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Neural correlates of retrospective memory confidence during face–name associative learning

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The ability to accurately assess one's own memory performance during learning is essential for adaptive behavior, but the brain mechanisms underlying this metamemory function are not well understood. We investigated the neural correlates of memory accuracy and retrospective memory confidence in a face–name associative learning task using magnetoencephalography in healthy young adults ($n = 32$). We found that high retrospective confidence was associated with stronger occipital event-related fields during encoding and widespread event-related fields during retrieval compared to low confidence. On the other hand, memory accuracy was linked to medial temporal activities during both encoding and retrieval, but only in low-confidence trials. A decrease in oscillatory power at alpha/beta bands in the parietal regions during retrieval was associated with higher memory confidence. In addition, representational similarity analysis at the single-trial level revealed distributed but differentiable neural activities associated with memory accuracy and confidence during both encoding and retrieval. In summary, our study unveiled distinct neural activity patterns related to memory confidence and accuracy during associative learning and underscored the crucial role of parietal regions in metamemory.

Key words: associative learning; magnetoencephalography; memory confidence; metamemory; neural oscillations.

Introduction

Despite the indisputable complexity of memories, they are often categorized as either remembered or forgotten, both in real life and in the laboratory. However, there is more to memory than just objective accuracy: memory retrieval is linked to subjective confidence in the accuracy of recalled information (Dunlosky and Bjork 2013). This process of metamemory monitoring (Nelson 1990; Koriat 2007; Chua et al. 2014) is crucial for guiding effective learning especially when no immediate external feedback is available. Metamemory monitoring encompasses the entire learning process (Chua et al. 2014). For example, judgment of learning (JOL) (Schwartz 1994; Müller et al. 2016; Irak et al. 2019) is an assessment made after memory encoding about how likely it will be remembered in the future. On the other hand, retrospective confidence judgment (RCJ) is made after memory retrieval and reflects the confidence in the accuracy of previously retrieved memories (Chua et al. 2006, 2009; Martín-Luengo et al. 2021). Recent behavioral studies have demonstrated that RCJ appears to be a better predictor of future memory performance compared to JOL (Robey et al. 2017; Putnam et al. 2022), as it prompts participants to more accurately utilize valid information to identify study items requiring further review.

Memory accuracy and confidence are often interrelated and hard to disassociate during learning (Chua et al. 2012; Roediger 3rd and DeSoto 2014). In the context of recognition memory, familiarity refers to a sense of prior exposure to a stimulus, while recollection involves the retrieval of specific details or contextual information (Yonelinas 2002; Woodruff et al. 2006; Migo et al.

2012). During memory retrieval, high-confidence correct answers are typically associated with recollection, whereas familiarity is associated with a broader range of lower confidence ratings (Yonelinas 2002; Skinner and Fernandes 2007). Importantly, memory confidence has been shown to modulate the brain activities related to both familiarity (Woodruff et al. 2006; Woroch and Gonsalves 2010; Yu and Rugg 2010) and recollection (Curran 2004; Kim and Cabeza 2007, 2009; Rutishauser et al. 2018). Furthermore, confidence ratings can be utilized to better parse out brain responses during encoding related to subsequently remembered versus forgotten items (Brewer et al. 1998; Wagner et al. 1998; Paller and Wagner 2002) by excluding instances where correct responses stem from lucky guessing rather than actual memory (Otten et al. 2001). Recent electroencephalography (EEG) studies incorporating subjective memory measures found a complex interaction of confidence with subsequent memory effect (Wiemer et al. 2021) and independent subsequent memory confidence effects (Wynn et al. 2019). Specifically, correctly memorized items with high confidence are associated with stronger event-related potentials (ERPs) in parietal channels compared to correctly memorized responses with low confidence during memory encoding (Wynn et al. 2019).

Synchronization and desynchronization of neural activity are thought to reflect the efficiency of information processing in the brain (Fries 2015; Hanslmayr et al. 2016; Parish et al. 2018). Successful memory encoding has been found to be associated with increased synchrony in the theta and gamma bands and decreased synchrony in the alpha and beta bands (Klimesch

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1996; Gruber et al. 2004; Osipova et al. 2006; Hanslmayr et al. 2012; Cruzat et al. 2021). Evidence of neural oscillations that support memory confidence during learning is scarcer compared to that supporting memory accuracy (Hanslmayr et al. 2009; Wynn et al. 2019, 2020). Some recent evidence suggests that decreases in alpha/beta power track the fidelity of internally generated stimulus-specific information (Griffiths et al. 2019), and alpha power modulations are associated with subjective perceptual experience and metacognitive abilities (Trajkovic et al. 2023). Despite evidence linking subjectively perceived memory confidence with distinct ERPs and oscillations during both memory encoding and retrieval (Wynn et al. 2018, 2019, 2020), pinpointing the brain origin for these metamemory-related electrophysiological activities remains a challenge due to the limitations of EEG's spatial resolution.

Memory confidence has been mapped to several brain regions in functional magnetic resonance imaging (fMRI) studies during encoding (Chua et al. 2004) and recognition (Chua et al. 2006). Left inferior frontal gyrus activity during encoding is sensitive to subsequent high confidence, regardless of accuracy, whereas the medial temporal lobes (MTLs) exhibit heightened activation specifically for subsequent responses that are both confident and accurate (Chua et al. 2004). Confidence assessment of memory seems to activate more medial and lateral parietal regions compared to a recognition task, and different levels of confidence judgments could modulate the neural activity in the hippocampus, cingulate, and other limbic regions (Chua et al. 2006). In addition, one study using single-unit recordings identified a population of memory-selective neurons in the human hippocampus and amygdala, whose activity signaled stimulus familiarity and confidence, as assessed by subjective reports (Rutishauser et al. 2015). Overall, converging evidence suggests that memory confidence is associated with neural activities at distributed brain regions including MTL, prefrontal and parietal cortices during memory encoding and retrieval (Kuchinke et al. 2013; Martín-Luengo et al. 2021; Wynn and Nyhus 2022). However, the sluggish temporal resolution of fMRI blood-oxygen-level-dependent (BOLD) responses hinders our understanding of the dynamic processes of memory confidence.

In this study, we investigated the neural correlates of memory accuracy and retrospective memory confidence to elucidate their dynamic and distinct neural patterns during associative learning. Magnetoencephalography (MEG) was used to capture brain activities at a millisecond resolution during face-name associative learning. We used event-related fields (ERFs), which are time- and phase-locked brain responses to stimuli, neural oscillations, and single-trial neural representations to systematically explore the rich information embedded in the MEG signal. In addition, we conducted source localization for these analyses, leveraging MEG's good spatial resolution to pinpoint the approximate location of the observed effects. We hypothesized a positive correlation between confidence and the accuracy of retrieved face-name associations in the behavioral measures. Regarding the ERFs, we expected to observe a memory accuracy-related effect similar to findings reported in previous studies (Rugg and Curran 2007; Kwon et al. 2023). However, we hypothesized that retrospective memory confidence would correlate with distinct but partially overlapping ERF brain responses compared to memory accuracy during both memory encoding and retrieval (Paller and Wagner 2002; Wynn et al. 2019, 2020). Furthermore, we hypothesized that neural oscillations, particularly in the alpha/beta bands, would also contribute to memory confidence, besides accuracy-related processes (Hanslmayr et al. 2012; Griffiths et al. 2019; Trajkovic

et al. 2023). Lastly, we utilized the rich behavioral information during learning to model the dynamic changes in memory confidence and accuracy using representational similarity analysis (RSA) (Kriegeskorte et al. 2008) at the single-trial level. While this novel analysis method is exploratory, we anticipate that the RSA will unveil distinct neural representations specifically associated with memory confidence and accuracy at the single-trial level.

Materials and methods

Ethics statement

The ethical approval for carrying out the study was obtained from the Ethics Committee of the University of Jyväskylä, Finland, and the study was conducted in accordance with the Declaration of Helsinki. All the participants gave their informed consent in written format prior to participation in the MEG experiments. After the MEG experiment, each participant received a gift card (10 euros) as compensation for their time in the MEG recording.

Participants

In total, 32 participants (mean: 25.1 yr, standard deviation (SD): 4.3 yr, range 20 to 35 yr, 9 males, 1 left-handed) were included in this study. They were mainly university students recruited by email lists and posters. Participants were screened for the following exclusion criteria: cardiovascular disease, severe sensory impairment (vision or hearing), neurological disorders, neurodevelopmental disorders (such as ADHD, dyslexia), neurodegenerative disease (e.g. dementia), medication affecting the central nervous system, brain injuries, and metal object in the body including dental braces and piercings.

Stimuli and task

Face stimuli were from the Chicago Face Database (Ma et al. 2015). Name stimuli were from lists of popular male and female names for people born between 1920 and 2019 from the U.S. Social Security Administration websites (<https://www.ssa.gov/oact/babynames/decades/century.html>). Forty faces were randomly selected from the database and paired with gender-matched names. The faces were selected based on the following criteria: age between 20 and 35 yr, an equal number of male and female faces, and an equal number of faces from four racial backgrounds (Ma et al. 2015). Another four face-name pairs were used for practice at the beginning of the experiment.

The experiment as illustrated in Fig. 1A started with a 3-min resting-state recording followed by a practice session. The actual task included six blocks of training and testing with a 2-min resting period between each block. During the 2-min resting period, the participants were instructed to relax and look at the fixation cross at the center of the screen. The resting period served to alleviate the potential working memory effect between encoding and immediate testing and to minimize participant fatigue after learning. All 40 faces were randomly presented in each training and testing block. All the trials in the training and testing phase started with a 500-ms fixation cross. In each trial of the training phase, a person's face was displayed on the screen (500 ms) followed by his/her name (1,000 ms). The trial was followed by a blank screen for a random duration of 500 to 1500 ms to give enough time for the encoding. In the testing phase, participants were first presented with the person's face only for 500 ms. Then, immediately after the face offset, a list of 4 names including the correct name for that face and 3 other names randomly drawn from the list of the remaining 19 gender-matched names were presented on the screen. The participants were asked to choose

the correct name for that face. After the participants made a selection using the response pad, they were asked to rate how certain they remembered the name correctly in a range of 1 to 4. Text labels were given for rating 1 (“I guessed”) and 4 (“I remembered”). Note that prior to the experiment, participants were carefully instructed to evaluate confidence using this scale. There was a maximum of 5-s response time for both selecting the name and the rating. There were also two repetitions of face-only (500 ms) trials followed by a fixation cross without presenting a selection of names and ratings for each face–name pair, and these trials were randomly mixed with the actual memory test trials during the test phase. There was a fixation cross presented for 700 to 1,500 ms (random) after each face-only trial until the next face presentation. The participants were instructed that there were those face-only trials, and they did not receive specific instruction on those trials. Only the face-only trials were used to investigate the neural correlates of memory confidence during retrieval. After each test session, the participants were allowed a short break and motivated by feedback: They were informed of accuracy (% of names correctly remembered) on the latest block and overall. No feedback was given for specific face–name pairs.

Recording

MEG data were recorded with the 306-channel Elekta Neuromag TRIUX system (MEGIN OY, Helsinki, Finland) in a magnetically shielded room located at the University of Jyväskylä. Data were band-pass filtered online at 0.1 to 330 Hz and stored at 1 kHz. Five head position indicator (HPI) coils were used to track the head position inside the MEG helmet continuously. Three of the HPI coils were placed on the participant’s forehead and one behind each ear. Before the MEG experiment, the position of three anatomic landmarks (nasion, left, and right preauricular points), the five HPI coils, and the head shape (>100 points evenly distributed over the scalp) were digitized using the Polhemus Isotrak digital tracker system (Polhemus, Colchester, VT, United States). The MEG gantry was in a 68° upright position during the recording with participants sitting comfortably in a chair.

The electrooculogram was recorded with two electrodes attached diagonally: one slightly below the left eye and the other slightly above the right eye. The electrocardiogram was recorded with one electrode placed on top of the right clavicle and the other one on the left lower ribs. The ground electrode was placed on the back of the neck. Respiration was monitored with a reusable fabric belt (RESPA00000; Spes Medica, Italy), which was fastened on top of the clothes on the lower chest area.

Data analysis

Behavioral data analysis

Trials were sorted based on accuracy and confidence rating during the retrieval phase. Accuracy was categorized into correct and incorrect based on the button responses. The trial counts for different confidence ratings exhibited considerable intersubject variation (mean \pm SD for rating 1: 64.2 ± 31.8 ; rating 2: 43.3 ± 24.6 ; rating 3: 35.0 ± 15.7 ; rating 4: 96.9 ± 31.5), as shown in Fig. 1E. Specifically, some participants had very few confidence ratings of 2 or 3. This variability may be partially attributed to differences in learning speed, but it also suggests that participants may have distinct preferences or criteria for mapping their retrospective memory performance onto their internal confidence representation. The limited availability of data for the middle range of confidence ratings posed a challenge for separate analyses of confidence ratings. Moreover, to facilitate comparison with previous literature on memory confidence that typically

utilized high and low confidence contrasts (Wynn et al. 2019, 2020), the confidence ratings were partitioned into two distinct categories for subsequent analysis: high confidence (HC, rating 4) and low confidence (LC, ratings 1 to 3). To control for the possible confounding effect of memory accuracy, we further divided the trials based on accuracy and confidence jointly, yielding four categories: HC-Correct, HC-Incorrect, LC-Correct, and LC-Incorrect (Fig. 1F). There were very few HC-incorrect trials for most of the participants, which indicates a good metamemory in this task. Thus, analysis was focused on the remaining three conditions. To quantify participants’ metacognitive ability, AUROC2 and type 2 d-prime (Dunlosky and Bjork 2013; Fleming and Lau 2014) were calculated based on accuracy and confidence ratings (Fig. 1G). All but one participant demonstrated fair metamemory: Participant nr 17 had scores lower than 1.5 times the interquartile range below the first quartile and was thus excluded from MEG analysis.

MEG data analysis

MEG data were first processed with Maxfilter (MEGIN OY, version 3.0.17) software to remove external noise interference and compensate for head movement during the recording. Bad MEG channels were identified manually and were excluded when running the Maxfilter program and the time series of the bad channels were reconstructed by Maxfilter. The movement-compensated temporal signal-space separation method (Taulu and Simola 2006) was used in the Maxfilter settings. MEG data were then analyzed using MNE Python (version: 1.1.0) (Gramfort et al. 2013). First, bad segments of MEG data were annotated and excluded from further analysis. A 40-Hz low-pass filter (zero-phase finite impulse response (FIR) filter with a “hamming” window) was applied to the MEG data. Fast independent component analysis (ICA) (Hyvärinen 1999) was employed to remove eye movement-related and cardiac artifacts. After applying ICA, MEG data were split into epochs 200 ms before and 2000 ms after the stimulus onset for the encoding trials and 1,000 ms after the stimulus onset for the face-only retrieval trials. A correction of 25 ms was applied to the epochs due to a time delay, which was measured with a photodiode, between the stimulus onset on the screen and the trigger signal in the recorded MEG data. Epochs were first rejected based on the maximum peak-to-peak amplitude ($\text{mag} = 5\text{e-}12$ T, $\text{grad} = 1500\text{e-}13$ T/m) and then visually inspected in case of some remaining artifacts. Baseline correction was done by subtracting the mean amplitude of the 200-ms data prior to the stimulus onset from all the data points in the epoch in each channel.

For source analysis of the ERF responses, a depth-weighted ($P = 0.8$) minimum-norm estimates method (MNE) (Hämäläinen and Ilmoniemi 1994; Lin et al. 2006) was used. Since individual MRIs were not available for this dataset, the Freesurfer average brain template (“fsaverage”) was used. The template brain was scaled uniformly and coregistered to the digitized head points of the participants using an automated approach described in Houck and Claus (2020). For the forward model, source space with the “ico4” option was used, which results in $\sim 2,562$ sources per hemisphere with an average of 6.2 mm between each source. A single-layer boundary-element model was created assuming the homogeneous conductivity of the intracranial volume. Noise-covariance matrix was estimated based on the baseline time window (-200 to 0 ms). Dynamic statistical parameter map (dSPM) was used for noise normalization after calculating the MNE inverse solution (Dale et al. 2000) with free source orientations. Pooling is performed by taking the norm of the free orientations for each source location in dSPM.

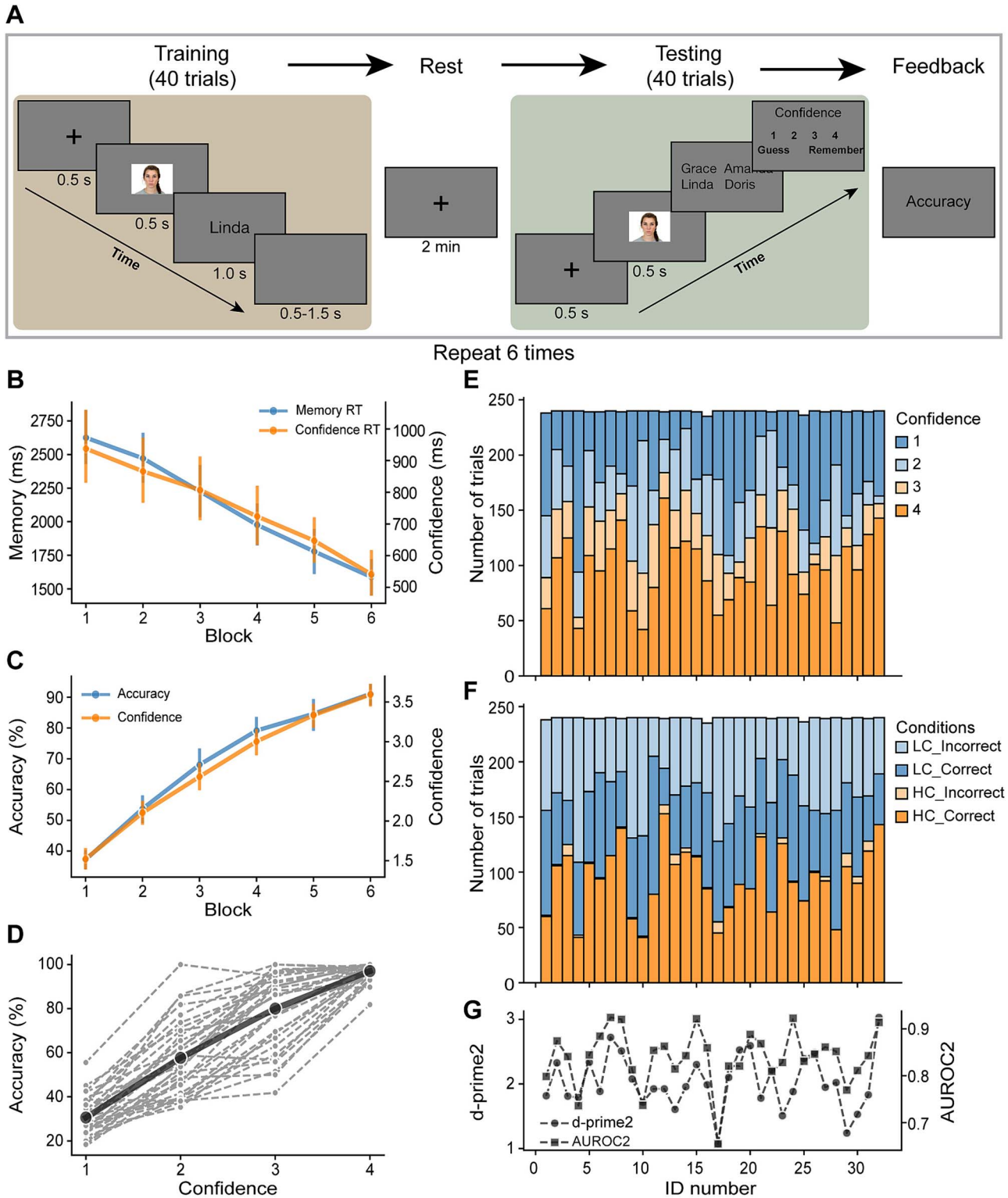


Fig. 1. Experimental design and behavioral performance. A) In the face-name task, participants were instructed to learn 40 unique associations over the course of 6 blocks of training and testing. B) Average reaction time for each block during memory retrieval and confidence rating. C) Accuracy and confidence rating for each block. In B and C, the vertical bars represent 95% confidence interval (CI). D) Accuracy averaged by confidence rating for each participant (gray lines) and the whole group (black line). E) Total number of memory retrievals in each confidence rating category for each participant (x axis). F) Total number of memory retrievals in four categories formed by combining information of accuracy (correct and incorrect) and confidence rating (LC=low confidence, ratings 1-3; HC=high confidence, rating 4) for each participant. G) Type 2 d-prime and AUROC2 for each participant (see methods for details).

Time–frequency analysis was conducted at both sensor and source space to provide the timing and location information of the neural oscillations. The same preprocessing was conducted for the time–frequency analysis as for the ERF analysis, except that we did not apply the 40-Hz low-pass filter and each trial was segmented with a longer length (–1.5 to 3 s for encoding trials and –1.5 to 2 s for the retrieval trials) to avoid edge effects caused by time–frequency decomposition. Corresponding ERF responses were subtracted from single trials in each condition. Sensor and source TFR (time–frequency representation) power was calculated using a Morlet wavelet with varying number of cycles equal to $F/2$ (at a given frequency F) in theta (4 to 7 Hz), alpha (8 to 13 Hz), beta (14 to 30 Hz), and gamma (40 to 90 Hz) frequency bands. Baseline correction was done by subtracting the mean of baseline values (–0.4 to –0.2 s) followed by dividing by the mean of baseline values. The same forward model was used in the TFR source analysis as in the source analysis of the ERF response. For the dSPM inverse solution, the regularization parameter λ_2 was changed to $1/9$ and the number of averages used to scale the noise covariance matrix was changed to 1 to account for the single trial data used for the time–frequency analysis.

Representational similarity analysis was used to further disentangle the neural representation of memory accuracy and confidence in the brain and also provide additional information on stimuli-related information processing during learning (Kriegeskorte et al. 2008). Both stimulus-related and learning-related representational dissimilarity matrices (RDMs) were constructed using the `mne-rsa` package (<https://users.aalto.fi/~#x007E;vanvlm1/mne-rsa/>, version 0.9) on single-trial data across the whole experiment. The following stimulus-related properties were used for calculating RDM models: grayscale image, age, gender, and identity of each face. The stimuli-related RDMs were constructed to control and partial out the potential effects of different properties of the visual stimuli (faces). In addition, it was used to validate the RSA pipeline since the stimuli-related brain processing has been more extensively explored with clear spatial and temporal information based on earlier studies (Liu et al. 2002; Haxby and Gobbini 2011; Vida et al. 2017; Ambrus et al. 2019; Dobs et al. 2019; Kaiser and Nyga 2020). The learning-related RDM models were calculated using the accuracy, confidence rating, reaction time of accuracy (RT_memory), and reaction time of confidence ratings (RT_confidence) associated with each trial. Pixel-level correlation was used as the distance metric to compute the dissimilarity matrix (DSM) for grayscale face images. Euclidean distance was used as the distance metric for age, rating, RT_memory, and RT_confidence. For accuracy (correct and incorrect), gender (male and female), and identity (40 different faces), the distance metric is defined as 0 if the corresponding properties for the pair of trials are the same and 1 if not (Vida et al. 2017). Representational similarity analysis was computed in both sensor and source space using a (spatio)temporal searchlight approach. For sensor-level RSA, we employed a searchlight approach over time (temporal radius = 10 ms), pooling data from all 306 sensors for each searchlight. To compensate for the varying signal units and magnitudes between magnetometers and gradiometers, we applied a noise covariance matrix calculated from prestimulus data to normalize the data. For source-level RSA, the same forward and inverse model was used as in the source-level time–frequency analysis since both analyses were done at the single-trial level. RSA searchlight was calculated for the 68 parcellation labels from Desikan-Killiany Atlas (Desikan et al. 2006) and with a 10-ms temporal

radius. Pearson's correlation was used as a distance metric to compute the neural DSM for each epoch. Spearman's ranked partial correlation (ρ) was used as the RSA metric to compare the neural and certain theoretical model DSM to partial out the effects of all the other model DSMs. The partial correlation coefficients were transformed into Fisher's Z-scores for statistical analysis.

Statistical analysis

As mentioned above, data from all 32 participants were included in the behavioral analyses and one participant was excluded from MEG analyses due to poor metamemory. Repeated-measures analysis of variance was used to examine changes in the behavioral response (accuracy, confidence ratings, and reaction time for both) across the six blocks of training. Spearman's ρ was used to analyze correlation between accuracy and confidence ratings. For the MEG data, individual trials during encoding and retrieval were grouped based on both accuracy and confidence of the specific face–name pair in the retrieval test within the same block. This provides accurate and dynamic information about memory confidence and accuracy for each face–name pair across the encoding and retrieval blocks. Due to the uneven distribution of trials into different accuracy and confidence categories (see Fig. 1), the effect of confidence on ERF and TFR was studied by comparing HC-Correct with LC-Correct trials. The effect of accuracy was studied by comparing LC-Correct with LC-Incorrect trials. For the two comparisons described above, trial numbers were equalized by minimizing the time differences between each event type to control for potential difference caused by a different signal-to-noise ratio.

To correct for multiple comparisons across time and spatial points, spatiotemporal cluster-based permutation statistical tests (Maris and Oostenveld 2007) were used. To avoid the issue of specifying a free yet somewhat arbitrary threshold for the initial clustering, the threshold-free cluster enhancement method ($h_power = 2.00$, $e_power = 0.50$, $start = 0$, $step = 0.2$) was utilized (Smith and Nichols 2009). The analysis time window spanned 0 to 2 s from face stimulus onset for encoding and 0 to 1 s for retrieval in all analyses (ERF, TFR, and single-trial RSA). The number of permutations was set to 1,000, and the statistical alpha level was set at 0.05 for all tests. In addition, we applied the Bonferroni correction where the significance level ($P = 0.05$) was divided by the number of tests conducted in each comparison (i.e. for the confidence effect in TFR analysis, the number of tests was 2 [sensor, source] \times 4 [frequency bands] = 8).

Results

Behavioral performance in the face–name associative learning task

Memory accuracy ($F(5, 155) = 252.03$, $P < 0.001$) and confidence ($F(5, 155) = 355.68$, $P < 0.001$) improved across the six blocks of training and testing while reaction times for the memory ($F(5, 155) = 78.17$, $P < 0.001$) and the confidence rating ($F(5, 155) = 27.72$, $P < 0.001$) decreased (see Fig. 1B,C). Accuracy and confidence rating correlated positively ($n = 32$, $\rho = 0.885$, $P < 0.001$) (see Fig. 1D). Type 2 d' -prime (2.03 ± 0.43) and AUROC2 (0.84 ± 0.06) (Fig. 1G) provided converging results that all but one participant (nr. 17, excluded from further analyses) had good metamemory. That is, overall, participants learned the 40 face–name pairs and were well aware of the accuracy of their memory during learning.

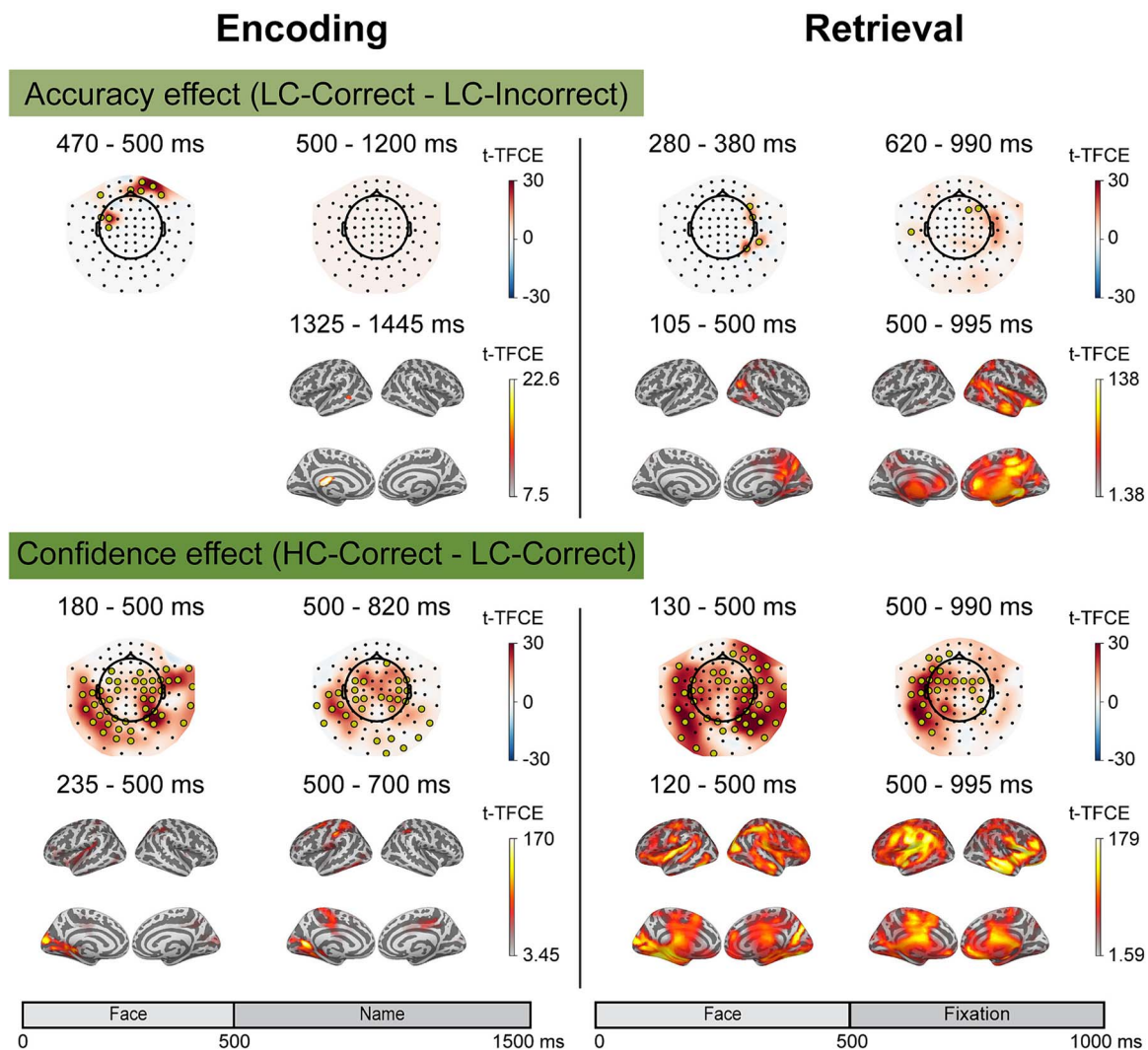


Fig. 2. Sensor and source ERF statistical results for accuracy and confidence effects during memory encoding and retrieval. The plots visualize significant effects ($P < 0.025$) during encoding (left) and retrieval (right) at both sensor (top rows) and source (bottom lows) level. For visualization purposes, the plots for the significant effects are split into two parts (face, name/fixation) based on the stimuli presented on the screen. The time windows (start-end, in ms) of the significant effects are displayed above the sensor and source plots. Sensor-level topographic plots show the t-TFCE values for the significant spatiotemporal points averaged in the time window. Yellow dots highlight the channels that are consistently significant during the time window. Source plots showed the t-TFCE values of the brain areas that showed significant effects over the time window.

ERF activity related to memory confidence and accuracy during learning

ERFs related to memory accuracy and confidence were investigated at sensor and source level (see Fig. 2 and Supplementary Fig. S1). There were significant effects ($P < 0.025$) of accuracy (LC-Correct > LC-Incorrect) during both encoding (sensor: 470 to 1,200 ms; source: 1,325 to 1,445 ms) and retrieval (sensor: 280 to 990 ms; source: 105 to 995 ms). There were also significant effects ($P < 0.025$) of memory confidence (HC-Correct > LC-Correct) during both encoding (sensor: 180 to 820 ms; source: 235 to 700 ms) and retrieval (sensor: 130 to 990 ms; source: 120 to 995 ms).

Oscillatory activity related to memory confidence and accuracy during learning

The neural oscillations that are correlated with accuracy and retrospective memory confidence were analyzed in a similar manner as the ERFs (see Fig. 3 and Supplementary Fig. S2 for a summary of results). No statistically significant accuracy effect ($P > 0.00625$)

was found for encoding or retrieval at any frequency bands. Significant confidence effects ($P < 0.00625$, HC-Correct < LC-Correct) were found only during memory retrieval and specifically at alpha (sensor: 15 to 1,000 ms; source: 245 to 1,000 ms) and beta (sensor: 0 to 1,000 ms; source: 0 to 1,000 ms) frequency bands. The effects at both frequency bands were most pronounced around the left and right parietal and occipital regions in the time window of 500 to 1,000 ms.

Neural representation of stimulus- and learning-related information during face-name associative learning

To disentangle the cognitive processes of perception and (meta)memory during encoding and retrieval, we employed RSA combined with spatiotemporal searchlight at source level (Fig. 4A). This approach enabled us to investigate the temporal dynamics and spatial location of these processes during learning at the single-trial level. In addition, sensor-level RSA was carried out using a temporal searchlight and pooling over all

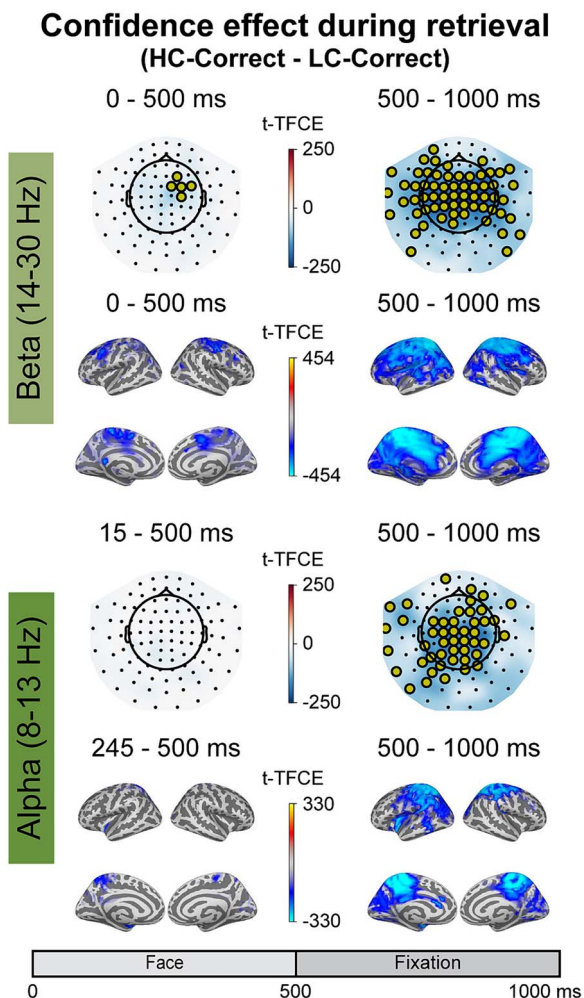


Fig. 3. Sensor and source TFR statistical results for memory confidence effect during retrieval. The plots visualize statistically significant effects ($P < 0.00625$) during retrieval at both sensor (top rows) and source (bottom lows) level. For visualization purposes, the plots for the significant effects are split into two parts (face, fixation) based on the stimuli presented on the screen. The time window (start–end, in ms) of the significant effects are displayed above the sensor and source plots. Sensor-level topographic plots show the t-TFCE values for the significant spatiotemporal points averaged in the time window. Yellow dots highlight the channels that are consistently significant during the time window. Source plots showed the t-TFCE values of the brain areas that showed significant effects over the time window.

306 channels. The sensor-level RSA results (reported in the [Supplementary Fig. S3](#)) were largely comparable to the source-level results concerning the timing of the significant effects. However, they appeared to be less pronounced, likely due to a loss of sensitivity resulting from channel pooling.

During memory encoding, significant partial correlations ($P < 0.025$) emerged between the pixel image representation and brain activity most pronounced in the occipital cortex in the time window of 70 to 390 ms. A similar significant effect was observed for face identity ($P < 0.025$, 40 to 990 ms) and gender ($P < 0.025$, 40 to 950 ms). Age effect was not detected ($P > 0.025$). Among the learning-related RDMs, significant partial correlation ($P < 0.025$) was found for both memory accuracy (220 to 1,000 ms) and confidence (240 to 1,540 ms). In addition, there was a significant effect of memory RT ($P < 0.025$, 780 to 1,210 ms). During the retrieval phase, the pixel image similarity pattern exhibited significant correlation with the neural similarity pattern most

pronounced in the left and right occipital cortices ($P < 0.025$, 70 to 680 ms). A similar effect was observed for face identity ($P < 0.025$, 20 to 990 ms) and gender ($P < 0.025$, 20 to 980 ms). Age effect was not detected ($P > 0.025$). Memory accuracy effect was significant ($P < 0.025$, 220 to 990 ms) as well as the confidence effect ($P < 0.025$, 220 to 990 ms). There were also significant effects ($P < 0.025$) between memory RT (190 to 990 ms) and confidence RT (140 to 990 ms).

Discussion

Neural correlates of memory accuracy and confidence have largely been investigated in separate experiments and mostly with a single learning episode for each item. In this study, we examined neural representations of both memory confidence and accuracy with MEG during an associative face–name learning task over multiple rounds of training and testing. Neural activity related to accuracy and confidence was systematically explored across spatial, temporal, and spectral dimensions with the analysis of ERF, TFR, and single-trial MEG activity in sensor and source space. We found that memory accuracy and retrospective confidence were associated with distinct yet partially overlapping neural activities during both encoding and retrieval. First, high confidence was related to stronger occipital ERF during encoding and stronger distributed ERF during retrieval, compared with lower confidence. In comparison, memory accuracy at the low confidence level seemed to be associated with activity in the medial temporal regions during both encoding and retrieval. Second, we found that a suppression of alpha/beta power in parietal and occipital regions during memory retrieval was predictive of higher retrospective confidence ratings. Finally, spatiotemporal RSA revealed that activity related to stimulus characteristics mainly emerged in the occipital cortices during encoding and retrieval. On the other hand, distinct neural activation related to memory accuracy and confidence was detected in distributed brain regions during encoding and retrieval.

Sensor- and source-level ERF brain responses during memory encoding significantly associated to subsequent memory confidence: Stronger ERF activity in occipital regions and parts of the parietal regions during encoding of the face–name pair was predictive of higher subjective confidence rating after successful memory retrieval of the names associated with the faces. Similar findings have been reported earlier using EEG: It was found that words subsequently remembered with high confidence evoked higher amplitude parietal responses at 400 to 800 ms after stimulus onset than words remembered with low confidence ([Wynn et al. 2019](#)). In a follow-up study, no such confidence-sensitive difference in brain responses was found using abstract pictures as stimuli and the authors concluded that the subsequent confidence effect was probably related to stimulus-specific processes ([Wynn et al. 2020](#)). It should be noted that in both studies, the analysis was based on the framework of parietal old/new effect in item recognition memory and therefore the analysis was limited to the specific time window and to parietal channels only. Our current results confirm and extend these findings and reveal a subsequent confidence effect in the parietal and occipital regions at ~200 to 600 ms after stimulus onset.

An association of ERF activity to retrospective memory confidence was also observed during retrieval and was related to more distributed brain regions. The effect was most pronounced in the left and right occipital regions starting ~130 ms after face presentation and centered on more anterior regions including left parietal, right temporal, and inferior frontal areas in the later time

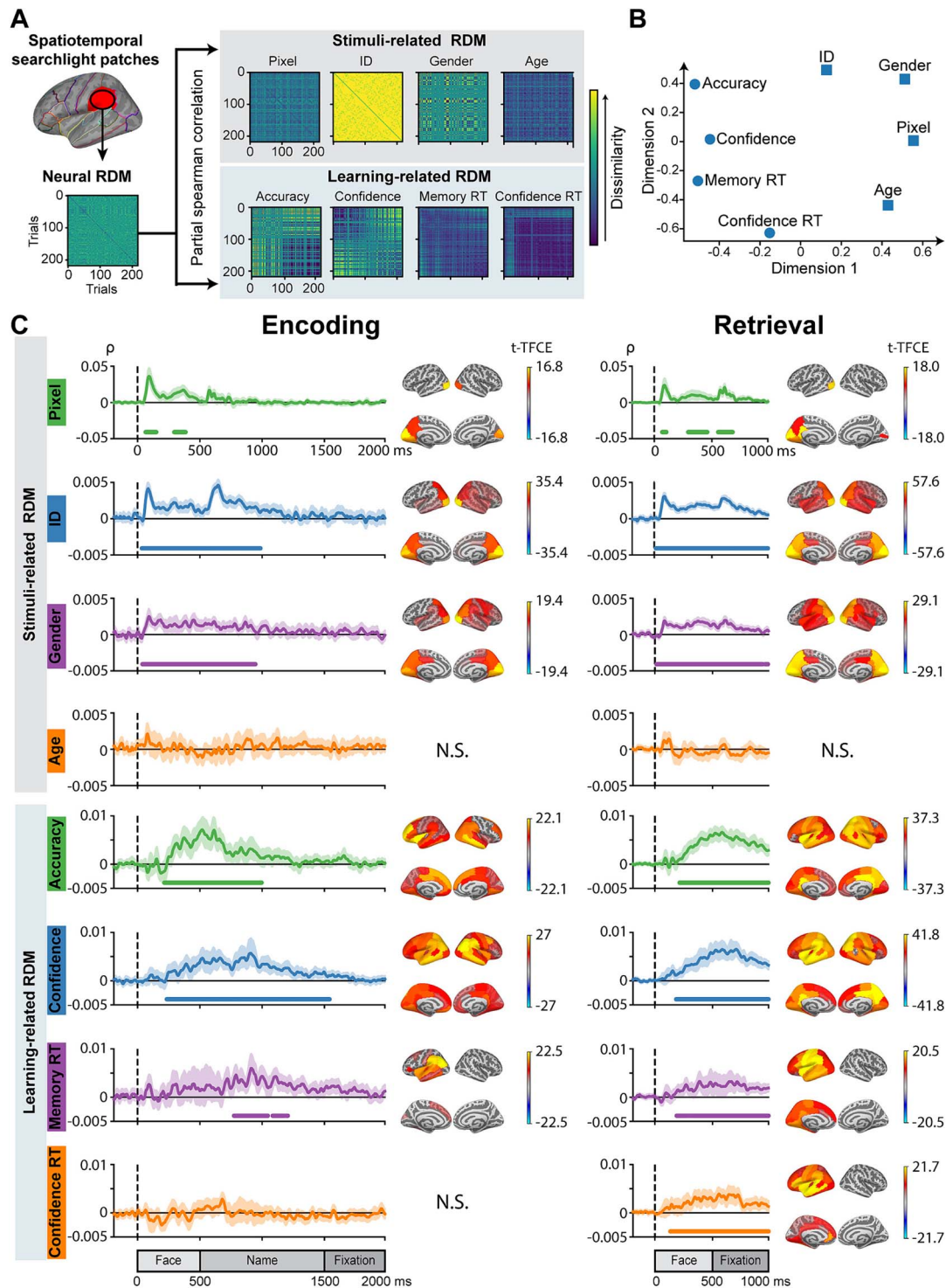


Fig. 4. Source-level representational similarity analysis (RSA) of stimuli- and learning-related processes during face-name association learning. A) A schematic illustration of the spatiotemporal RSA pipeline, utilizing representational dissimilarity matrices (RDMs) from a single participant as an example. The RDMs are generated for all pairs of single trials, which are arranged temporally along the x and y axes. Neural RDMs are created by calculating the dissimilarity in brain source activation (using a spatiotemporal searchlight approach) between each trial, during either encoding or retrieval phases. Similarly, stimuli-related (pixel, ID, gender, age) and learning-related (accuracy, confidence, reaction time for accuracy [memory RT], reaction time for confidence [confidence RT]) RDMs are generated based on the attributes of the face stimuli and the memory confidence and accuracy of each trial. Partial Spearman's rank correlations (ρ) are computed between the neural pattern RDM and each target RDM, controlling for the variances of the other seven RDMs. The resulting partial correlation (ρ) values are then mapped back to the central source location of each searchlight. B) Multidimensional scaling analyses (MDS) are applied to visualize the representational geometries of the stimuli and learning-related RDMs in a 2-dimensional space. C) RSA results for stimuli-related (top) and learning-related (bottom) processes during the encoding (left) and retrieval (right) phases. For each RDM model, partial Spearman ρ from significant parcellation labels are extracted and plotted as a time course (left panels) with a 95% confidence interval band. The colored dots/lines below the time course lines highlight the time points of the significant effects ($P < 0.025$). The spatial extent of the significant effect is visualized on the cortical surface by averaging the t-TFCE values of the significant parcellation labels over time (right panels). Nonsignificant effects are marked as N.S. in the location of source plots and the t-TFCE values extracted from the whole brain parcellation labels are plotted.

window. The medial brain regions are also actively engaged during the whole time window. Similar findings of higher parietal ERF response amplitude associated with high confidence compared with low confidence have been reported earlier for both word and abstract picture stimuli (Wynn et al. 2019, 2020). The localization of the confidence effects during retrieval is, in general, consistent with the metamemory literature showing that subjective aspects of memory are related to distributed brain networks including the parietal and frontal brain regions (Vaccaro and Fleming 2018; Martín-Luengo et al. 2021; Wynn and Nyhus 2022; Xue et al. 2023).

Memory accuracy was associated with higher ERF responses following the face presentation during both encoding and retrieval. The effect of accuracy at low confidence levels during encoding appeared to be more closely associated with activities originating from deeper brain regions on the left medial surface, occurring in a later time window when names are displayed on the screen during memory encoding. During retrieval, the accuracy effect was found in the right occipital regions during face presentation and later was found in regions centered around the left and right medial regions. Comparable accuracy effects have been reported by one earlier EEG study using a face-name task: ERPs were more positive at 200 to 800 ms after stimulus onset for subsequently remembered associations compared to forgotten associations (Guo et al. 2005). Although MEG is not optimal for studying the hippocampus (Ruzich et al. 2019; López-Madrone et al. 2022), our source-level analyses revealed a clear effect presumably localized to the MTL and nearby regions. Thus, our results support the abundance of evidence suggesting that the MTL is a key brain region for successful memory formation and retrieval (Squire and Zola-Morgan 1991; Sperling et al. 2003; Zeineh et al. 2003; Dickerson and Eichenbaum 2010; Vaz et al. 2019).

According to the information via desynchronization hypothesis (Hanslmayr et al. 2012, 2016), alpha/beta oscillatory activity suppression in the neocortex allows for a rich representation of memory content since a desynchronized system has more flexibility to encode information. We found alpha/beta oscillatory power suppression at parietal and occipital regions during memory retrieval for high-confidence compared with low-confidence correctly retrieved face-name pairs. Our finding is consistent with an fMRI study that reported increased activation in the right posterior superior parietal cortex for low-confidence responses, regardless of memory accuracy (Moritz et al. 2006). Previous studies have also indicated that the posteromedial portion of the parietal lobe, the precuneus, might be involved in metamemory (Fleming et al. 2010; McCurdy et al. 2013; Morales et al. 2018; Rutishauser et al. 2018; Vaccaro and Fleming 2018; Ye et al. 2018) and in successful episodic memory retrieval (Cavanna and Trimble 2006).

Several earlier studies have reported sustained power decreases in the alpha/beta band related to accurate memory formation (Sederberg et al. 2003; Hanslmayr et al. 2009; Michelmann et al. 2018) and retrieval (Hanslmayr et al. 2009; Staesina et al. 2016). Furthermore, reductions in alpha/beta power correspond with the fidelity of internally generated, stimulus-specific memory reinstatement in the neocortex induced by hippocampal pattern completion during memory retrieval (Griffiths et al. 2019; Griffiths et al. 2021). Thus, it is somewhat surprising that we did not observe a difference in alpha/beta suppression between accurately versus inaccurately retrieved named faces. This might have been affected by the fact that for assessing accuracy effects we used only the low-confidence trials, where memory representation might still lack robustness or stability. Overall, alpha/beta power

suppression in the occipital and parietal regions is likely a common neural pattern in both successful memory retrieval and high retrospective memory confidence, although distinguishing between these intertwined processes poses a significant challenge using traditional analysis approaches.

Spatiotemporal RSA analysis on single-trial data revealed interesting brain activity patterns during memory encoding and retrieval that represent both stimulus-related and learning-related information in the brain. The results illustrated in Fig. 4C indicate a spatiotemporal separation between stimuli-related and (meta)memory processes during encoding and retrieval. Specifically, most stimulus-related neural representations were significant in the left and right occipital cortices during the presentation of face stimuli. This is consistent with earlier studies (Ambrus et al. 2019; Dobs et al. 2019; Kaiser and Nyga 2020; Tsantani et al. 2021) on face processing related to pixel-level image, identity, and gender information. Most importantly, we found dissociable neural representations related to memory confidence and accuracy during encoding and retrieval. Both accuracy and confidence effects were observed in late time windows (>200 ms from face onset), following the stage of face processing (Ambrus et al. 2019; Dobs et al. 2019). This temporal pattern suggests that accuracy and confidence-related processes unfold after the initial perceptual processing of stimuli.

Compared with the spatially localized effects observed for stimulus-related representations, accuracy and confidence effects exhibited a more widespread spatial distribution across the cortical surfaces. This suggests that both accuracy and confidence-related processes of face-name learning engage distributed networks of brain regions (Sperling et al. 2001; Yu et al. 2021) and coordination of neural activity across extended time periods (Guo et al. 2005). The accuracy effect during encoding appeared to be most pronounced around the left frontal and left and right temporal cortices. This pattern is largely in line with earlier studies showing significantly greater activation in the anterior hippocampal formation bilaterally and left inferior prefrontal cortex for successfully encoded face-name associations (Sperling et al. 2003). Conversely, during memory retrieval, the accuracy effect was centered around the left and right temporal (including MTL and surrounding structures) and parietal regions, which are heavily implicated in associative memory retrieval processes (Zeineh et al. 2003; Chua et al. 2004; Mayes et al. 2007; Klamer et al. 2017). The effects of confidence seemed most pronounced in the parietal regions during both encoding and retrieval, although neighboring temporal and frontal regions were also notably engaged. This observation suggests that confidence processing entails a network of brain regions, including the parietal cortex, MTL, and prefrontal cortex (PFC), a finding corroborated by earlier studies on metamemory (Moritz et al. 2006; Martín-Luengo et al. 2021; Wynn and Nyhus 2022).

It should be noted that the confidence effect in the RSA is based on the assumption that neural activity that represents memory confidence is linear. Although it has been shown in fMRI studies that the memory confidence pattern could be nonlinear in those brain regions (Wynn and Nyhus 2022), linear effects seem to be the most predominant pattern. Furthermore, the left temporal and parietal and sensorimotor regions are linked to the reaction time of memory tests during both encoding and retrieval, as well as to confidence ratings during retrieval. This association may potentially signify the involvement of these regions in metacognition (Qiu et al. 2018; Fleming 2024) and decision-making (Schall 2003; Shadlen and Kiani 2013).

To summarize, based on our results from ERF, TFR, and single-trial MEG data analysis, the parietal regions seem to be consistently involved in metamemory. Parietal regions are associated with many aspects of (meta)memory including, for example, attentional control (Cabeza et al. 2008, 2011), multisensory integration (Avillac et al. 2007; Shimamura 2011), and the subjective feeling of memory recollection. In one study the activity of single neurons in the posterior parietal cortex represented memory strength and recognition confidence (Rutishauser et al. 2018). According to our results, there is a negative correlation between memory confidence and oscillatory power in the alpha/beta frequency bands (i.e. alpha/beta suppression) in the parietal lobe around the precuneus located on the medial surface. This pattern seems to be analogous to that reported based on fMRI signals and indicating decreasing parietal activity with increasing confidence in different cognitive tasks (Hebart et al. 2016; Vaccaro and Fleming 2018; Rouault et al. 2022). In general, the medial parietal regions have been hypothesized to be part of the “Default Mode Network” (Buckner et al. 2008; Bowman et al. 2017) that is thought to deactivate during focused cognitive processing such as memory encoding and retrieval (Miller et al. 2008; Vannini et al. 2011). In addition, we also found metamemory-related effects in the activity of frontal brain regions. It has been reported that false memory confidence depends on the prefrontal reinstatement of true memory (Kim et al. 2022), and that patients with frontal lobe damage perform worse than controls on tests of retrospective confidence, i.e. have impaired metamemory (Pannu et al. 2005). Together with the precuneus, the prefrontal cortex is suggested to belong to a domain-general network responsible for metamemory across different cognitive tasks (Fleming et al. 2012; Molenberghs et al. 2016; Qiu et al. 2018; Vaccaro and Fleming 2018; Rouault et al. 2022).

Several limitations of the study should be noted. First, we utilized only one metamemory measure during learning, namely the retrospective confidence judgments obtained after each trial during memory retrieval. In general, retrospective memory confidence seemed to correlate more strongly with neural activity during retrieval than during encoding. Ideally, it would be interesting to also include prospective metamemory judgments during encoding and to compare the behavioral and neural correlates of different metamemory measures. Second, MEG might not be the optimal method for localizing brain activity within deep brain regions like the MTL due to the decreased signal-to-noise ratio as a function of source depth. Nonetheless, other studies have indicated that MEG can capture hippocampal activity (Attal and Schwartz 2013; Ruzich et al. 2019), particularly during learning and memory tasks (Taylor et al. 2012; Backus et al. 2016; Shah-Basak et al. 2018; Liu et al. 2019; Wimmer et al. 2020, 2023; Xu et al. 2020). In our study, the MTL was primarily implicated in memory accuracy, consistent with the abundant evidence on the role of the hippocampus/MTL in learning. Lastly, our results demonstrated that memory confidence effects can be detected from ERF, TFR, and single-trial MEG signals during learning. However, the exact underlying neural mechanisms in different types of brain signals that support confidence computation and representation still require further investigation.

In conclusion, we found that healthy young participants exhibited remarkable metamemory during face-name learning and that neural activity specific to metamemory can be identified with MEG. Face-name memory has been reported sensitive to early Alzheimer’s disease (Werheid and Clare 2007; Rentz et al. 2011). To build upon these findings, it would be

interesting to investigate neural signatures of metamemory in populations susceptible to memory impairment. Furthermore, it would be fascinating to explore how external modulation of metamemory-related neural responses might affect memory accuracy and learning overall. We contend that the quantification of memory should transcend a binary approach and encompass the subjective aspect of memory. Incorporating the subjective dimension of memory in future studies will lead to a more comprehensive understanding of (meta)memory processes and their implications for decision-making, education, and memory-related disorders.

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Author contributions

Weiyong Xu (Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Software, Validation, Visualization, Writing—original draft, Writing—review & editing), Xueqiao Li (Visualization, Writing—review & editing), Tiina Parviainen (Methodology, Resources, Supervision, Writing—original draft, Writing—review & editing), and Miriam S. Nokia (Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Writing—original draft, Writing—review & editing).

Supplementary material

Supplementary material is available at *Cerebral Cortex* online.

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Data and code availability

The dataset is not publicly available due to legal restrictions but is available from the corresponding author with a formal data sharing agreement. MEG and EEG data are considered pseudonymous personal data under the GDPR and, therefore, cannot be openly shared. According to the principle outlined by the Finnish Data Protection ombudsman in 2017, only anonymous data can be published openly. Analysis scripts are available at the GitHub repository (<https://github.com/weiyongxu/FaceName-Brain>).

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