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Research Report

How neural representations of newly learnt faces change over time: Event-related brain potential evidence for overnight consolidation

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ABSTRACT

Previous experiments have shown that a brief encounter with a previously unfamiliar person leads to the establishment of new facial representations, which can be activated by completely novel pictures of the newly learnt face. The present study examined how stable such novel neural representations are over time, and, specifically, how they become consolidated within the first 24 h after learning. Using event-related brain potentials (ERPs) in a between-participants design, we demonstrate that clear face familiarity effects in the occipito-temporal N250 are evident immediately after learning. These effects then undergo change, with a nearly complete absence of familiarity-related ERP differences 4 h after the initial encounter. Critically, 24 h after learning, the original familiarity effect re-emerges. These findings suggest that the neural correlates of novel face representations are not stable over time but change during the first day after learning. The resulting pattern of change is consistent with a process of consolidation.

1. Introduction

Imagine you have just had a 10-min conversation with somebody you had never previously met. Would you recognise this person's face if you bumped into them in the street tomorrow, or in a photograph taken under different conditions? Recognising the people that we know, such as our friends, relatives, and colleagues, is of critical importance for our social interactions, and humans are highly skilled at familiar face recognition. At the same time, recognising that we have seen the face of a person we are not particularly familiar with, or even the simultaneous matching of different photos of an unfamiliar person, can be surprisingly difficult (Bruce et al., 1999; Burton,

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Wilson, Cowan, & Bruce, 1999; Hancock, Bruce, & Burton, 2000; Young & Burton, 2018). Critically, all familiar faces have been unfamiliar at some point in the past and have become familiar with exposure over time. However, we know very little about what happens to our memory of a new face after an initial encounter. Therefore, the present study examined how representations of newly learnt faces develop over the first 24 h after having met somebody for the first time, using event-related brain potentials (ERPs).

Face learning can be conceptualised as establishing an image-invariant representation of a new face, allowing recognition from a wide range of pictures (Burton, Jenkins, & Schweinberger, 2011; Young & Burton, 2017). Pictures of the same identity can appear very different, as they vary with respect to environmental factors (such as lighting or viewing angle) and changes in the face itself (e.g. changes in emotional expression or due to speech movements, changes in make-up, hair- or beard-style etc.). It is this considerable within-person variability that makes unfamiliar face recognition (or matching) difficult (Jenkins, White, Van Montfort, & Burton, 2011). Face learning, therefore, involves learning how different the same face can look in varying conditions (Burton, Kramer, Ritchie, & Jenkins, 2016; Kramer, Young, & Burton, 2018).

Of relevance for the present study, theoretical accounts of face learning make no assumptions about the stability of a new representation. This appears to be a substantial gap, given the abundance of literature on how memory representations change over time (starting with the seminal work of Ebbinghaus, 1885). A potentially very important mechanism in this respect involves consolidation of newly learnt items. Memory consolidation is assumed to stabilize newly encoded information and to integrate it with pre-existing long-term knowledge (Marshall & Born, 2007; Squire, Genzel, Wixted, & Morris, 2015). Experiments have shown that a 24-h gap between learning and test results in the consolidation of newly learnt words (Dumay & Gaskell, 2012; Gaskell & Dumay, 2003). In contrast, evidence for consolidation of face learning has been limited at best, with most studies relying on paradigms that test old/new recognition of previously seen single images of unfamiliar faces rather than the image-invariant recognition that underlies real-life face recognition (Santos et al., 2022; but see Solomonova et al., 2017).

Importantly, to achieve consolidation of an existing memory trace, the underlying neural representation needs to be modified. Substantial evidence points to an important role of sleep (Diekelmann, Wilhelm, & Born, 2009; Stickgold, 2005), and the hippocampus has been identified as a critical brain structure (e.g., Marshall & Born, 2007). More specifically, to prevent interference with pre-existing long-term memories, new information is thought to be encoded temporarily into an intermediate buffer and then, in an offline process (i.e., during sleep), gradually transferred to a long-term store. This intermediate storage is supposed to critically involve the medial temporal lobe, and most notably the hippocampus, while neocortical structures are assumed to contain consolidated long-term memories (e.g. Frankland & Bontempi, 2005; Squire et al., 2015). Interestingly, neocortical areas such as the fusiform gyrus and the inferior occipital lobe (see e.g. Kovacs, 2020) and the hippocampus (Sliwinska et al., 2022) have been reported to be involved in face learning.

A number of studies have examined face learning using EEG and event-related potentials (ERPs). The human EEG consists of changes in electrical voltage measured on the surface of the head, reflecting summed post-synaptic potentials and therefore neural activity (e.g., Jackson & Bolger, 2014). ERPs reflect averaged EEG activity time-locked to a specific event, such as the presentation of a visual stimulus. The main finding from ERP face learning experiments consists of more negative amplitudes for newly learnt relative to unfamiliar faces at occipito-temporal channels from approximately 200 ms onwards (Andrews, Burton, Schweinberger, & Wiese, 2017; Kaufmann, Schweinberger, & Burton, 2009; Tanaka, Curran, Porterfield, & Collins, 2006). This N250 familiarity effect can be observed after a 10-min real-life interaction with a previously unfamiliar person, even if participants are tested with highly variable, never-before-seen images of the newly learnt identity (Popova & Wiese, 2023b). Previous research has further shown that the N250 effect increases with rising levels of familiarity, as it is bigger for more, relative to less, familiar faces (Andrews et al., 2017; Popova & Wiese, 2023a; Wiese, Hobden, et al., 2022; Wiese, Tüttenberg, et al., 2019). Moreover, familiarity effects tend to increase over the 200–400 ms time range, which is therefore typically split into two consecutive time windows in learning studies (Andrews et al., 2017; Kaufmann et al., 2009; Popova & Wiese, 2023b).

Finally, ERP familiarity effects have also been observed in a subsequent 400–600 ms time window, both for newly learnt (Kaufmann et al., 2009; Popova & Wiese, 2023b) and highly familiar faces (Wiese, Hobden, et al., 2022; Wiese, Tüttenberg, et al., 2019). While in the case of highly familiar faces, this Sustained Familiarity Effect (SFE) is substantially larger than the N250 effect, a corresponding increase has not been observed for newly learnt faces (Popova & Wiese, 2023b). The time range following the N250 is commonly associated with accessing identity-specific semantic and episodic information (Schweinberger & Neumann, 2016). Accordingly, the full effect might not occur for newly learnt faces because of the limited availability of identity-specific knowledge for somebody just met. Critically for the present study, it remains unclear how stable the new representations underlying the N250 and subsequent familiarity effects are after the initial encounter with a new person, and to what extent such representations change as they are consolidated.

The aim of the present study was therefore to examine the stability or change, i.e. potential forgetting and/or consolidation, of newly learnt facial identity representations over time. More specifically, we tested whether an initial N250 familiarity effect to a newly learnt face would remain stable if a time gap between study and test was introduced, or whether such effects would change as the memory is consolidated. To answer this question, we examined 120 participants who were split into four groups of 30 participants each. Adopting a naturalistic learning approach (Ambrus, Eick, Kaiser, & Kovacs, 2021; Campbell, Louw, Michniak, & Tanaka, 2020; Popova & Wiese, 2023b; Sliwinska et al., 2022), all participants engaged in a real-life interaction with a pre-experimentally unfamiliar person and were later tested with highly variable, never-before-seen images of this and of an unfamiliar control identity. Crucially, each group was tested after a different study-test gap, with Group 1 being tested immediately after the interaction, Group 2 after 1 h, Group 3 after 4 h, and Group 4 after 24 h.

We expected to replicate our previous finding of clear N250 familiarity effects in the immediate testing (0h gap) condition (Popova & Wiese, 2023b). Critically, if the neural representation of the new identity changed over time, this should be reflected in ERP familiarity effects. In contrast, if the new representation remained stable over the tested time interval, no differences in N250 familiarity effects should be observable. Importantly, if overnight consolidation resulted in a strengthening of the representation, we would expect the N250 familiarity effect in the 24h gap condition to be stronger than at the last point of measurement before sleep (4h condition).

2. Methods

We report how we determined our sample size, all data exclusions, all inclusion/exclusion criteria, whether inclusion/exclusion criteria were established prior to data analysis, all manipulations, and all measures in the study.

2.1. *Participants*

The tested population consisted of 128 Durham University under- and postgraduate students, eight of whom were excluded for counterbalancing reasons established prior to data analysis (see below). Given the between-subjects factor of study-test gap (four factor levels, see below), 30 participants per gap condition were analysed. The sample size was determined prior to data collection in a power analysis using G*Power (Faul, Erdfelder, Lang, & Buchner, 2007) based on the 10-min condition of our previous experiment (Popova & Wiese, 2023b; paired-sample t-test, dz = .53, power = .8), which suggested N = 30 to detect an N250 learning effect. The final sample consisted of twelve male and 18 female participants (mean age = 20.0 years, SD = 1.7) in Group 1 (0h time gap), ten male and 20 female participants (mean age = 19.8 years, SD = 1.2) in Group 2 (1h time gap), nine male and 21 female participants (mean age = 20.1 years, SD = 1.5) in Group 3 (4h time gap), and twelve male and 18 female participants (mean age = 19.7 years, SD = 1.5) in Group 4 (24h time gap). All participants had normal or corrected to normal vision, and did not take central-acting medication. They gave written informed consent to participate and received course credit or monetary compensation of £8/h. The study was approved by the ethics committee of Durham University's Department of Psychology.

2.2. *Stimuli*

Stimuli consisted of 50 naturally varying “ambient” face images for each of eight confederates (or identities, IDs; see Fig. 1 for examples). Images were cropped around the head, resized to 190 x 285 pixels, and converted to grayscale. Eight images of butterflies were used to create a task demand. All depicted individuals were fully informed about the purpose of the experiment and voluntarily provided the pictures. All were female students at Durham University in their early-to mid-twenties. All participants were unfamiliar with the assigned confederates in all cases.

The eight IDs were combined into four pairs (with approximately the same hair colour and length). Each participant was tested with one pair, with one ID as the to-be-learnt person while the other was used as the unfamiliar face. Both members of each pair were learnt equally often by different participants, and accordingly the same images were used for the learnt and unfamiliar conditions across participants (see Fig. 1a).

2.3. *Procedure*

The experiment consisted of a learning session and a subsequent EEG test session. One of the eight IDs was chosen as the to-be-learnt person for a given participant. Before the experiment, participants were informed that they would have a chat with an unfamiliar fellow student for 10 min. While learning was not explicitly mentioned, participants were further told that they would subsequently be shown images of faces, and that some of these faces might be familiar. During the learning session, the confederate interacted with the participant in a naturalistic face-to-face conversation. This was carried out in a room close to the EEG lab, with only the participant and the confederate present. To allow for a more naturalistic situation, the discussion was not scripted, but typical conversation topics included the participants' experiences at university (e.g., colleges, sports teams, societies etc.), their courses, hobbies, where they are from, or their living situation. Both the participant and confederate asked for and provided information (as would be expected in a natural conversation), and accordingly participants learned some identity-specific semantic information about the confederate. Participants were not explicitly instructed to attend to the other person's face, but confederates were asked to ensure that their face was visible at all times.

Following the learning session, participants were either immediately taken to the EEG lab (0h gap condition) or were asked to come to the lab after a specified gap of either one, four, or 24 h. These timepoints were chosen based on research (starting with Ebbinghaus, 1885; Nelson, 1985) showing that forgetting is more pronounced shortly after learning. We therefore chose time points roughly following a logarithmic rather than a linear function. Upon arrival in the lab, participants were prepared for EEG recording (taking approximately 15 min) and seated in an electrically shielded and sound-attenuated chamber (Global EMC^{TM}), with their heads resting on a chin rest 80 cm from a computer monitor. Fifty photos each of the newly learnt ID and of the unfamiliar person from the same pair, as well as 16 trials with pictures of butterflies were presented in random order. The images were presented using EPrime (Psychology Software Tools, Pittsburgh, PA) at a visual angle of $3.6^\circ \times 5.4^\circ$ on a uniform grey background in the centre of the screen for 1,000 ms. Trials were separated by a 1,500–2,500 ms fixation cross (2,000 ms on average). Participants were instructed to watch the screen at all times. To ensure that participants were paying attention to the stimuli, they were asked to press a response key with their right index finger whenever a butterfly was presented (see Fig. 1b). Face recognition itself is involuntary in the sense that one cannot

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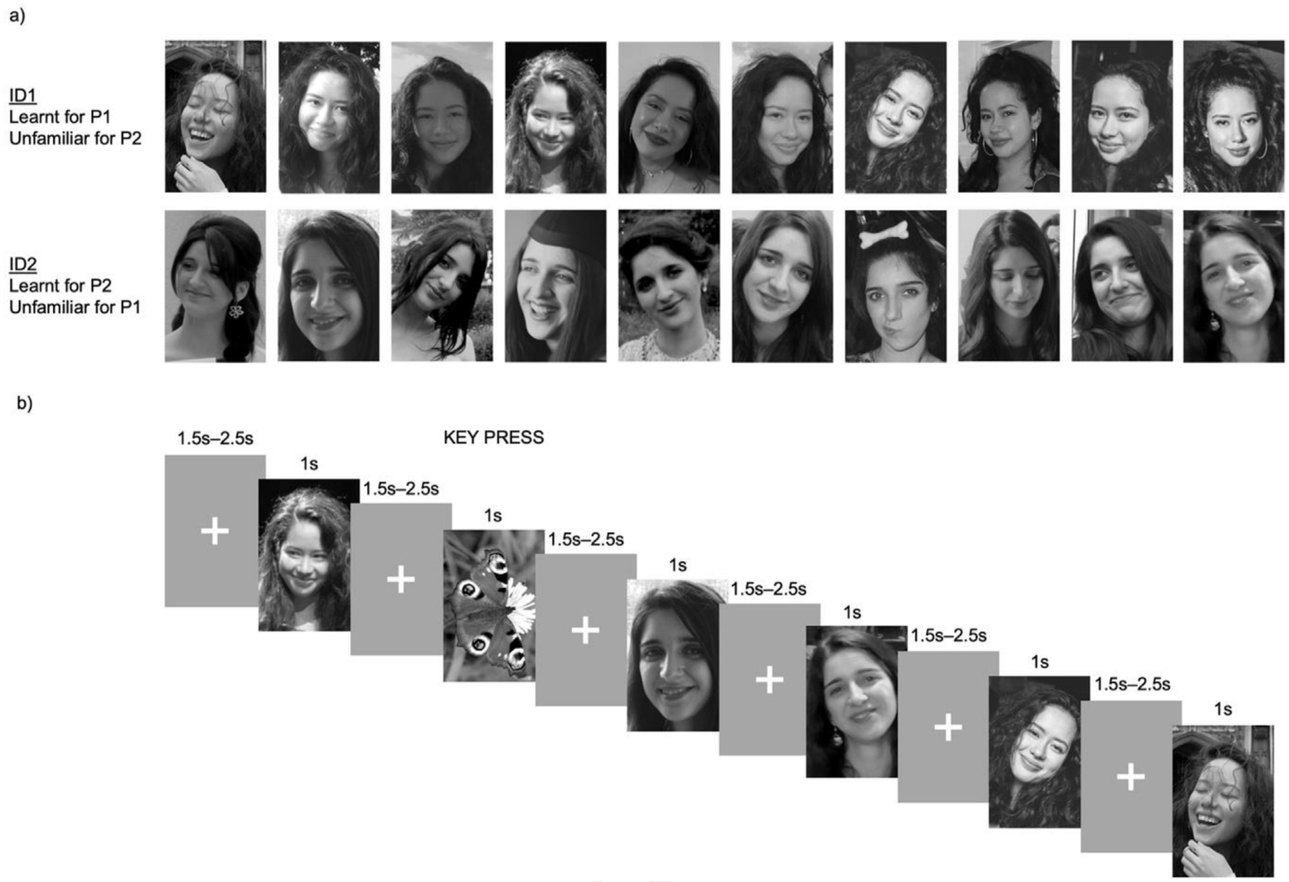

Fig. 1 – a) Example stimuli from the experiment. Note that identities were balanced across conditions, such that Participant 1 (P1) would for example learn ID1 and Participant 2 (P2) would learn ID2, while the respective other ID of the pair would be unfamiliar at test. b) Trial structure of the experiment. Images are published with explicit consent of the depicted individuals.

look at a face and decide to not recognise it, so we purposefully did not choose explicit familiarity judgments to reduce potential task-related top-down effects, which would not occur during spontaneous real-life face recognition. Both speed and accuracy were emphasised.

After the main experiment, participants were asked to rate the visual recognisability of the learnt and the unfamiliar identity. They were simultaneously presented with eight randomly selected images of each of the two identities separately and asked how likely they would recognize the person if they saw her in the street on a scale from 1 (highly unlikely) to 5 (highly likely).

2.4. *EEG recording and data analysis*

64-channel EEG (EEGo, ANT Neuro, Enschede, The Netherlands) was recorded using sintered Ag/Ag-Cl electrodes. The sampling rate was set to 1024 Hz, allowing for accurate measurement from DC to 266 Hz (see https://www.ant-neuro.com/products/eego_mylab/specs). AFz was used as the ground electrode and CPz served as the recording reference. Blinks were corrected using independent component analysis as implemented in BESA Research Software (Version 6.3, Grafelfing, Germany). Data were segmented into epochs from −200 to 1,000 ms relative to stimulus onset, with the first 200 ms serving as a baseline. Artefact rejection was implemented using a 100 μV amplitude threshold and a 75 μV gradient criterion. The remaining trials were re-referenced to the common average reference and averaged for each participant group (0h, 1h, 4h, 24h time gap conditions) as well as for learnt and unfamiliar faces separately. Average number of trials were 47.1 (SD = 4.8, min = 29) for newly learnt and 47.0 (SD = 4.3, min = 31) for unfamiliar faces in the 0h-group, 47.6 (SD = 2.5, min = 41) for newly learnt and 48.1 (SD = 2.5, min = 40) for unfamiliar faces in the 1h-group, 47.9 (SD = 2.5, min = 39) for newly learnt and 47.9 (SD = 2.6, min = 39) for unfamiliar faces in the 4h-group, and 47.1 (SD = 4.9, min = 29) for newly learnt and 47.2 (SD = 5.3, min = 28) for unfamiliar faces in the 24h-group.

Similar to previous work on face learning (Andrews et al., 2017; Kaufmann et al., 2009; Popova & Wiese, 2023b), early (200–300 ms) and late (300–400 ms) N250 time windows were analysed. Moreover, a time window from 400 to 600 ms (SFE) was analysed at the same electrodes (Wiese, Anderson, et al., 2022; Wiese, Hobden, et al., 2022). While we only analysed electrodes TP9/TP10 in the planned analyses of our previous

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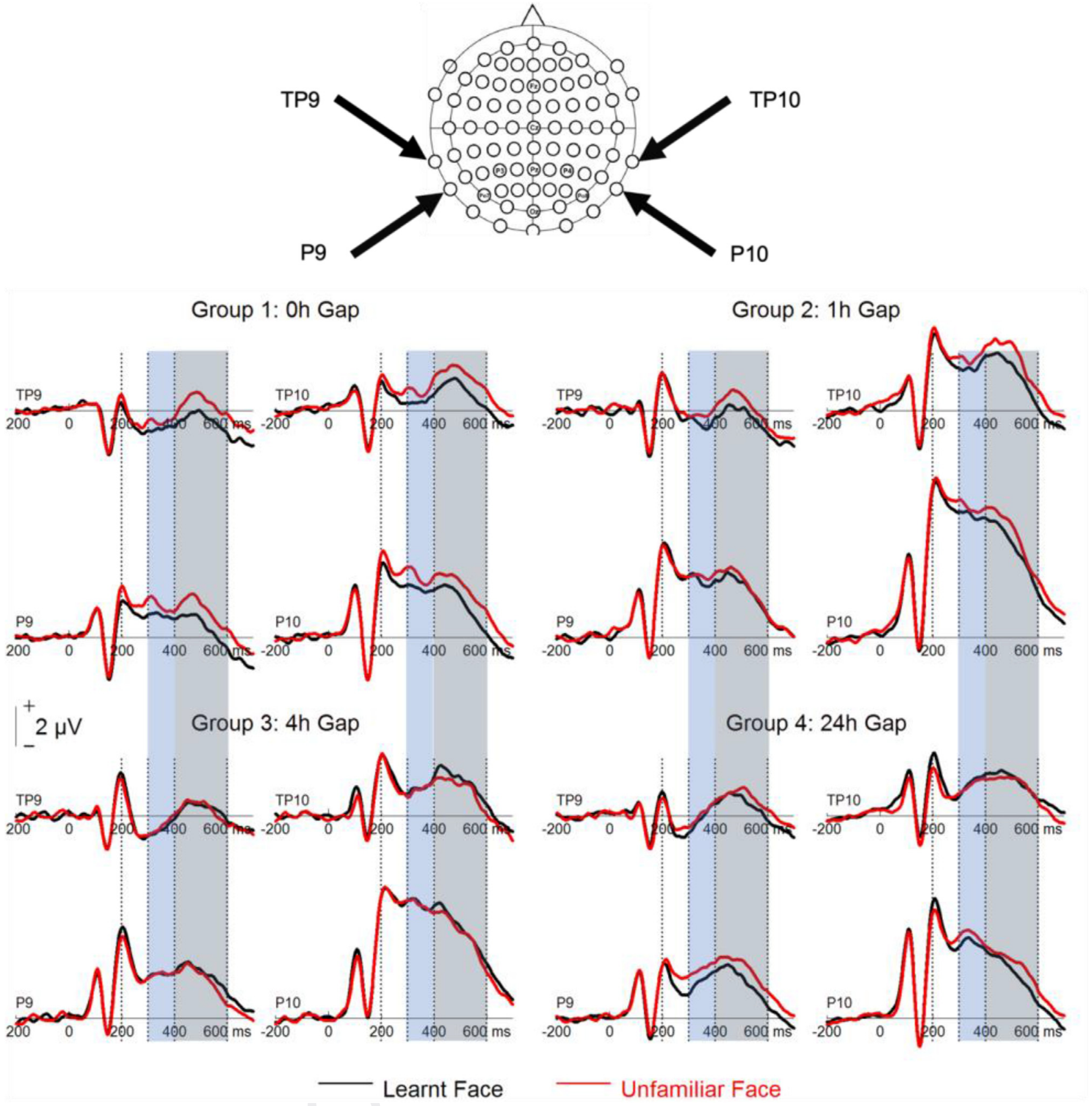

Fig. 2 – Grand average event-related potentials for the four time gap conditions at occipito-temporal channels TP9/TP10 and P9/P10. Dashed lines indicate early (200–300 ms) and late (300–400 ms; blue areas) N250 as well as SFE (400–600 ms; grey areas) time windows.

real-life learning study (Popova & Wiese, 2023b), exploratory analyses also showed clear differences between learnt and unfamiliar faces at P9/P10. We therefore decided to add this electrode pair to the planned analyses of the present study (see also Wiese, Anderson, et al., 2022; Wiese, Hobden, et al., 2022). Mixed-model ANOVAs with the between-subjects factor of time gap (0h, 1h, 4h, 24h) and the within-subject factors familiarity (learnt, unfamiliar), hemisphere (left, right), and site (TP, P) were conducted for each time window separately. To test for change in familiarity effects over time, significant interactions involving time gap and familiarity in the omnibus ANOVAs were followed up by corresponding t-tests. Following an estimation approach in data analysis (Cumming, 2012), effect sizes and appropriately sized confidence intervals (CIs) are reported throughout. Cohen's d was bias-corrected[1] (d_{unb}) and calculated using the mean standard deviation rather than

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[1] Cohen's d overestimates the population effect size and is therefore corrected using the following formula (e.g., Cumming, 2012, p. 294): $d(unb.) = \left(1 - \frac{3}{4\,df-1}\right)*d$

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Table 1 – Follow-up t-tests.

Time window	Site	Gap	M_{diff}	95 % CI	t(29)	p	d_{unb}	95 % CI
300–400 ms	TP9/TP10	0h	.439	[-.124, 1.002]	1.594	.122	.181	[-.049, .417]
		1h	.435	[-.200, 1.066]	1.408	.170	.096	[-.042, .238]
		4h	.037	[-.537, .611]	.131	.897	.011	[-.157, .180]
		24h	.029	[-.329, .387]	.165	.870	.010	[-.109, .129]
	P9/P10	0h	.539	[.020, 1.059]	2.124	**.042***	.162	[.006, .324]
		1h	.286	[-.367, .940]	.896	.378	.056	[-.070, .185]
		4h	−.018	[-.652, .616]	−.058	.954	−.004	[-.156, .147]
		24h	.493	[.048, .937]	2.268	**.031***	.121	[.011, .235]
400–600 ms	TP9/TP10	0h	.812	[.204, 1.420]	2.731	**.011***	.336	[.080, .606]
		1h	.675	[.021, 1.330]	2.110	**.044***	.203	[.006, .408]
		4h	−.184	[-.810, .442]	−.602	.552	−.064	[-.281, .150]
		24h	.093	[-.429, .615]	.365	.718	.037	[-.166, .241]
	P9/P10	0h	.809	[.238, 1.380]	2.899	**.007***	.269	[.075, .474]
		1h	.410	[-.267, 1.087]	1.238	.226	.111	[-.070, .297]
		4h	−.234	[-.877, .408]	−.746	.462	−.071	[-.266, .121]
		24h	.562	[.075, 1.048]	2.362	**.025***	.169	[.021, .323]

the standard deviation of the difference as the denominator.[2] Finally, to fully explore the data, we ran mass univariate tests comparing learnt and unfamiliar faces at all electrodes and time points for each gap condition separately.

The study procedures and analysis plans were not preregistered. All study data and analysis code are available on the Open Science Framework platform (https://osf.io/5yn96/?view_only=2f832b29fe544722a1153c7160e8b2b2). The conditions of our ethical approval do not permit the public archiving of the photos of the facial identities used in this study and images cannot be shared with anyone outside of the author team. Images of selected individuals who have provided their explicit consent are used as examples in Fig. 1.

3. Results

3.1. *Event-related potentials*

Visual inspection of grand average ERPs (see Fig. 2) suggested clear familiarity effects at occipito-temporal channels immediately after the learning phase. These effects seemed to become progressively weaker for the 1h and 4h gap conditions. Interestingly, however, ERPs 24 h after learning suggested the re-occurrence of the original effect. Formal tests of these observations are reported below.

A mixed-model ANOVA with the within-subjects factors site (TP, P), hemisphere (left, right), and familiarity (newly learnt, unfamiliar), as well as the between-subjects factor gap (0h, 1h, 4h, 24h) in the 200–300 ms time window revealed a trend for a significant interaction of hemisphere by familiarity by time gap, $F(3, 116) = 2.581$, $p = .057$, $\eta^2_p = .063$, 90 % CI [0, .126]. No other trends or significant interactions involving the factors familiarity and time gap were observed.

A corresponding analysis in the 300–400 ms time window revealed a significant main effect of familiarity, $F(1, 116) = 4.547$, $p = .035$, $\eta^2_p = .038$, 90 % CI [.001, .108], which was qualified by a significant interaction of site by familiarity by time gap, $F(3, 116) = 3.698$, $p = .014$, $\eta^2_p = .087$, 90 % CI [.010, .159]. Follow-up paired-sample t-tests (see Table 1 and Fig. 3), testing for effects of familiarity in each time gap condition and at each electrode pair separately, yielded significantly more negative amplitudes for newly learnt relative to unfamiliar faces at the more posterior electrode pair P9/P10 in both the 0h and 24h gap conditions, but not in the 1h or 4h conditions. No significant effects were observed at TP9/TP10. Direct comparisons of familiarity effects at TP9/TP10 and P9/P10 revealed no reliable differences between time gap conditions, all $t < 1.389$, all $p > .169$.

A mixed-model ANOVA in the 400–600 ms time window again yielded a significant main effect of familiarity, $F(1, 116) = 6.717$, $p = .011$, $\eta^2_p = .055$, 90 % CI [.007, .133], again qualified by an interaction of site by familiarity by time gap, $F(3, 116) = 3.985$, $p = .010$, $\eta^2_p = .093$, 90 % CI [.014, .166]. Follow-up tests at the more posterior electrode pair P9/P10 again demonstrated the above-described pattern of significant familiarity effects in the 0h and 24h, but not in the 1h or 4h conditions. At more anterior electrodes TP9/TP10, significant familiarity effects were detected in the 0h and 1h conditions.

Direct comparisons of familiarity effects between groups at TP9/TP10 revealed no reliable difference between the 0h and the 1h gap conditions, $M_{0h\ gap} = .812$ μV, 95 % CI [.203, 1.420], $M_{1h\ gap} = .676$ μV, 95 % CI [.021, 1.330], $t(58) = .311$, $p = .757$, $d_{unb} = .079$, 95 % CI [−.426, .586], while significantly larger familiarity effects were detected in the 0h relative to the 4h gap condition, $M_{4h\ gap} = -.186$ μV, 95 % CI [−.812, .440], $t(58) = 2.336$, $p = .023$, $d_{unb} = .595$, 95 % CI [.083, 1.118]. The comparison of the 0h with the 24h condition yielded no significant effect, $M_{24h\ gap} = .094$ μV, 95 % CI [−.428, .616],

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[2] Using the mean SD as the denominator results in a measure comparable to Cohen's d for between-group designs (which uses the pooled SD). From a statistical point of view, there is no justification why an effect size should differ exclusively on the basis of the chosen experimental design (paired versus independent samples), and accordingly a similar way to calculate the measure should be used. We note that (i) given typically highly correlated ERP data, our method provides a more conservative estimate, and that (ii) we provide all necessary information (i.e. mean and CI of the difference) for the interested reader to calculate d_z based on the SD of the difference (e.g. for the purpose of power calculations).

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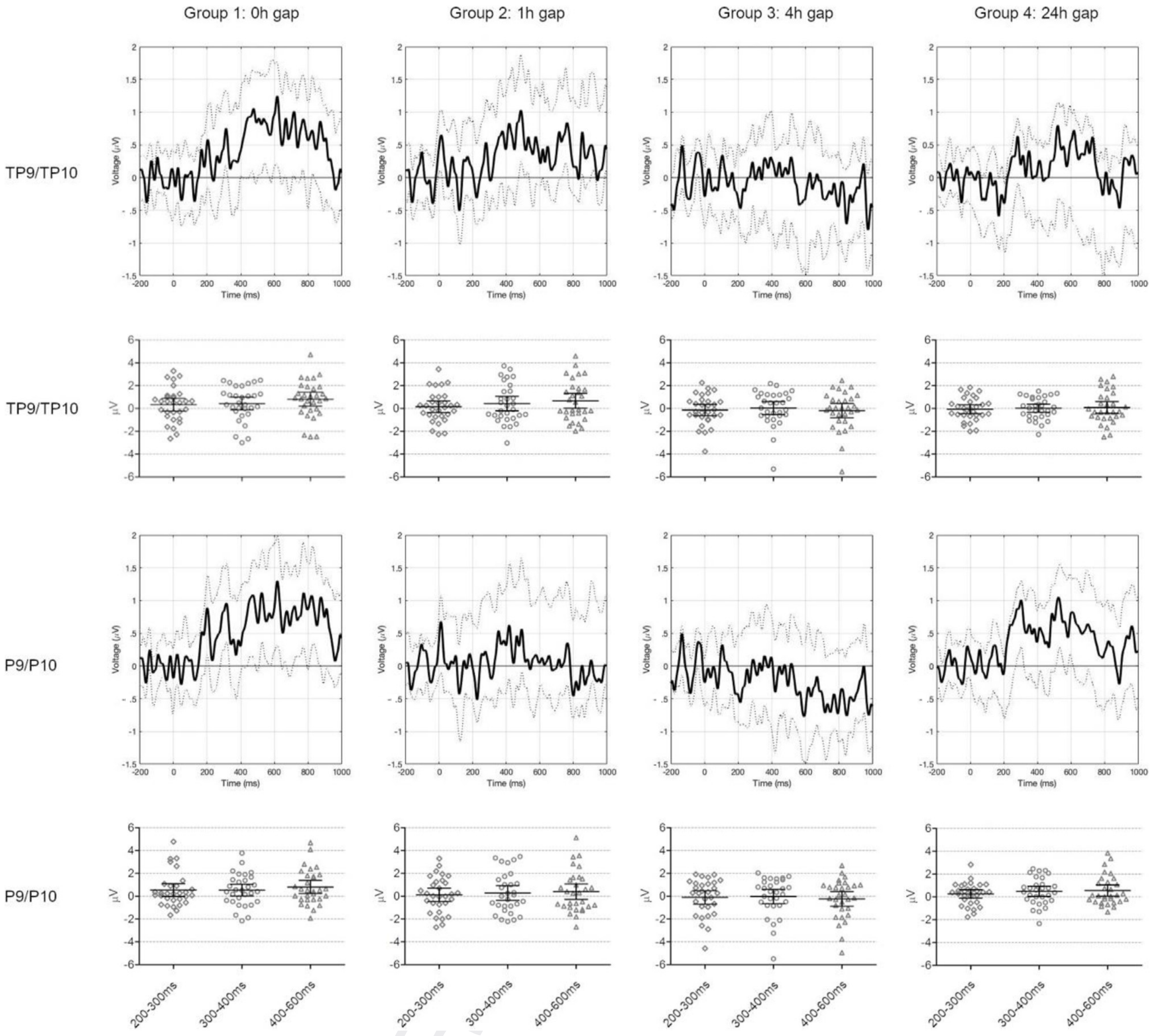

Fig. 3 – First/third row: Mean difference waveforms (unfamiliar – familiar; ± 95 % CIs) at electrodes TP9/TP10 (first row) and P9/P10 (third row) for each time gap condition separately. Second/fourth row: Mean (black lines; ± 95 % CIs) and individual (grey symbols) familiarity effects (unfamiliar – learnt conditions) at electrodes TP9/TP10 (second row) and P9/P10 (fourth row) in the three analysis time windows for each gap condition separately.

$t(58) = 1.830$, $p = .072$, $d_{unb} = .466$, 95 % CI [−.043, .984]. As the absence of significant effects in NHST cannot be interpreted as evidence for the null hypothesis, additional Bayesian independent samples t-tests were carried out. These tests revealed moderate evidence for the null hypothesis when comparing the 0h and 1h gap conditions, $BF_{01} = 3.659$, error % = .010, but only anecdotal evidence for the null for the 0h as compared with the 24h condition, $BF_{01} = .945$, error % = .010.

Corresponding analyses at electrodes P9/P10 yielded no significant difference between the 0h and 1h condition, $M_{0h\ gap} = .810$ μV, 95 % CI [.240, 1.380], $M_{1h\ gap} = .410$ μV, 95 % CI [−.267, 1.086], $t(58) = .925$, $p = .359$, $d_{unb} = .236$, 95 % CI [−.270, .746], while familiarity effects were again significantly larger in the 0h relative to the 4h condition, $M_{4h\ gap} = -.234$ μV, 95 % CI [−.877, .408], $t(58) = 2.487$, $p = .016$, $d_{unb} = .634$, 95 % CI [.120, 1.159]. Again, the comparison between the 0h gap and 24h gap groups did not reveal a significant effect, $M_{24h\ gap} = .560$ μV, 95 % CI [.074, 1.046], $t(58) = .681$, $p = .498$, $d_{unb} = .174$, 95 % CI [−.332, .682]. Bayesian independent samples t-tests comparing the 0h

Table 2 – Mean (± 95 % CI) ratings of visual recognisability ("How likely would you recognise this person in the street?"; 1 = highly unlikely, 5 = highly likely) for newly learnt and unfamiliar faces for each gap condition separately.

Group	Newly learnt		Unfamiliar	
	M	95 % CI	M	95 % CI
Group 1: 0h gap	4.00	[3.60, 4.40]	3.00	[2.60, 3.40]
Group 2: 1h gap	4.17	[3.87, 4.46]	2.47	[2.08, 2.86]
Group 3: 4h gap	3.57	[3.14, 3.99]	2.63	[2.17, 3.10]
Group 4: 24h gap	3.87	[3.44, 4.29]	2.43	[1.94, 2.93]

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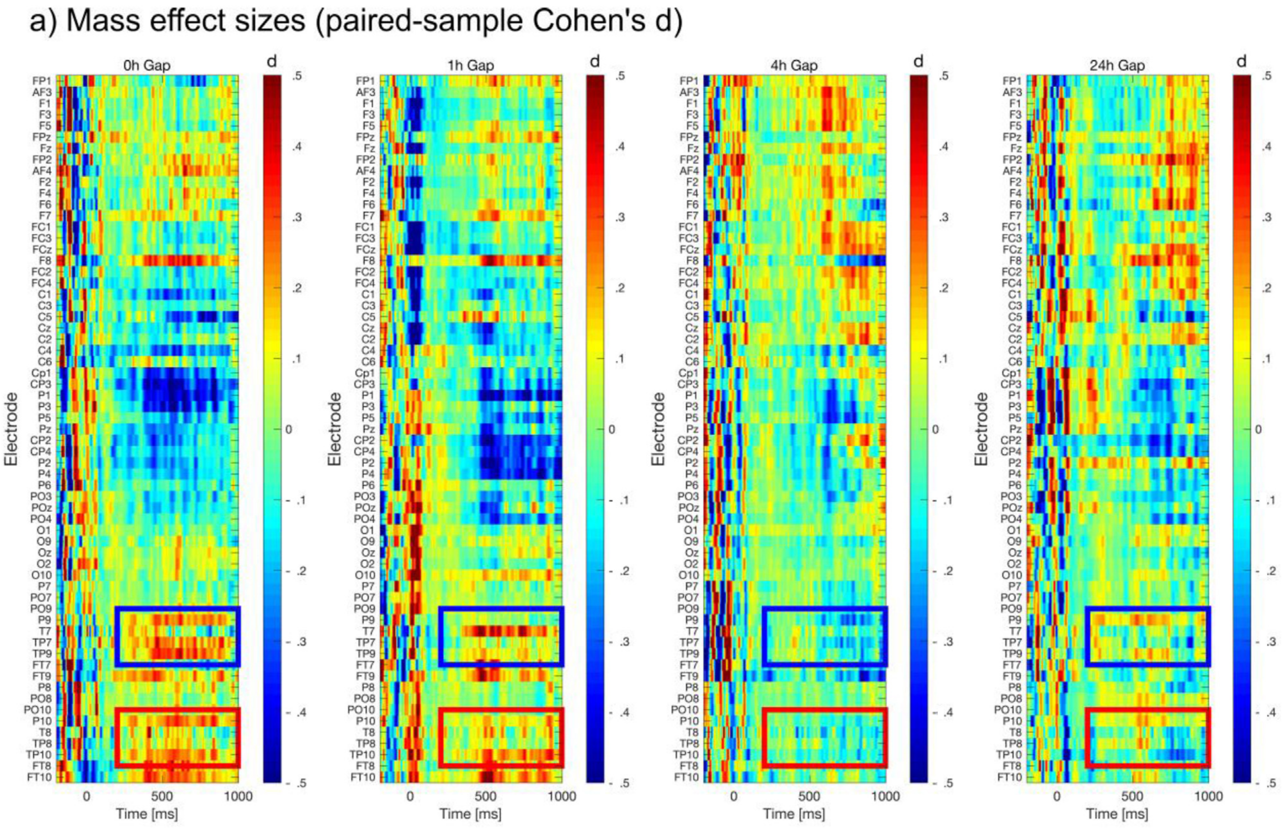
a) Mass effect sizes (paired-sample Cohen's d)

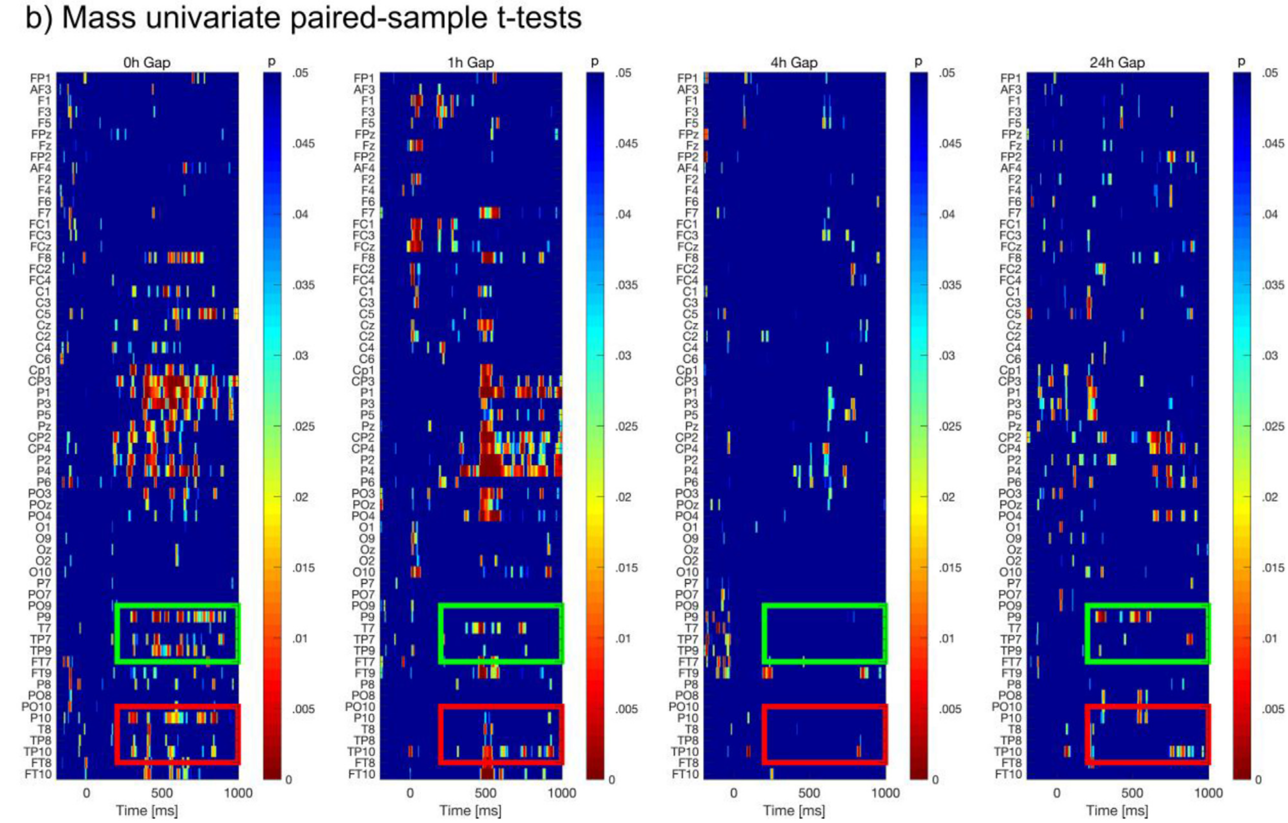
b) Mass univariate paired-sample t-tests

Fig. 4 – a) Repeated-measures Cohen's d (using the average SD rather than the SD of the difference) for the difference in ERPs between learnt and unfamiliar faces at each time point (horizontal axis) and electrode (vertical axis) for each of the four gap conditions separately. Red (right hemisphere) and blue (left hemisphere) boxes correspond to occipito-temporal electrodes

and 1h gap conditions revealed anecdotal evidence for the null hypothesis of no difference, $BF_{01} = 2.662$, error % = .010, while moderate evidence for the null was obtained in the 0h and 24h gap comparison, $BF_{01} = 3.139$, error % = .010.

Finally, to test whether familiarity effects in the late time window (400–600 ms) largely carried over from earlier segments or represented processing over and above differences in the N250, we additionally computed a mixed-model ANOVA on mean amplitudes in the 400–600 ms window corrected for amplitudes in the 300–400 ms time window (see Popova & Wiese, 2023b; Wiese, Hobden, et al., 2022). This procedure entailed measuring the late time window relative to the directly preceding one and not to the pre-stimulus baseline, which was achieved by subtracting the amplitudes measured in the 300–400 ms time window from those in the 400–600 ms time window. This analysis neither yielded a significant main effect of familiarity, $F(1, 116) = 1.257$, $p = .265$, $\eta^2_p = .011$, 90 % CI [0, .610], nor the above-observed interaction of site by familiarity by time gap, $F(3, 116) = .537$, $p = .658$, $\eta^2_p = .014$, 90 % CI [0, .042]. The only significant effect involving the familiarity factor was an interaction of site by hemisphere by familiarity, $F(1, 116) = 5.931$, $p = .016$, $\eta^2_p = .049$, 90 % CI [.005, .124]. However, post-hoc t-tests, examining familiarity effects at each electrode separately, did not reveal any significant results, all $t < 1.696$, all $p > .092$. It therefore appears that familiarity effects in the 400–600 ms time windows were mostly driven by those in earlier segments.

3.2. *Rating results*

Visual recognisability ratings are reported in Table 2. A mixed-model ANOVA with the within-subjects factor familiarity (newly learnt, unfamiliar) and the between-subjects factor time gap condition (0h, 1h, 4h, 24h) revealed a significant main effect of familiarity, $F(1, 116) = 102.669$, $p < .001$, $\eta^2_p = .470$, 90 % CI [.360, .553], indicating higher recognisability of the newly learnt relative to the unfamiliar identity. Neither the effect of time gap condition, $F(3, 116) = 1.267$, $p = .289$, $\eta^2_p = .032$, 90 % CI [0, .078], nor the interaction was significant, $F(3, 116) = 2.121$, $p = .101$, $\eta^2_p = .052$, 90 % CI [0, .111].

Further analyses revealed small to moderate correlations of the difference in visual recognisability ratings with ERP familiarity effects in the 400–600 ms time window at TP9/TP10, $r(118) = .228$, 95 % CI [.051, .391], $p = .012$, and P9/P10, $r(118) = .263$, 95 % CI [.088, .422], $p = .004$. No significant correlations between recognisability ratings and familiarity effects were detected in the 200–300 ms or 300–400 ms time windows, all $r < .157$, all $p > .089$.

3.3. *Exploratory mass univariate analysis*

Fig. 4 provides effect size measures (repeated-measures Cohen's d) and mass univariate paired-samples t-tests for each point in time by electrode position for each of the four time gap conditions separately. These mass univariate tests revealed clear familiarity effects at left (blue boxes in Fig. 4a, green boxes in Fig. 4b) and right (red boxes in Fig. 4a and b) occipito-temporal channels in the 0h gap group. Moreover, polarity-reversed familiarity effects (see Fig. 4a) were observed at centro- and posterior parietal channels, presumably to some extent reflecting the opposite side of the dipoles underlying occipito-temporal effects. Familiarity effects appeared to gradually fade out in the 1h and 4h group, the latter of which showed nearly no corresponding effects at occipito-temporal electrodes. However, some effects were still observed at centro- and posterior parietal channels. Critically, and paralleling the findings of the planned analyses reported above, familiarity effects at occipito-temporal electrodes re-emerged in the 24h condition.

4. Discussion

Using event-related brain potentials, the present study examined the stability of newly formed face representations over time. Immediately following a brief real-life interaction, we observed clear ERP familiarity effects in the N250 time range for a newly learnt relative to an unfamiliar face, reflecting the establishment of an initial neural representation of the new facial identity. These effects were revealed with highly variable and previously unseen images of the familiarised and unfamiliar faces to create a strong test of recognition of the learnt face. Familiarity effects were smaller but still detectable after a 1-h gap between learning and test, but almost absent after a 4-h gap, suggesting that the initial neural representation substantially changed over this time period. Critically, however, ERP familiarity effects re-emerged after a 24-h gap between learning and test, suggestive of strengthening of the representations overnight via memory consolidation. The present findings therefore demonstrate the potential interplay of different processes after the initial formation of a novel face representation, and especially memory consolidation (presumably during sleep). These findings are discussed in more detail below.

Building on recent studies on learning from real-life encounters (Ambrus et al., 2021; Campbell et al., 2020; Sliwinska et al., 2022), previous research from our lab has demonstrated that 10 min of naturalistic interaction are sufficient to establish an initial image-independent representation of a newly learnt face (Popova & Wiese, 2023b). Critically, the current results further demonstrate that this initial neural representation is not stable over time, but undergoes substantial change during the first 24 h after learning. The introduction of a 1-h gap between learning and test still yielded significant familiarity effects following the N250 range, both in the planned analyses and the exploratory mass univariate tests. However, familiarity effects as evidenced by ERPs had already begun to fade across the 1-h interval, as they were less expanded in time/electrode space and restricted to the

of interest. b) *p*-values for mass univariate repeated-measures t-tests, comparing learnt to unfamiliar faces at each time point and electrode for each of the four gap conditions separately. Red (right hemisphere) and green (left hemisphere) boxes correspond to occipito-temporal electrodes of interest.

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400–600 ms time window in the planned analysis. After a 4-h gap, only marginal evidence for familiarity effects was observed in the ERPs, consisting of limited centro- and posterior parietal effects in the mass univariate analysis. It thus appears that the initial neural representation had undergone significant change at this point. Critically, however, familiarity effects re-emerged after a 24-h gap in the late N250 time window. Interestingly, while initial effects were detected at both P and TP electrode sites, this re-emergence was observed exclusively at the more posterior electrodes P9/P10 in our planned analyses. It is therefore possible that a somewhat different set of neurons responded in the 24h relative to 0h condition, resulting in a slight change of dipole orientation. Alternatively, however, the slight difference in the topography of the learning effect might reflect sample variability, and future replication of the present pattern would be necessary to allow for stronger conclusions. More generally, the strengthening of familiarity effects after 24 h was also evident in exploratory tests, and may suggest overnight consolidation of the underlying facial representation, which is in line with previous reports of consolidation after face learning particularly during REM sleep (Solomonova et al., 2017). While we are not aware of other mechanisms that could explain these findings, the interpretation of our results in terms of memory consolidation requires further elaboration. If representations have changed in a way that renders them less detectable from ERPs after 4 h, how is it possible for them to reappear?

Of course, there is considerable precedent for the observation that memory traces can remain effective even after the original methods used to detect learning no longer do so. For example, studies demonstrating savings in relearning, originally reported by Ebbinghaus in 1885 (see Nelson, 1985), show that apparently forgotten material can be reacquired more quickly on re-exposure. These effects also apply to simple CS/US pairings such as a tone and an eye-blink (e.g., Medina, Garcia, & Mauk, 2001). While such effects have clear differences with the phenomena reported here, it is worth noting that they are highly robust, and are generally explained in terms of “residual plasticity” or “implicit processes”, which are a consequence of initial learning (McDougle, Bond, & Taylor, 2015).

In the present study, we observed a reduction of ERP familiarity effects at the intermediate time gaps even though the learnt face was explicitly recognised (Table 2). We see at least two potential explanations for this interesting and somewhat counterintuitive pattern. First, it has been suggested that neocortical regions, such as the fusiform gyrus and inferior occipital areas, are involved in face learning and recognition (e.g., Kovacs, 2020). It therefore seems plausible that representations in these structures underlie the initial ERP familiarity effects observed immediately after learning. However, current models implicate the hippocampus as a critical structure in memory consolidation in general (e.g., Frankland & Bontempi, 2005; Marshall & Born, 2007), and recent studies have also shown the involvement of the hippocampus in face learning (Sliwinska et al., 2022). This structure lies at a relatively large distance from the surface of the skull and it is widely assumed that such deeper sources may be only detectable by surface-recorded EEG if they produce a sufficiently strong signal (Jackson & Bolger, 2014). The hippocampal formation is also folded, and as neural signals from folded structures tend to at least partly cancel each other (Jackson & Bolger, 2014), it seems unlikely that any presumably small hippocampal effects, generated by previously unseen ambient images of a briefly encountered person, were measurable in the present study. This allows for the possibility that an undetected hippocampal representation may have remained intact over the time-period examined in the present study. This hippocampal representation may then have driven the re-establishment of cortical representations via consolidation during sleep (e.g., Marshall & Born, 2007).

Second, exploratory mass univariate analyses demonstrated familiarity effects at centro- and posterior parietal electrode sites. While these effects presumably mostly represent the opposite end of the dipoles underlying occipito-temporal activity, it appears noteworthy that they were still detected after 4 h, when activation at more ventral electrodes had ceased. It therefore seems possible that these effects to some extent reflect additional sources. It is well-established that remembered items in recognition memory experiments elicit more positive amplitudes relative to new items at similar scalp locations (so-called old/new effects; e.g., Rugg & Curran, 2007). Such parietal old/new effects in recognition memory experiments are often interpreted as reflecting the recollection of specific study phase detail (Curran & Hancock, 2007). In our experiment, however, participants could not possibly remember a particular context in which a specific image was previously seen, as all images were completely novel at test. Others have argued that parietal old/new effects in face recognition memory experiments reflect explicit memory based on a “feeling of knowing”, in the absence of specific study phase detail (MacKenzie & Donaldson, 2007; Yovel & Paller, 2004). It therefore appears possible that the remaining memory traces at centro- and posterior parietal scalp locations in the present study reflect similar processes and guided the consolidation process that led to the re-emergence of the original occipito-temporal familiarity effects.

A further question that needs to be addressed concerns how to functionally interpret the consolidation effect observed in the present experiment. Word learning studies have shown an integration of the newly learnt material with existing knowledge structures after one night, which was not evident immediately after learning (Dumay & Gaskell, 2012). In the case of the present experiment, we did not detect an additional effect after 24h that was not present immediately after learning. Instead, it seems that the same familiarity effects observed directly after learning re-emerged after 24 h. We note, however, that the use of ERPs represents a very different measure relative to previous studies on word learning. Future studies should compare implicit and explicit recognition of newly learnt faces, and contrast face and picture memory, to test for episodic memory as compared to the integration of new facial representations into existing knowledge structures.

It furthermore seems important to discuss what specific processes or representations underlie the familiarity effects we have observed here. It is commonly assumed that the 200–400 ms time range reflects access to visual representations of individual faces (e.g., Schweinberger & Neumann, 2016). We have further argued in previous work that the

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Sustained Familiarity Effect (SFE) found in a subsequent time range (400–600 ms) represents processes related to the integration of identity-specific semantic with visual information, or to the sustained activation of person-specific representations to prepare a potential interaction (Wiese, Ingram, et al., 2019; Wiese, Tüttenberg, et al., 2019). Importantly, however, as we have also previously suggested, to infer such additional processing relative to visual recognition in the earlier N250 time range, it seems necessary to show that familiarity effects in the 400–600 ms time range are not simply carried over from earlier segments (Wiese, Hobden, et al., 2022). Similar to previous studies of learning a new face from a brief interaction (Popova & Wiese, 2023b), the present results provide no evidence for an increased familiarity effect in the later time window relative to earlier effects. In line with the above reasoning, we therefore cannot interpret the effects observed here in the 400–600 ms time window as reflecting additional processing relative to the N250 time range. Alternatively, it seems possible that access to visual representations may take more time in the case of newly learnt relative to highly familiar faces. In line with this, the late time window revealed the most consistent familiarity effects, which were larger in effect sizes than those observed in earlier time windows and yielded significant between-group comparisons as well as significant correlations with behavioural data.

Finally, the present study provides some initial insights into the relationship between neural representations of novel faces and the participants' subjective experience of recognisability. More specifically, we observed a positive correlation between subjective recognisability and the ERP familiarity effect in the late 400–600 ms time window. In other words, those participants who showed larger ERP effects also demonstrated larger increases in rated recognisability. Note, however, that this correlation was observed across all participants, independent of the time gap condition. Accordingly, it could partly reflect individual differences in face learning, with better learners showing larger ERP effects. However, average ERP effects decreased between the 0h and 4h conditions, and it seems likely that participants in the latter condition would have shown larger ERP familiarity effects had they been tested earlier. Nevertheless, the correlation establishes a relationship between self-reported and objective ERP markers of learning.

As discussed in a previous paper (see Popova & Wiese, 2023a, 2023b), unstructured interactions during learning as used in the present study have the clear advantage of increasing ecological validity, as learning happens under more realistic conditions as compared to the use of pictures/video material or scripted interactions. The disadvantage is a relative reduction in experimental control, as for instance the extent to which participants were paying attention to the confederates' faces is unclear. Future studies may entail specific tasks during real-life learning to experimentally manipulate such factors. Moreover, in the present study we have not examined any potential moderating factors, such as age or sex of the participants and/or to-be-learnt faces. Specifically, as a reviewer has commented, only female confederates were used in the present study, while participant sex and potentially sexual orientation varied. Nonetheless we are neither aware of any research suggesting a difference in how female and male facial identities are learnt, nor of differences in face identity learning related to participant sex or sexual orientation. Indeed, we consider it unlikely that such factors would affect the nature of the basic learning and consolidation mechanism, even if they could influence the rate of learning itself. However, we accept that future studies may examine such potential moderators.

In conclusion, the present study examined neural correlates of learning and consolidating previously unfamiliar facial identities. We found that an initial neural representation, as observed in the N250 time range immediately after learning, is substantially reduced in strength within the next 4 h. Critically, however, this representation is restored after a 24-h gap between learning and test, suggestive of strengthening via consolidation during sleep. Our findings emphasise the dynamic changes that novel face representations undergo during the first 24 h after learning and demonstrate that the initial representation is not stable but changes over time. Our results therefore offer a first step towards a theoretical understanding of the temporal dynamics of face learning.

Author statement

Holger Wiese – Conceptualization; Formal analysis; Investigation; Methodology; Project administration; Resources; Supervision; Visualization; Writing – original draft; Writing - review & editing. Tsvetomila Popova- Data curation; Formal analysis; Investigation; Project administration. Maya Schipper - Data curation; Formal analysis; Investigation. Deni Zakriev - Data curation; Formal analysis; Investigation. A. Mike Burton - Conceptualization; Writing – original draft; Writing - review & editing. Andrew W. Young - Conceptualization; Writing – original draft; Writing - review & editing

Open practices section

The study in this article earned Open Data badge for transparent practices. The data used in this study are available at: https://osf.io/5yn96/?view_only=2f832b29fe544722a1153c7160e8b2b2.

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