigott, S.E., Parrent, A.G., Pruessner, J.C., Yonelinas, A.P., Köhler, S., 2007. Impaired familiarity with preserved recollection after anterior temporal-lobe resection that spares the hippocampus. *Proc. Natl. Acad. Sci.* 104 (41), 16382–16387. <https://doi.org/10.1073/pnas.0705273104>.
- Bruce, V., & Young, A. A. W. (1986). Understanding face recognition. *77*(3), 305–327. doi: 10.1111/j.2044-8295.1986.tb02199.x.
- Burton, A.M., Jenkins, R., Schweinberger, S.R., 2011. Mental representations of familiar faces. *Br. J. Psychol.* 102 (4), 943–958. <https://doi.org/10.1111/j.2044-8295.2011.02039.x>.
- Calder, A.J., Burton, A.M., Miller, P., Young, A.W., Akamatsu, S., 2001. A principal component analysis of facial expressions. *Vision Res.* 41 (9), 1179–1208. [https://doi.org/10.1016/S0042-6989\(01\)00002-5](https://doi.org/10.1016/S0042-6989(01)00002-5).
- Calder, A.J., Young, A.W., 2005. Understanding the recognition of facial identity and facial expression. *Nat. Rev. Neurosci.* 6 (8), 641–651. <https://doi.org/10.1038/nrn1724>.
- Carlson, T. A., Grootswagers, T., & Robinson, A. K. (2020). An Introduction to Time-Resolved Decoding Analysis for M/EEG. In *The Cognitive Neurosciences* (pp. 679–690). The MIT Press. doi: 10.7551/mitpress/11442.003.0075.
- Coelho, C.M., Cloete, S., Wallis, G., 2011. The face-in-the-crowd effect: when angry faces are just cross(es). *J. Vis.* 10 (1), 7. <https://doi.org/10.1167/10.1.7>.
- Collin, C.A., Chamberland, J., LeBlanc, M., Ranger, A., Boutet, I., 2022. Effects of Emotional Expression on Face Recognition May Be Accounted for by image Similarity. *Soc. Cogn.* 40 (3), 282–301. <https://doi.org/10.1521/soco.2022.40.3.282>.
- Dalski, A., Kovács, G., Ambrus, G.G., 2022a. Evidence for a General Neural Signature of Face Familiarity. *Cereb. Cortex* 32 (12), 2590–2601. <https://doi.org/10.1093/cercor/bhab366>.
- Dalski, A., Kovács, G., Ambrus, G.G., 2023. No semantic information is necessary to evoke general neural signatures of face familiarity: evidence from cross-experiment classification. *Brain Struct. Funct.* 228 (2), 449–462. <https://doi.org/10.1007/s00429-022-02583-x>.
- Dalski, A., Kovács, G., Wiese, H., Ambrus, G.G., 2022b. Characterizing the shared signals of face familiarity: long-term acquaintance, voluntary control, and concealed knowledge. *Brain Res.* 1796, 148094. <https://doi.org/10.1016/j.brainres.2022.148094>.
- D'Argembeau, A., Van der Linden, M., 2011. Influence of facial expression on memory for facial identity: Effects of visual features or emotional meaning? *Emotion* 11 (1), 199–202. <https://doi.org/10.1037/a0022592>.
- D'Argembeau, A., Van der Linden, M., Comblain, C., Etienne, A.-M., 2003. The effects of happy and angry expressions on identity and expression memory for unfamiliar faces. *Cogn. Emot.* 17 (4), 609–622. <https://doi.org/10.1080/02699930302303>.
- Deen, B., Husain, G., Freiwald, W.A., 2024. A familiar face and person processing area in the human temporal pole. *PNAS* 121 (28), e2321346121. <https://doi.org/10.1073/pnas.2321346121>.
- Ely, M.M., Ambrus, G.G., 2025. Shared neural dynamics of facial expression processing. *Cogn. Neurodyn.* 19 (1), 45. <https://doi.org/10.1007/s11571-025-10230-4>.
- Ely, M.M., Kelsey, C., Ambrus, G.G., 2026. Shared Neural Codes for Emotion Recognition in Emoji and Human Faces. *Psychophysiology* 63 (3).
- Foa, E.B., Gilboa-Schechtman, E., Amir, N., Freshman, M., 2000. Memory Bias in Generalized Social Phobia. *J. Anxiety Disord.* 14 (5), 501–519. [https://doi.org/10.1016/S0887-6185\(00\)00036-0](https://doi.org/10.1016/S0887-6185(00)00036-0).
- Fox, E., Lester, V., Russo, R., Bowles, R.J., Pichler, A., Dutton, K., 2000. Facial Expressions of Emotion: are Angry Faces Detected more Efficiently? *Cognit. Emot.* 14 (1), 61–92. <https://doi.org/10.1080/026999300378996>.
- Gainotti, G., 2007. Face familiarity feelings, the right temporal lobe and the possible underlying neural mechanisms. *Brain Res. Rev.* 56 (1), 214–235. <https://doi.org/10.1016/j.brainresrev.2007.07.009>.
- Gobbini, M.I., Haxby, J.V., 2007. Neural systems for recognition of familiar faces. *Neuropsychologia* 45 (1), 32–41. <https://doi.org/10.1016/j.neuropsychologia.2006.04.015>.
- Grootswagers, T., Wardle, S.G., Carlson, T.A., 2017. Decoding dynamic brain patterns from evoked responses: a tutorial on multivariate pattern analysis applied to time series neuroimaging data. *J. Cogn. Neurosci.* 29 (4), 677–697. <https://doi.org/10.1162/jocn.a.01068>.
- Hancock, P.J.B., Bruce, V., Burton, A.M., 2000. Recognition of unfamiliar faces. *Trends in Cognitive Sciences* 4 (9), 330–337. [https://doi.org/10.1016/S1364-6613\(00\)01519-9](https://doi.org/10.1016/S1364-6613(00)01519-9).
- Hebart, M.N., Baker, C.I., 2018. Deconstructing multivariate decoding for the study of brain function. *Neuroimage* 180, 4–18. <https://doi.org/10.1016/j.neuroimage.2017.08.005>.
- Jackson, M.C., Raymond, J.E., 2008. Familiarity Enhances Visual Working memory for Faces. *J. Exp. Psychol. Hum. Percept. Perform.* 34 (3), 556–568. <https://doi.org/10.1037/0096-1523.34.3.556>.

- Jackson, M.C., Wu, C.-Y., Linden, D.E.J., Raymond, J.E., 2009. Enhanced visual short-term memory for angry faces. *J. Exp. Psychol. Hum. Percept. Perform.* 35 (2), 363–374. <https://doi.org/10.1037/a0013895>.
- Johansson, M., Mecklinger, A., Treese, A.-C., 2004. Recognition memory for Emotional and Neutral Faces: an Event-Related potential Study. *J. Cogn. Neurosci.* 16 (10), 1840–1853. <https://doi.org/10.1162/0898929042947883>.
- Karimi-Rouzbahani, H., Ramezani, F., Woolgar, A., Rich, A., Ghodrati, M., 2021. Perceptual difficulty modulates the direction of information flow in familiar face recognition. *Neuroimage* 233, 117896. <https://doi.org/10.1016/j.neuroimage.2021.117896>.
- Klink, H., Kaiser, D., Stecher, R., Ambrus, G.G., Kovács, G., 2023. Your place or mine? the neural dynamics of personally familiar scene recognition suggests category independent familiarity encoding. *Cereb. Cortex* 33 (24), 11634–11645.
- Kok, R., Taubert, J., Van der Burg, E., Rhodes, G., Alais, D., 2017. Face familiarity promotes stable identity recognition: Exploring face perception using serial dependence. *R. Soc. Open Sci.* 4 (3). <https://doi.org/10.1098/rsos.160685>.
- Kottror, T.M., 1989. Recognition of faces by adults. *Psychol. Stud.* 34 (2), 102–105.
- Kramer, R.S.S., Young, A.W., Burton, A.M., 2018. Understanding face familiarity. *Cognition* 172, 46–58. <https://doi.org/10.1016/j.cognition.2017.12.005>.
- Landi, S.M., Viswanathan, P., Serene, S., Freiwald, W.A., 2021. A fast link between face perception and memory in the temporal pole. *Science* 373 (6554), 581–585. <https://doi.org/10.1126/science.abi6671>.
- Langeslag, S.J.E., Morgan, H.M., Jackson, M.C., Linden, D.E.J., Van Strien, J.W., 2009. Electrophysiological correlates of improved short-term memory for emotional faces. *Neuropsychologia* 47 (3), 887–896. <https://doi.org/10.1016/j.neuropsychologia.2008.12.024>.
- Lee, H.J., Cho, Y.S., 2019. Memory facilitation for emotional faces: Visual working memory trade-offs resulting from attentional preference for emotional facial expressions. *Mem. Cognit.* 47 (6), 1231–1243. <https://doi.org/10.3758/s13421-019-00930-8>.
- Lí, C., Burton, A.M., Ambrus, G.G., Kovács, G., 2022. A neural measure of the degree of face familiarity. *Cortex* 155, 1–12. <https://doi.org/10.1016/j.cortex.2022.06.012>.
- Liu, C.H., Chen, W., Ward, J., 2014. Remembering faces with emotional expressions. *Front. Psychol.* 5. <https://doi.org/10.3389/fpsyg.2014.01439>.
- Lundqvist, D., Flykt, A., & Öhman, A. (1998). The Karolinska Directed Emotional Faces. Department of Clinical Neuroscience, Psychology section, Karolinska Institutet.
- McLelland, V.C., Chan, D., Ferber, S., Barense, M.D., 2014. Stimulus familiarity modulates functional connectivity of the perirhinal cortex and anterior hippocampus during visual discrimination of faces and objects. *Front. Hum. Neurosci.* 8. <https://doi.org/10.3389/fnhum.2014.00117>.
- Moerel, D., Grootswagers, T., Robinson, A.K., Shatek, S.M., Woolgar, A., Carlson, T.A., Rich, A.N., 2022. The time-course of feature-based attention effects dissociated from temporal expectation and target-related processes. *Sci. Rep.* 12 (1), 6968. <https://doi.org/10.1038/s41598-022-10687-x>.
- Mogg, K., Bradley, B.P., 1999. Orienting of attention to Threatening Facial Expressions Presented under Conditions of Restricted Awareness. *Cognit. Emot.* 13 (6), 713–740. <https://doi.org/10.1080/026999399379050>.
- Öhman, A., Lundqvist, D., Esteves, F., 2001. The face in the crowd revisited: a threat advantage with schematic stimuli. *J. Pers. Soc. Psychol.* 80 (3), 381–396. <https://doi.org/10.1037/0022-3514.80.3.381>.
- Ozdemir, B., Ambrus, G.G., 2025. From encoding to recognition: Exploring the shared neural signatures of visual memory. *Brain Res.* 1857, 149616. <https://doi.org/10.1016/j.brainres.2025.149616>.
- Popova, T., Wiese, H., 2022. The time it takes to truly know someone: Neurophysiological correlates of face and identity learning during the first two years. *Biol. Psychol.* 170, 108312. <https://doi.org/10.1016/j.biopsycho.2022.108312>.
- Popova, T., Wiese, H., 2023. How quickly do we learn new faces in everyday life? Neurophysiological evidence for face identity learning after a brief real-life encounter. *Cortex* 159, 205–216. <https://doi.org/10.1016/j.cortex.2022.12.005>.
- Ramon, M., Vizioli, L., Liu-Shuang, J., Rossion, B., 2015. Neural microgenesis of personally familiar face recognition. *Proc. Natl. Acad. Sci.* 112 (35), E4835–E4844. <https://doi.org/10.1073/pnas.1414929112>.
- Righi, S., Marzi, T., Toscani, M., Baldassi, S., Ottonello, S., Viggiano, M.P., 2012. Fearful expressions enhance recognition memory: Electrophysiological evidence. *Acta Psychol.* 139 (1), 7–18. <https://doi.org/10.1016/j.actpsy.2011.09.015>.
- Rugg, M.D., Yonelinas, A.P., 2003. Human recognition memory: a cognitive neuroscience perspective. *Trends Cogn. Sci.* 7 (7), 313–319. [https://doi.org/10.1016/S1364-6613\(03\)00131-1](https://doi.org/10.1016/S1364-6613(03)00131-1).
- Savage, R.A., Lipp, O.V., Craig, B.M., Becker, S.I., Horstmann, G., 2013. In search of the emotional face: Anger versus happiness superiority in visual search. *Emotion* 13 (4), 758–768. <https://doi.org/10.1037/a0031970>.
- Schindler, S., Bublatzky, F., 2020. Attention and emotion: an integrative review of emotional face processing as a function of attention. *Cortex* 130, 362–386. <https://doi.org/10.1016/j.cortex.2020.06.010>.
- Švegar, D., Kardum, I., Polić, M., 2013. Happy face superiority effect in change detection paradigm. *Psihologijske Teme* 22 (2), 249–269.
- Tay, P.K.C., Yang, H., 2017. Angry faces are more resistant to forgetting than are happy faces: directed forgetting effects on the identity of emotional faces. *J. Cogn. Psychol.* 29 (7), 855–865. <https://doi.org/10.1080/20445911.2017.1323907>.
- Teichmann, L., Moerel, D., Baker, C., Grootswagers, T., 2022. An Empirically Driven Guide on using Bayes Factors for M/EEG Decoding. *Aperture Neuro* 2, 1–10. <https://doi.org/10.52294/ApertureNeuro.2022.2.MAOC6465>.
- Vuilleumier, P., Pourtois, G., 2007. Distributed and interactive brain mechanisms during emotion face perception: evidence from functional neuroimaging. *Neuropsychologia* 45 (1), 174–194. <https://doi.org/10.1016/j.neuropsychologia.2006.06.003>.
- Wetzels, R., Matzke, D., Lee, M.D., Rouder, J.N., Iverson, G.J., Wagenmakers, E.-J., 2011. Statistical evidence in Experimental Psychology. *Perspect. Psychol. Sci.* 6 (3), 291–298. <https://doi.org/10.1177/1745691611406923>.
- Wiese, H., Anderson, D., Beierholm, U., Tüttenberg, S.C., Young, A.W., Burton, A.M., 2022. Detecting a viewer's familiarity with a face: evidence from event-related brain potentials and classifier analyses. *Psychophysiology* 59 (1), 1–21. <https://doi.org/10.1111/psyp.13950>.
- Wiese, H., Hobden, G., Siilbek, E., Martignac, V., Flack, T.R., Ritchie, K.L., Young, A.W., Burton, A.M., 2021. Familiarity is familiarity: Event-related brain potentials reveal qualitatively similar representations of personally familiar and famous faces. *J. Exp. Psychol. Learn. Mem. Cogn.* <https://doi.org/10.1037/xlm0001063>.
- Wiese, H., Schipper, M., Popova, T., Burton, A.M., Young, A.W., 2023. Personal familiarity of faces, animals, objects, and scenes: Distinct perceptual and overlapping conceptual representations. *Cognition* 241, 105625. <https://doi.org/10.1016/j.cognition.2023.105625>.
- Wiese, H., Schweinberger, S.R., 2011. Accessing semantic person knowledge: Temporal dynamics of nonstrategic categorical and associative priming. *J. Cogn. Neurosci.* <https://doi.org/10.1162/jocn.2010.21432>.
- Yonelinas, A.P., Jacoby, L.L., 1996. Noncritical recollection: Familiarity as automatic, irrelevant recollection. *Conscious. Cogn.* <https://doi.org/10.1006/ccog.1996.0008>.