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Event-related potentials reveal the development of stable face representations from natural variability

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Event-related potentials reveal the development of stable face representations from

natural variability

Sally Andrews[1,5], A. Mike Burton[1,6], Stefan R. Schweinberger[2,3], Holger Wiese[2,4]

1. *School of Psychology, University of Aberdeen, UK*

2. *DFG Research Unit Person Perception, Friedrich Schiller University Jena, Germany*

3. *Department of General Psychology and Cognitive Neuroscience, Friedrich Schiller University Jena, Germany*

4. *Department of Psychology, Durham University, UK*

5. *Division of Psychology, Nottingham Trent University, UK*

6. *School of Psychology, University of York*

Running head: Developing stable face representations

Address for correspondence

Holger Wiese, Department of Psychology, Durham Univsersity, Queen's Campus, E007

Wolfson Building, Stockton-on-Tees, TS17 6BH, UK. E-Mail: holger.wiese@durham.ac.uk,

Phone: 0044 191 3340433

1   **Abstract**

2   Natural variability between instances of unfamiliar faces can make it difficult to

3   reconcile two images as the same person. Yet for familiar faces, effortless recognition occurs

4   even with considerable variability between images. To explore how stable face

5   representations develop, we employed incidental learning in the form of a face sorting task.

6   In each trial, multiple images of two facial identities were sorted into two corresponding piles.

7   Following the sort, participants showed evidence of having learnt the faces, performing more

8   accurately on a matching task with seen than unseen identities. Furthermore, ventral temporal

9   event-related potentials were more negative in the N250 time range for previously-seen than

10   previously-unseen identities. These effects appear to demonstrate some degree of abstraction,

11   rather than simple picture learning, as the neurophysiological and behavioural effects were

12   observed with novel images of the previously-seen identities. The results provide evidence of

13   the development of facial representations, allowing a window onto natural mechanisms of

14   face learning.

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3

1 **Introduction**

2

3   Successfully recognizing the face of a familiar person requires activation of a stable

4 face representation. Such representations must be sensitive to structural and textural

5 differences between different identities, but tolerant of transient within-person variability in

6 appearance. The same person can appear visually different on different occasions, and this

7 variability can sometimes exceed the differences between two people (Adini, Moses &

8 Ullman, 1996). The ability to identify a familiar face is thus a remarkable challenge to the

9 visual system, yet familiar observers are able to do so with ease and accuracy. By contrast,

10 recognizing or even matching unfamiliar faces from new instances is surprisingly hard

11 (Bruce et al., 1999; Clutterbuck & Johnston, 2002; Jenkins, White, van Montfort & Burton,

12 2011). Although this remarkable difference in processing familiar and unfamiliar faces has

13 been shown in a number of studies (Bruce et al., 2001; Jenkins et al., 2011), we remain

14 largely unclear about the processes involved in the transition between these two states, i.e.,

15 face learning. Specifically, the precise mechanisms of forming representations that allow

16 identification of a person across different instances are largely unknown.

17   Recent investigations have begun to address the question of how stable

18 representations form. These investigated the benefits of learning multiple *different* instances

19 of the same person, with familiarity measured using previously unseen instances of those

20 faces (Longmore, Liu & Young, 2008; Etchells & Johnston, 2014, Kaufmann, Schweinberger

21 & Burton, 2009). Etchells and Johnston (2014) found that extensive learning of two different

22 viewpoints (i.e. front-facing, three-quarter view) increased subsequent matching accuracy

23 (Clutterbuck & Johnston, 2005). Moreover, experiencing many natural images of a person's

24 face shows evidence of generalizability to previously unseen natural images (White et al.,

25 2014).

1   Whereas behavioural studies provide information about the outcome of a cascade of

2   cognitive sub-processes, event-related brain potentials (ERP) allow the examination of these

3   neuro-cognitive sub-stages in more detail (see e.g., Luck, 2005). ERPs are voltage changes in

4   the human electroencephalogram (EEG), thus reflecting the summed activity of post-synaptic

5   potentials (see e.g., Jackson & Bolger, 2014), which are time-locked to certain events such as

6   the presentation of a visual stimulus. ERP waveforms consist of a series of positive and

7   negative components or peaks, which represent neural correlates of specific perceptual and

8   cognitive processing stages. For instance, all visual stimuli elicit a positive-going P1

9   component, which peaks at occipital channels about 100 ms after stimulus onset. The P1

10   reflects early visual processes, as it is highly sensitive to low-level stimulus characteristics,

11   such as luminance or contrast (e.g., Luck, 2005).

12   The earliest ERP component closely related to face rather other visual object

13   processing is the N170 (Bentin et al., 1996; Eimer, 2011), a negative deflection peaking at

14   occipito-temporal channels roughly 170 ms after stimulus onset. N170 is often interpreted to

15   reflect the structural encoding of faces or the detection of a face-like pattern (Eimer, 2000;

16   Schweinberger & Burton, 2003; Amihai, Deouell, & Bentin, 2011), i.e., processing stages

17   prior to the identification of an individual face. In line with this, a number of studies found no

18   difference in N170 amplitude for familiar relative to unfamiliar faces (Bentin & Deouell,

19   2000; Eimer, 2000; Schweinberger et al., 2002; Henson et al., 2003). Other studies, however,

20   found larger N170 amplitudes for familiar relative to unfamiliar faces (experiment 2 in Wild-

21   Wall, Dimigen & Sommer, 2008; Caharel et al., 2005, 2006), or larger amplitudes for

22   unfamiliar relative to familiar faces (Marzi & Viggiano, 2007). Accordingly, the question

23   whether N170 is sensitive to face familiarity is not entirely resolved. It should be noted,

24   however, that even those studies supporting this suggestion are not consistent regarding the

25   direction of a potential N170 familiarity effect, and that such effects are typically small.

5

1   An ERP component showing clear sensitivity to facial familiarity is typically

2   observed to peak approximately 250 ms following stimulus onset. Immediate repetitions of

3   familiar faces have been shown to result in increased negativity relative to non-repetitions at

4   occipito-temporal scalp sites (Begleiter, Porjesz & Wang, 1995; Schweinberger, Pfütze &

5   Sommer, 1995), an effect known as N250r (r for repetition). While an N250r is also observed

6   for unfamiliar faces, the effect is much smaller (Schweinberger et al., 1995), and largely

7   restricted to the repetition of identical images (see Zimmermann & Eimer, 2013).

8   Interestingly, an N250r for familiar faces has been shown even when different images of the

9   same identity are presented as the second stimulus (Schweinberger, Pickering, Jentzsch,

10   Burton & Kaufmann, 2002). Increases in negativity here are smaller than when the same

11   image is repeated, suggesting that the effect is in part image-sensitive. Similarly, a degree of

12   viewpoint-independence of the N250r may develop after face learning (Zimmermann &

13   Eimer, 2013). While it has been a considerable challenge to experimentally separate the

14   image-independent and image-specific parts of the N250r (for promising approaches, see

15   Bindemann et al., 2008, and Doerr et al., 2011), one might argue that the image-independent

16   part of the N250r reflects the transient activation of stable representations – akin to face

17   recognition units (see Bruce & Young, 1986).

18   More recently, a similar negativity has been observed with intervening faces between

19   identity repetitions, which shares a similar onset to N250r, but extends until around 400ms

20   post stimulus onset (e.g. Itier & Taylor, 2004). Thus, repetition effects have been analysed

21   separately in two subsequent time windows (e.g., Kaufmann et al., 2009), representing an

22   'early' (app. 200 – 280 ms) and a 'late N250' (app. 280 – 400 ms), respectively (Wiese,

23   2012). Importantly, the N250 effect is evident for *familiar* faces when images of different

24   identities appear between repetitions, while in the case of *unfamiliar* faces, the presence of

25   different identities between repetitions eliminates the effect (Pfütze, Sommer, &

6

1   Schweinberger, 2002). Indeed, Itier & Taylor (2004) demonstrated that seeing the same face

2   multiple times (with non-immediate repetitions) produces a more long-term N250. Studies on

3   face repetition therefore suggest that the more negative N250 for repeated faces reflects the

4   transient activation of an individual face representation, with stronger activations for better-

5   known faces. Generally in line with this idea, a larger N250 has also been observed for

6   famous relative to unfamiliar faces (Gosling & Eimer, 2011).

7   Of most relevance to the present experiment, N250 is sensitive to face learning. More

8   specifically, following learning, pre-experimentally unfamiliar faces show an enhanced N250

9   that is equivalent to highly familiar faces (Pierce, Scott, Boddington, Droucker, Curran &

10   Tanaka, 2011; Tanaka, Curran, Porterfield & Collins, 2006). Importantly, Kaufmann and

11   colleagues observed an increased N250 for different instances of the learned identities,

12   showing that the effect was not due to the formation of a pictorial representation (Kaufmann

13   et al., 2009). Moreover, in this study N250 amplitude further increased with increasing

14   familiarity of the faces over different experimental blocks. Therefore, a larger N250 to

15   different-image, non-immediate repetitions of faces reflects an index of familiarity that can

16   be used to track the establishment of face representations (Kaufmann et al., 2009). At the

17   same time, increasing N250 amplitudes in the course of learning appear to reflect the

18   acquisition of a stable face representation, independent of the repetition of specific images.

19   Whether and to what extent N250r as measured in repetition priming paradigms and

20   the N250 face learning effect reflect the same underlying processes is not entirely clear at

21   present and of substantial theoretical interest (see also Schweinberger & Neumann, in press).

22   As described above, N250r is typically measured as the difference between repeated and non-

23   repeated familiar faces, and therefore likely reflects facilitated access of a well-established

24   representation due to its pre-activation by the prime. At the same time, the N250 effect in

25   learning experiments is usually measured as the difference between newly learnt and

1   unfamiliar faces. It probably reflects access to a newly formed representation for the learnt

2   faces, whereas no corresponding representation exists for unfamiliar faces. Accordingly, this

3   effect may be similar, although probably less pronounced (see below), to the difference in

4   N250 between famous and unfamiliar faces (Gosling & Eimer, 2011), which may also reflect

5   accessing a representation of an individual face in the former but not in the latter case.

6   As noted earlier, face learning involves the development of representations that allow

7   the recognition of faces under highly variable conditions. Such variability might be

8   encountered across a complex combination of dimensions. For example, a face may appear

9   different between encounters because of textural differences due to lighting, health, and

10   tiredness changes, in addition to differences because of changes in viewpoint, expression, and

11   distance from the observer. Whereas some ERP studies on face learning did not take any of

12   these dimensions into account (Tanaka et al., 2006; Pierce et al., 2011), as identification of

13   the newly learnt face was tested with the same image at all occasions, Kaufmann and

14   colleagues (2009) observed an enhanced N250 for newly learnt faces for previously unseen

15   instances. Another recent study by Schulz, Kaufmann, Kurt, and Schweinberger (2012)

16   extended these findings by showing distinct contributions of distinctiveness for face learning

17   and its correlate in the N250. However, in both studies, variability between images was rather

18   restricted to head turning, small differences in viewpoint, or speaking, but otherwise

19   experimentally constrained to maintain other dimensions of variability. At the same time, it

20   has been shown that high-quality, full-frontal images of unfamiliar people, taken on the same

21   day but with different cameras and under different lighting conditions, are relatively hard to

22   match (Bruce et al., 1999). Sources of image variability in this latter study were quite

23   different from those in previous ERP studies on face learning, which therefore only

24   superficially, and incompletely, capture the apparent changes of an unfamiliar person's

25   appearance in real life.

1 Interestingly, previous studies using adaptation techniques in functional brain imaging

2 found a sensitivity of the so-called fusiform face area (FFA) for facial identity when different

3 images with limited variability (i.e., changes in viewpoint) were used (Ewbank & Andrews,

4 2008). At the same time, FFA was not sensitive to identity when images with natural

5 variability were presented (Davies-Thompson et al., 2009), although a more anterior

6 subregion of fusiform gyrus has been reported to exhibit identity-sensitive responses for such

7 face images (Eger, Schweinberger, Dolan, & Henson, 2005). It is therefore important to

8 understand whether the N250 learning effects observed in studies with limited variability

9 extend to variability that might naturally be experienced, i.e. across 'ambient images'

10 (Jenkins et al, 2011; Sutherland et al, 2013; see Figure 1). Jenkins et al. (2011) recently

11 demonstrated that sorting naturally varying images is remarkably difficult for unfamiliar

12 faces. In their task, unfamiliar observers were asked to sort 40 ambient images into as many

13 identities as they perceived. The most common number of identities perceived was nine, even

14 though only two identities were actually present. Accordingly, telling unfamiliar faces apart

15 seems to be much easier than telling unfamiliar faces together. Familiar observers, on the

16 other hand, sorted the identities quickly and accurately, with seemingly no difficulty,

17 reflecting the ability to accommodate entirely novel instances once a stable representation has

18 been established.

19   The present experiment examines how the formation of stable representations affects

20 the neural processing of newly learnt faces. To do this, we used 'ambient images' and an

21 incidental learning technique, based on the sorting procedure of Jenkins et al. (2011). This

22 reflects a further critical difference to previous ERP studies on face learning, which used

23 explicit learning tasks. The use of an implicit learning task is arguably closer to face learning

24 in daily life, as we usually do not explicitly try to encode the faces of the people we have just

25 met. Observers were asked to sort 40 unfamiliar face images of two different people into

1 separate piles for each identity. However, unlike the Jenkins et al study, we instructed our

2 participants that only two different people were present. Under these constraints, naturally

3 varying instances are sorted into their respective identities with very few misidentification

4 errors (Andrews et al., 2015). Therefore, the constraint of being told the correct number of

5 identities appears to enable the incidental learning of these identities during sorting.

6   To determine whether resulting representations for these identities can be observed in

7 ERP familiarity correlates, we investigated any putative differences between novel, newly

8 learnt and pre-experimentally familiar (famous) faces in the N250. We assumed that face

9 learning, as implemented in the present study, would result in the establishment of a stable

10 representation that would on the one hand not be available for novel faces, but that would on

11 the other hand not be as refined as the representation of highly familiar faces. Accordingly,

12 N250 for newly learnt faces was expected to lie in-between the N250 for famous and novel

13 faces. Importantly, we also investigated whether any observable differences in neural

14 processing exist between images of learnt identities that were seen during learning, and

15 completely new instances of learnt faces that have not been seen before. If the sorting task

16 results in the establishment of stable representations, we hypothesised that N250 would be

17 more negative for learnt than novel faces. Moreover, any potential difference in the same-

18 image versus different-image conditions would inform about the extent to which the observed

19 N250 learning effect reflects image-dependent or image-independent learning. At the same

20 time, no difference between the images that were seen in the earlier learning phase and

21 previously unseen images of the learnt identities would be strongly indicative of the implicit

22 formation of stable (rather than image-dependent) representations of facial identities (Burton

23 et al., 2005; Burton, Jenkins, & Schweinberger, 2011). Whereas some studies found learning

24 effects in the early N250 (Kaufmann et al., 2009), others observed effects that extended well

1   into the later N250 time range (Schulz et al., 2012). It was therefore not clear whether

2   learning effects in the present study would occur in the early or late N250.

3   In addition, to estimate behavioural effects of face learning, and to ascertain their

4   relationship to any ERP findings, we measured performance in a subsequent perceptual

5   matching task. This task indicates differences in levels of familiarity, such that highly

6   familiar faces are matched with greater accuracy than less familiar faces (Clutterbuck &

7   Johnston, 2002; 2005).

8

9   **Methods**

10   **Participants**

11   Twenty-four (19 female) undergraduate students with a mean age of 21.95 years (SD

12   = 3.42, range = 18-30) from the Friedrich Schiller University of Jena participated in the

13   experiment for course credit or a reimbursement of 5 €/h. All participants reported normal or

14   corrected to normal vision, and reported no previous neurological or psychiatric conditions.

15   All were native German speakers and all were right-handed (as measured by the Edinburgh

16   Handedness Inventory; Oldfield, 1971). All participants gave written informed consent to

17   participate.

18   **Design & materials**

19   There were three components to the current design. All participants completed an

20   initial sorting task, followed by an ERP task, finishing with a face matching task. All portions

21   of the design were manipulated within-subjects.

22   Stimuli were 85 images each of 6 identities unfamiliar to our participants (Dutch

23   celebrities; Chantal Janzen, Gigi Ravelli, Hanna Verboom, Nicolette Kluijver, Renate

24   Verbaan and Wendy van Dijk), 20 images each of 2 pre-experimentally familiar celebrities

25   (Cameron Diaz, Heidi Klum), and 12 images of different butterflies (used as target stimuli

1   during the ERP task, see below). Images were obtained from a Google Image search, and

2   were the first unique images where the face/butterfly occupied at least 190 x 285 pixels, and

3   where faces were roughly front-facing. These were then size-adjusted and cropped to 190 x

4   285 pixels in height, and converted to greyscale.

5   For each unfamiliar identity, three image sets were randomly selected, comprising

6   two sets of 20 images each to be used in the sorting and EEG tasks and a further set of 45

7   images to be used in the matching task (match Set). Each identity was paired with another, so

8   that two identities always co-occurred (unfamiliar set 1 consisted of Chantal Janzen with

9   Hanna Verboom, unfamiliar set 2 consisted of Gigi Ravelli with Renate Verbaan, and

10 unfamiliar set 3 consisted of Nicolette Kluijver with Wendy van Dijk). There were therefore

11 3 pairs of identities; for each pair of faces, there were 40 images in set A, 40 images in set B,

12 and 90 images in set C. Mean luminance for all face stimuli to be used in the EEG portion of

13 the study was calculated using image analysis software (ImageJ; Schneider, Rasband &

14 Eliceiri, 2012) and entered into a one-way between subjects ANOVA (factor levels famous

15 set, unfamiliar set 1-A, unfamiliar set 1-B, unfamiliar set 2-A, unfamiliar set 2-B, unfamiliar

16 set 3-A, unfamiliar set 3-B). Results from this analysis revealed no differences in mean

17 luminance between the sets ($F(6, 273) = 1.00$, $p > .05$, $\eta\rho^2 = .02$).

18   For the sorting task, the 80 images (40 in set A, 40 in set B) of each of the 3

19 unfamiliar ID pairs were printed at a size of 3 x 4 cm, at maximum DPI and laminated. The

20 ID pair used for the sorting task was counterbalanced across participants, so that each of the 6

21 unfamiliar face sets (3 ID pairs x 2 image sets [A, B]) were seen by an equal number of

22 participants during the sorting task.

23   For the ERP task, 172 trials were completed in total. These were 40 trials for same

24 images of the IDs seen in the sorting task (seen-in-sort-sIMG), 40 trials for different images

25 of the IDs seen in the sorting task (seen-in-sort-dIMG), 40 famous ID trials (famous), 40

1   previously unseen unfamiliar ID trials (new-to-ERP), and 12 butterfly trials, which were not

2   analysed. Images were presented sequentially for 1000ms at 190 x 285 pixels in the centre of

3   the screen. Trials were preceded by a fixation with a randomly selected duration (ranging

4   from 700-1300ms in 100ms intervals; M = 1000ms). Participants sat at a distance of 90cm

5   from the screen, with head position maintained with an adjustable chinrest. This resulted in a

6   visual angle of approximately 4.04° x 6.38° for each image. Image order was randomly

7   selected for each participant.

8   For the matching task, 180 trials were completed in total. These were 15 same-ID and

9   15 different-ID trials for each of the 2 IDs that were first seen in the sorting task (seen-in-

10   sort), 15 same- and 15 different-ID trials for each of the 2 IDs that were first seen in the ERP

11   task (seen-in-ERP), and 15 same- and 15-different ID trials each for 2 previously unseen

12   unfamiliar IDs (new-to-match). Each image was presented at 190 x 285 pixels, with image

13   pairs presented side-by-side.

14   **Procedure**

15   Participants were prepared for the EEG portion of the experiment prior to the sorting

16   task. They were then handed a pile of shuffled cards of two identities, and asked to sort the

17   images into separate piles so that all the images of the same person were together. They were

18   told that only two identities were present, and that they should generate only two piles. They

19   were also encouraged to place images of the same person next to one another, so they could

20   see all images at the same time. There was no time restriction, and participants were able to

21   move images freely back and forth between piles before settling on their final decision.

22   In the ERP task, participants were presented with sequentially presented images,

23   which remained on screen for 1s and were preceded by a fixation. Participants were required

24   to respond using a keypress when a butterfly was presented, but to withhold any response

25   following the presentation of faces. Speed and accuracy of responses was stressed.

1   In the face matching task, participants were presented with pairs of faces, and were

2   required to indicate via keypresses whether pairs were of the same person, or two different

3   people. There was no time restriction, and participants were encouraged to respond as

4   accurately as possible.

5   **EEG recording and analyses**

6   EEG was recorded from 32 active sintered Ag/Ag–Cl electrodes using a Biosemi

7   Active II system (BioSemi, Amsterdam, Netherlands). Please note that BioSemi systems

8   work with a "zero-Ref" set-up with ground and reference electrodes replaced by a CMS/DRL

9   circuit (cf. http://www.biosemi.com/faq/cms&drl.htm for further information). EEG was

10   recorded continuously with a 512-Hz sample rate from DC to 155 Hz. Recording sites

11   corresponded to an extended version of the 10–20-system (Fz, Cz, Pz, Iz, FP1, FP2, F3, F4,

12   C3, C4, P3, P4, O1, O2, F7, F8, T7, T8, P7, P8, F9, F10, FT9, FT10, TP9, TP10, P9, P10,

13   PO9, PO10, I1 and I2). Blinks were corrected using the algorithm implemented in BESA

14   5.1.8 (see Berg & Scherg, 1994). EEG was then segmented from –200 ms until 1000ms

15   relative to stimulus onset, with the first 200 ms serving as a baseline. Artifact rejection was

16   carried out using an amplitude threshold of 100μV and a gradient criterion of 50μV.

17   Remaining trials were recalculated to average reference, averaged according to experimental

18   condition and digitally low-pass filtered at 40 Hz (12 db/oct, zero phase shift). In the

19   resulting waveforms, mean amplitude of the P1 (85-115 ms) was analyzed at O1/O2, while

20   mean amplitudes of N170 (130-160 ms), and early and late N250 (240-280 ms, 280-400ms)

21   were analyzed at electrode sites P9/P10, PO9/PO10, and TP9/TP10 as in previous studies on

22   face learning (Kaufmann et al., 2009). The mean number of trials was 35.8 in the seen-in-

23   sort-sIMG (SD = 4.9; range = 24 - 40), 35.6 in the seen-in-sort-dIMG (SD = 4.8; range = 22 -

24   40), 36.3 in the famous (SD = 4.4; range = 24 – 40), and 35.5 in the new-to-ERP conditions

25   (SD = 5.0; range = 23 - 40), respectively.

1

Results

3 **Sorting task**

4   Intrusion errors were calculated for each participant. We define intrusion errors as an

5 instance of one ID appearing in a pile containing mostly images of the other ID. The median

6 number of errors from sorting the 40 images was 0.5 (mode = 1; range = 0 - 19), and 6

7 participants sorted the identities perfectly.

8 **Matching task**

9   Correct responses were entered into a one-way repeated measures ANOVA with 3

10 levels (exposure; new-to-match, seen-in-ERP, seen-in-sort). Data from two participants were

11 missing due to technical errors, leaving data from 22 participants. The resulting output

12 revealed a significant main effect of exposure ($F(2, 42) = 10.41$, $p < .001$, $\eta\rho^2 = .33$). Tukey's

13 HSD showed this effect was due to a significant difference between new-to-match IDs and

14 seen-in-sort IDs ($M = .80$ +/- 0.03 *SEM* and $M = .89$ +/- 0.03 *SEM*, respectively; $p < .05$), and

15 also between new-to-match IDs and seen-in-ERP IDs ($M = .80$ +/- 0.03 *SEM* and $M = .85$ +/-

16 0.03 *SEM*, respectively; $p < .05$).

17 **ERP task**

18   During the EEG task, participants detected all target stimuli. Two participants

19 wrongly pressed the response key when a face was presented, but both only in one trial.

20 Mean response time for correct responses was 509.5 ms (+/- 50.8 SD).

21   ERP waveforms are depicted in Figure 2, and scalp-topographical voltage maps of

22 exposure effects relative to the novel condition are shown in Figure 3. In the interests of

23 stringency and readability, only effects that involve the factor 'exposure' will be reported in-

24 text. A complete list of all effects from P1 and N170 can be found in Table 1, while a

25 complete list of all effects from Early and Late N250 can be found in Table 2.

1 **P1**

2   P1 amplitude was analysed using a 4 (exposure; new-to-ERP, seen-in-sort-sIMG,

3 seen-in-sort-dIMG, famous) x 2 (hemisphere; left, right) repeated measures ANOVA, which

4 revealed no significant effect of exposure ($F(3, 69) = 1.11$, $p = .350$, $\eta\rho^2 = .046$), or

5 interaction between exposure and hemisphere ($F(3, 69) = 2.42$, $p = .073$, $\eta\rho^2 = .10$). This

6 finding indicates that potential low-level differences between faces in the different

7 experimental conditions did not affect the ERP results.

8 **N170**

9   N170 amplitude was analysed using a 4 (exposure; new-to-ERP, seen-in-sort-sIMG,

10 seen-in-sort-dIMG, famous) x 2 (hemisphere; left, right) x 3 (site; TP, P, PO) repeated

11 measures ANOVA. Again, there was no significant effect of exposure ($F(3, 69) = 1.01$, p

12 $= .393$, $\eta\rho^2 = .042$), and no interaction between hemisphere and exposure ($F(6, 138) = 1.94$, p

13 $= .079$, $\eta\rho^2 = .078$; see Figure 2).

14 **Early N250**

15   A corresponding ANOVA for the early N250 time window revealed a significant

16 main effect of exposure ($F(3, 69) = 4.46$, $p = .010$, $\eta\rho^2 = .163$). There were no significant

17 interactions either between exposure and site ($F(6, 138) = 1.12$, $p = .354$, $\eta\rho^2 = .046$), or

18 between exposure and hemisphere ($F(6, 138) = 1.92$, $p = .135$, $\eta\rho^2 = .077$), although

19 somewhat larger exposure effects were seen over the right hemisphere. There was also no

20 significant three-way interaction between hemisphere, site and exposure ($F(6, 138) = 1.09$, p

21 $= .373$, $\eta\rho^2 = .045$). Follow-up contrasts on the main effect showed this effect to be driven by

22 a difference between new-to-ERP and famous IDs ($F(1, 23) = 18.36$, $p < .001$, $\eta\rho^2 = .444$),

23 with famous IDs being significantly more negative. There was also a trend for seen-in-sort-

24 dIMG to show more negative amplitudes than new-to-ERP IDs ($F(1, 23) = 3.09$, $p = .092$,

25 $\eta\rho^2 = .119$), whereas the difference between seen-in-sort-sIMG and new-to ERP IDs was not

1　significant ($F(1, 23) = 2.09$, $p = .162$, $\eta\rho^2 = .083$). At the same time, famous IDs elicited

2　more negative amplitudes than both seen-in-sort-sIMG ($F(1, 23) = 5.13$, $p = .033$, $\eta\rho^2 = .182$)

3　and seen-in-sort-dIMG conditions ($F(1, 23) = 4.92$, $p = .037$, $\eta\rho^2 = .176$).

4　**Late N250**

5　　A corresponding analysis was conducted in the 280 – 400ms time window. This

6　revealed a significant main effect of exposure ($F(3, 69) = 15.30$, $p < .001$, $\eta\rho^2 = .400$). There

7　were no significant interactions either between exposure and site ($F(6, 138) = 0.76$, $p = .603$,

8　$\eta\rho^2 = .032$), or between exposure and hemisphere ($F(6, 138) = 0.59$, $p = .738$, $\eta\rho^2 = .025$),

9　although somewhat larger exposure effects were observed over the right hemisphere. There

10　was also no significant three-way interaction between hemisphere, site and exposure ($F(6,$

11　$138) = 0.96$, $p = .455$, $\eta\rho^2 = .040$). Follow-up orthogonal contrasts showed that new-to-ERP

12　IDs were less negative than both seen-in-sort-sIMG trials ($F(1, 23) = 13.29$, $p < .001$, $\eta\rho^2$

13　$= .366$), and seen-in-sort-dIMG trials ($F(1, 23) = 18.78$, $p < .001$, $\eta\rho^2 = .449$), and further that

14　famous trials were more negative than both seen-in-sort-sIMG ($F(1, 23) = 7.77$, $p = .010$, $\eta\rho^2$

15　$= .252$) and seen-in-sort-dIMG trials ($F(1, 23) = 9.84$, $p = .005$, $\eta\rho^2 = .300$). There was no

16　difference between seen-in-sort-sIMG and seen-in-sort-dIMG trials ($F(1, 23) = 0.82$, $p = .375$,

17　$\eta\rho^2 = .035$)[1]. These main findings are shown in Figure 2.

18

19　　　　　　　　　　　　　　　**Discussion**

20　　The present experiment explores the influence of experiencing within-person

21　variability from ambient images during incidental face learning, using behavioural and ERP

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[1] Please note that a corresponding ANOVA, in which two participants with error rates of more than 2 *SD* above the mean in the sorting task were excluded, yielded highly similar results. A significant main effect of exposure ($F(1, 21) = 14.51$, $p < .001$, $\eta\rho^2 = .409$) was related to more negative amplitudes for seen-in-sort-sIMG, seen-in-sort-dIMG, and famous relative to new-to-ERP IDs (all $F(1, 21) > 13.26$, all $p < .002$, all $\eta\rho^2 > .387$). Famous trials were more negative than both seen-in-sort-sIMG and seen-in-sort-dIMG trials (both $F(1, 21) > 6.24$, both $p < .021$, both $\eta\rho^2 = .229$), and there was no difference between seen-in-sort-sIMG and seen-in-sort-dIMG trials ($F(1, 21) = 0.98$, $p = .332$, $\eta\rho^2 = .045$.

1   measures of familiarity. Whereas no familiarity effects were detected in the N170, we found

2   that faces learnt through experience with natural within-person variability showed enhanced

3   negativity, relative to novel faces, in the late N250 time range (280 – 400 ms), which is

4   similar to previous results from explicit face learning experiments (Kaufmann et al., 2009;

5   Schulz et al., 2012, Tanaka et al., 2006; Pierce et al., 2011). Of particular importance, N250

6   to same-exemplar and different-exemplar conditions were indistinguishable. We therefore

7   conclude that an image-independent, or stable, representation was established during the

8   sorting task, presumably as a result of exposure to natural variability of the newly learnt

9   facial identities. Our ERP results are consistent with behavioural measures of familiarity

10   (simultaneous matching task; Clutterbuck & Johnston, 2002; 2005), confirming earlier

11   findings that experience of natural variability enables the formation of stable face

12   representations. The present results are the first to demonstrate a corresponding effect in the

13   N250, which has been previously linked to face learning, but has not been examined in a

14   study that directly compared repeated and novel images of newly learnt faces. However, late

15   N250 for newly learnt faces was less negative than N250 for famous faces, and larger

16   negativity for famous but not newly learnt faces was also observed in the earlier N250 time

17   window (180 – 280 ms). This suggests that the representations acquired during sorting were

18   somewhat weaker and needed more time to be accessed compared to those for highly

19   overlearned faces.

20   It is becoming increasingly clear that within-person variability should be considered,

21   rather than controlled, when exploring face identification and face learning (Burton, 2013;

22   Jenkins & Burton, 2011). By incorporating this natural variability into face learning

23   procedures, we have recently found that experience of natural variability might in fact be

24   necessary in order to form stable representations, as has been suggested by Bruce (1994).

25   This requirement appears to arise because individuals have *idiosyncratic* variability, i.e. the

1   ==ways in which faces vary are different between identities (Burton, Kramer, Ritchie & Jenkins,==

2   ==2016).== Using the same behavioural matching task, but different target identities, we again

3   found that simply experiencing natural variability between instances of the same person is

4   sufficient to form representations that are sensitive to previously unseen images of that

5   person (Andrews et al., 2015).

6   If such an incidental learning technique enables the formation of stable

7   representations, one would expect that evidence of face representations would be evident

8   from familiarity-sensitive ERPs. N250 has been shown to track the acquisition of new face

9   representations formed from only one face image (e.g., Pierce et al., 2011; Tanaka et al.,

10   2006, Wiese, Kaufmann, & Schweinberger, 2014) or from constrained variability (e.g.,

11   Kaufmann et al., 2009, Schulz et al., 2012). Importantly, however, no previous study

12   examined effects of natural within-person variability on N250, which appears crucial for face

13   learning (Bruce, 1994). We therefore substantially extend previous ERP findings to faces

14   learnt from ambient images, with natural variability==. Our finding of highly similar N250==

15   ==amplitudes for same- and different-image conditions== further shows that the resulting

16   representations are identity- rather than image-specific. Moreover, we observed a later ERP

17   face learning effect than previous studies (Kaufmann et al., 2009; Pierce et al., 2011; Schulz

18   et al., 2012), suggesting that newly established stable representations derived from natural

19   rather than restricted image variability are accessed at a somewhat later point in time.

20   ==Alternatively, the later effect could be driven by the implicit rather than explicit learning==

21   ==approach used in the present study – an idea that may be tested by subsequent research. At==

22   ==the same time, the== finding of an earlier N250 effect for highly overlearnt famous faces may

23   suggest that access becomes more efficient with increasing experience with a particular facial

24   identity.

1   We argue that the increases in negativity would not occur for faces learnt from a

2   single image when tested with a different exemplar. There is strong evidence to suggest that

3   N250 is evident for faces learnt from one image when later tested with the same image

4   (Tanaka et al., 2006; Pierce et al., 2011), yet there is no evidence to suggest that seeing a

5   different image of a previously seen unfamiliar face results in greater N250 than faces that

6   have never been seen previously (Pfütze et al., 2002). In behaviour, learning faces from a

7   single instance does not result in good recognition of different instances of the face (Logie,

8   Baddely & Woodhead, 1987). Even learning faces from two different instances does not

9   reliably enable subsequent recognition when tested with a different image (Longmore et al.,

10   2008). These findings support our argument that experience of multiple images of the same

11   person is necessary in order to form stable face representations that are tolerant of natural

12   variability. It is therefore highly unlikely that greater N250 to new instances of faces seen in

13   the sorting task could result from single image learning, although this conclusion is not based

14   on empirical findings and therefore reflects an outstanding question for future research.

15   Our incidental learning procedure involves experiencing natural variability when all

16   images of that person are present simultaneously. This technique cannot fully account for

17   how faces are learnt naturalistically, as different instances can normally only be seen at the

18   same time if seen from photographs. Behavioural data in the present study also show some

19   evidence for identity learning even when different images of the respective person were not

20   seen at the same time; during the matching task, identities that were only seen during the ERP

21   task were recognized more accurately than completely novel identities. While naturally

22   varying instances of unfamiliar faces are often not identified as the same person (Jenkins et

23   al., 2011), the debilitating effects of variability can be overcome by providing the viewers

24   with the information that they should expect to see only two people. We suggest that

25   participants also expected this context during the ERP task for then novel faces; observers

1   had recently been informed that different face images were of only two different identities,

2   and during the ERP task saw two other identities who were already familiar. It is therefore

3   plausible that stable representations formed online for unfamiliar identities introduced during

4   the EEG part of the experiment. Overall, sequential presentation of faces with context

5   information maybe a promising new method for understanding how faces are learnt.

6   A notable finding from this experiment was the observation of graded familiarity,

7   both from ERPs and behaviourally. More specifically, late N250 for newly learnt faces was

8   more negative than for faces novel to the EEG part, but not as negative as for highly

9   overlearnt famous faces. Moreover, matching was best for faces learnt during the sorting task,

10 but was still better for identities introduced during the previous ERP part than for novel faces.

11 Under normal situations, it is likely that faces become increasingly familiar, as we have more

12 experience with them (Jenkins & Burton, 2011), and behavioural experiments on face

13 learning have begun to show such graded effects (Clutterbuck & Johnston, 2002; 2005). As

14 greater experience with faces necessarily means experience of more natural variability, it is

15 possible that graded effects of familiarity indicate a continued consolidation and refinement

16 of face representations. That is, with more instances comprising a representation, it becomes

17 less likely that non-identity specific information is erroneously encoded into any resulting

18 representation. We suggest that examining both behavioural and neural correlates of different

19 levels of familiarity might prove useful in developing a comprehensive understanding of face

20 processes underlying learning and identification.

21   In conclusion, the present study is the first to demonstrate a neural correlate of the

22 implicit formation of image-independent face representations, which were established using

23 an incidental learning technique with ambient images. Previous research has focussed on our

24 explicit *memory* for faces, and our ability to identify individual faces (Bonner et al., 2003;

25 Longmore et al., 2008; Reynolds & Pezdek, 1992). Here we addressed the question of how

1   different instances of the same person are implicitly combined into a stable representation,

2   which may more closely resemble face learning in real life. We found an enhanced late N250

3   for implicitly learnt facial identities, reflecting access to new representations formed from

4   natural variability. We suggest that future research into face learning should consider how

5   between- *and* within-person variability contributes to the joint problem of telling faces apart,

6   while also telling faces together.

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1 *Table 1. ANOVA results for ERP modulations at P1, N17 and P2*

Effect	Latency	*df*	*F*	*p*	$\eta\rho^2$
P1	85-115				
Hemisphere		1, 23	1.77	.196	0.07
Exposure		3, 69	1.11	.351	0.05
Hemisphere x exposure		3, 69	2.42	.073	0.1
N170	130-160				
Hemisphere		1, 23	0.16	.693	0.01
Site		2,46	1.52	.229	0.06
Exposure		3, 69	1.01	.394	0.04
Hemisphere x site		2,46	1.29	.285	0.05
Hemisphere x exposure		3, 69	0.11	.954	0.01
Site x exposure		6, 138	1.94	.079	0.08
Hemisphere x site x exposure		6, 138	1.03	.409	0.04

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3

1   *Table 2*. ANOVA results for ERP modulations at Early and Late N250

Effect	Latency	*df*	*F*	*p*	$\eta\rho^2$
Early N250	180-280				
Hemisphere		1, 23	32.60	< .001	0.59
Site		2,46	43.00	< .001	0.65
Exposure		3, 69	4.46	.006	0.16
SIS-sIMG vs NTM		1, 23	2.09	.162	0.08
SIS_sIMG vs famous		1, 23	5.13	.033	0.18
SIS_dIMG vs NTM		1, 23	3.09	.092	0.12
SIS_dIMG vs famous		1, 23	4.92	.037	0.18
SIS_sIMG vs SIS_dIMG		1, 23	0.03	.865	0.001
Hemisphere x site		2,46	6.77	.003	0.23
Hemisphere x exposure		3, 69	1.91	.135	0.08
Site x exposure		6, 138	1.12	.354	0.05
Hemisphere x site x exposure		6, 138	1.09	.373	0.05
Late N250	240-280				
Hemisphere		1, 23	35.67	< .001	0.61
Site		2,46	39.95	< .001	0.64
Exposure		3, 69	15.30	< .001	0.4
SIS-sIMG vs NTM		1, 23	13.29	.001	0.37
SIS_dIMG vs famous		1, 23	7.77	.010	0.25
SIS_dIMG vs NTM		1, 23	18.78	< .001	0.45
SIS_dIMG vs famous		1, 23	9.84	.005	0.3
SIS_sIMG vs SIS_dIMG		1, 23	0.82	.375	0.04
Hemisphere x site		2,46	2.66	.081	0.1
Hemisphere x exposure		3, 69	0.59	.624	0.03
Site x exposure		6, 138	0.76	.603	0.03
Hemisphere x site x exposure		6, 138	0.96	455	0.04

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1   **Figure Captions**

2

3   *Figure 1*. Examples of ambient face images from two identities.

4

5   *Figure 2.* Early- and late-N250 ERP modulations across temporal and occipital-temporal sites

6   for left and right hemispheres, showing mean amplitudes by exposure

7   *Figure 3.* Scalp-topographical voltage maps (spherical spline interpolation, 110° equidistant

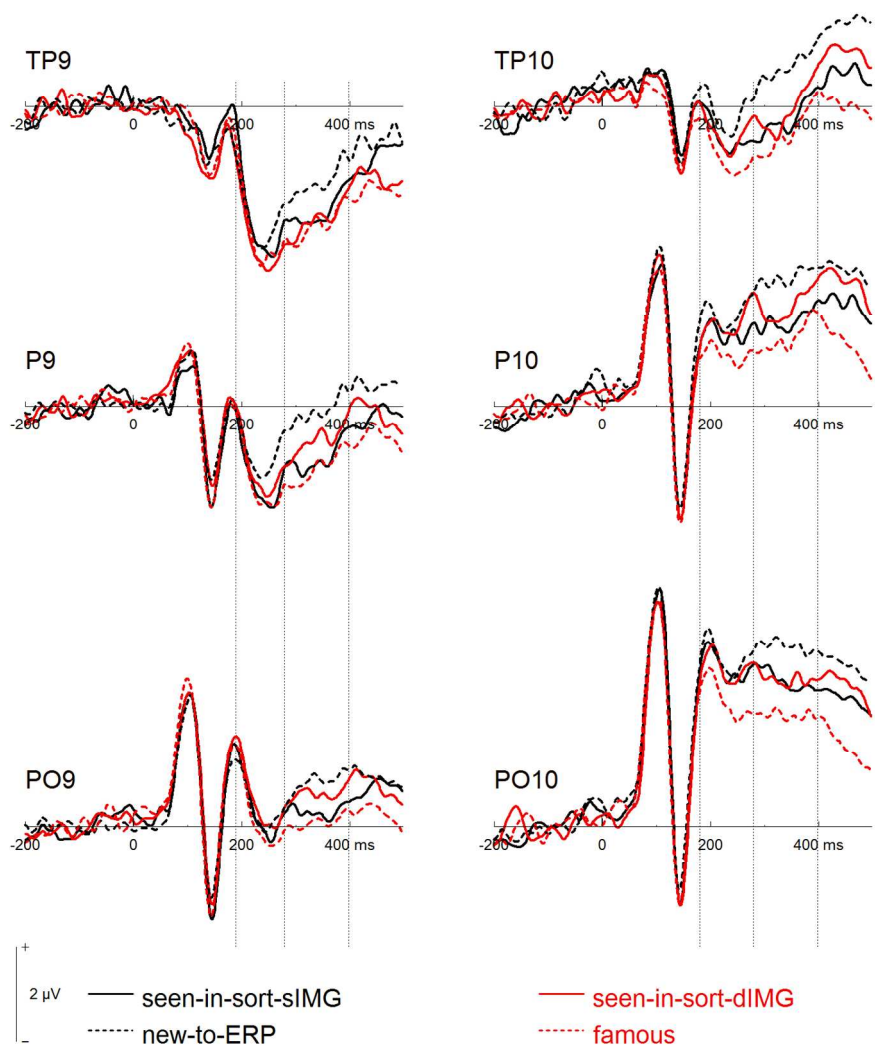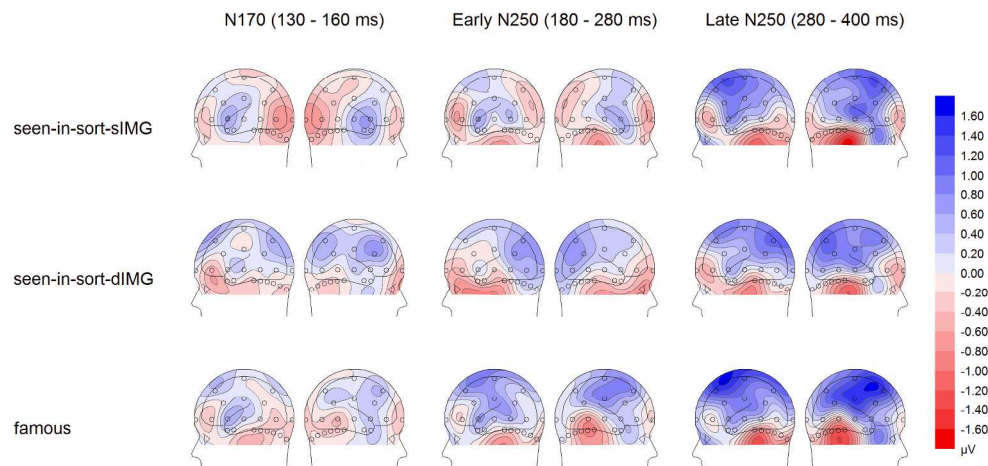8   projection) of the different waves between new-to-ERP and previously seen face identities.
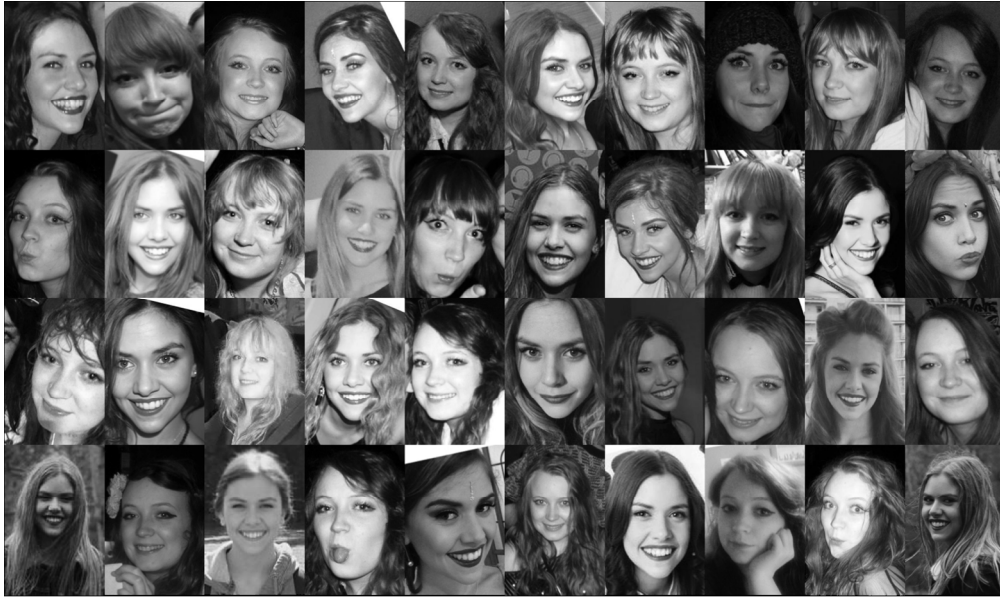
Figure 1

Figure 2

Figure 3
846x448mm (72 x 72 DPI)