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Face learning and the emergence of view-independent face recognition: An event-related brain potential study

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ABSTRACT

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Keywords: Face perception Face recognition Visual face memory Event-related brain potentials Recognizing unfamiliar faces is more difficult than familiar face recognition, and this has been attributed to qualitative differences in the processing of familiar and unfamiliar faces. Familiar faces are assumed to be represented by view-independent codes, whereas unfamiliar face recognition depends mainly on view-dependent low-level pictorial representations. We employed an electrophysiological marker of visual face recognition processes in order to track the emergence of view-independence during the learning of previously unfamiliar faces. Two face images showing either the same or two different individuals in the same or two different views were presented in rapid succession, and participants had to perform an identity-matching task. On trials where both faces showed the same view, repeating the face of the same individual triggered an N250r component at occipito-temporal electrodes, reflecting the rapid activation of visual face memory. A reliable N250r component was also observed on view-change trials. Crucially, this view-independence emerged as a result of face learning. In the first half of the experiment, N250r components were present only on view-repetition trials but were absent on viewchange trials, demonstrating that matching unfamiliar faces was initially based on strictly viewdependent codes. In the second half, the N250r was triggered not only on view-repetition trials but also on view-change trials, indicating that face recognition had now become more view-independent. This transition may be due to the acquisition of abstract structural codes of individual faces during face learning, but could also reflect the formation of associative links between sets of view-specific pictorial representations of individual faces.

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1. Introduction

It is generally believed that face recognition is an easy and effortless task that we perform expertly on countless occasions each day. While this may indeed be the case for recognizing familiar faces (family, friends, or celebrities), our ability to identify unfamiliar faces is often surprisingly poor, and this can have serious consequences in real-life contexts such as eyewitness testimonies or passport checks (e.g., Burton & Jenkins, 2011). The difficulty of recognizing unfamiliar faces has been demonstrated in a number of different experimental tasks. In face-matching studies (e.g., Bruce et al., 1999; Bruce, Henderson, Newman, & Burton, 2001), participants have to decide whether a target face is present among a set of simultaneously shown photographs of other faces, similar to the situation faced by witnesses in a police line-up. This task is easy when the target face is familiar, or when the target face image is physically identical to one of the other photographs. But it is much more difficult when an unfamiliar individual has to

be identified and different images of this individual are being shown. Perhaps even more surprisingly, observers are also far from perfect when deciding whether two simultaneously presented face photographs show the same or two different unfamiliar individuals, even when these photographs are taken on the same day (Burton, White, & McNeill, 2010). The same task is trivially easy with two images of familiar individuals (Burton & Jenkins, 2011).

The fact that our ability to recognize unfamiliar faces is much poorer than familiar face recognition suggests that there are systematic qualitative differences in the perceptual encoding or memory storage of familiar and unfamiliar faces. Results from repetition priming experiments point to an important role of visual face memory: Repeated presentations of faces of the same individual facilitate recognition of familiar but not unfamiliar faces (Ellis, Young, Flude, & Hay, 1987; Ellis, Young, & Flude, 1990), suggesting that representations of recently encountered familiar faces in visual memory are more robust than memory traces of unfamiliar faces (but see Goshen-Gottstein & Ganel, 2000, and Martin & Greer, 2011, for evidence that unfamiliar faces can produce small repetition priming effects). However, the critical difference between familiar and unfamiliar face processing may







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already emerge at an earlier stage in face processing where individual faces are perceptually encoded. According to Hancock, Bruce, and Burton (2000), the encoding of unfamiliar faces is based primarily on low-level image-dependent pictorial cues, whereas familiar faces are processed and encoded in a more abstract and flexible structural fashion. Pictorial codes contain image-specific visual information about a face, whereas structural codes contain those view-invariant visual cues that define facial identity (see also Bruce & Young, 1986, on the roles of pictorial and structural codes in face processing). As a consequence of this difference, the recognition of familiar faces remains largely intact when they are encountered in different views during first exposure and subsequent test, whereas unfamiliar face recognition is strongly disrupted by such view changes (e.g., Bruce, 1982). There is also corresponding neuropsychological evidence for double dissociations between familiar and unfamiliar face recognition from patients with acquired prosopagnosia. Malone, Morris, Kay, and Levin (1982) described one patient whose ability to recognize familiar faces improved while problems in matching individual unfamiliar faces remained, and another patient with persistent familiar face recognition impairments who recovered his ability to match unfamiliar faces, suggesting that neural mechanisms for familiar and unfamiliar face recognition are anatomically and functionally distinct.

In spite of these behavioural differences between familiar and unfamiliar face recognition, neurophysiological and neuroimaging studies have so far provided little systematic insight into their neural basis. For example, it is not yet clear whether and to what degree activity in the human fusiform face area (FFA; Kanwisher, McDermott, & Chun, 1997) is modulated by the familiarity of a face (see Natu & O'Toole, 2011, for a recent review). Neuroimaging evidence suggests that both familiar and unfamiliar face representations are view-dependent and thus image-specific in the FFA, whereas view-invariance is only found outside the FFA (Pourtois, Schwartz, Mohamed, Lazeyras, & Vuilleumier, 2005a; Pourtois, Schwartz, Seghier, Lazeyras, & Vuilleumier, 2005b). However, Ewbank and Andrews (2008) provided evidence that the FFA may also be sensitive to the difference between pictorial and structural representations of unfamiliar and familiar faces, respectively: Activity in the FFA was suppressed when faces of the same individual were repeated, and this repetition suppression effect was view-dependent for unfamiliar faces but view-independent for familiar faces. Event-related brain potential (ERP) studies of face processing have primarily focused on the facesensitive N170 component, which is triggered at lateral posterior electrodes 150-190 ms after stimulus onset. Because N170 amplitudes are typically unaffected by face familiarity (Eimer, 2000a; Bentin & Deouell, 2000) or facial identity repetition (Schweinberger, Pickering, Burton, and Kaufmann, 2002a), this component is assumed to reflect early stages in the structural encoding of faces that precede face recognition (Eimer, 2000b; Rossion et al., 2000).

A more promising electrophysiological marker of face recognition has been observed slightly later than the N170 component at inferior occipito-temporal electrodes. Between 200-300 ms after stimulus onset, repetitions of familiar faces trigger an enhanced negativity that is typically maximal between 230 ms and 280 ms, is often larger over the right hemisphere, and is accompanied by an anterior positivity (e.g., Schweinberger, Pfütze, & Sommer, 1995; Schweinberger, Pickering, Burton, and Kaufmann, 2002a; Schweinberger, Huddy, & Burton, 2004; Begleiter, Porjesz, & Wang, 1995). This N250r component is assumed to reflect a successful match between a perceptual face representation and a memory trace of this face (Schweinberger & Burton, 2003), and reflects both short-term perceptual as well as long-term memory representations of facial identity (Dörr, Herzmann, & Sommer, 2011). Similar N250 components have not just been found for immediate face repetitions, but also in response to participants' own faces (Tanaka, Curran, Porterfield, & Collins, 2006) and to previously known famous faces (Gosling & Eimer, 2011), and have been interpreted as reflecting the activation of stored long-term face memories of familiar individuals. Importantly, the N250r to familiar faces shows some degree of image-independence (e.g., Cooper, Harvey, Lavidor, & Schweinberger, 2007; Bindemann, Burton, Leuthold, & Schweinberger, 2008), in line with the hypothesis that familiar face recognition is primarily based on abstract structural codes of individual faces. The observation that N250r amplitudes are larger for same-image repetitions of a famous face than for repetitions of different images of this face (Schweinberger, Pickering, Jentzsch, Burton, & Kaufmann, 2002b) suggests that the underlying face recognition processes may not be entirely view-independent.

Reliable N250r components have also been found for unfamiliar face repetitions (e.g., Herzmann, Schweinberger, Sommer, & Jentzsch, 2004; Itier & Taylor, 2004), but they were considerably smaller than the N250r to familiar faces, and were abolished when other face images were presented between the first and second appearance of a specific unfamiliar face (Pfütze, Sommer, & Schweinberger, 2002). These observations suggest that facespecific memory traces are activated more strongly by repetitions of familiar faces that have pre-existing long-term representations than by previously unknown repeated faces. Because the N250r reflects early visual stages of face recognition processes, and has been linked to the activation of view-independent face recognition units (FRUs) in Bruce and Young's (1986) model (e.g., Kaufmann, Schweinberger, & Burton, 2009), this component is ideally suited to investigate qualitative differences in familiar and unfamiliar face recognition. If unfamiliar face recognition is based on viewdependent low-level pictorial cues, the N250r should be strongly attenuated or even completely abolished when repeated presentations show the same unfamiliar face in different views.

But what happens when novel faces gradually become more familiar through repeated exposure? Once new visual memory traces for individual faces are established in the course of face learning, their activation by another presentation of the same face should elicit an N250 component. This is indeed the case: Tanaka et al. (2006) asked participants to recognize a previously studied target face that was presented among other non-target faces as well as the participant's own face. Initially, only the own face triggered an N250 component, reflecting the activation of a stored long-term face representation. In the second half of the experiment (after the target face had been encountered about 35 times), an N250 component also emerged in response to this target face. This result demonstrated that familiarity with this face acquired in the course of the experiment had resulted in the formation of a new face representation in visual memory. However, the viewdependence of this representation could not be assessed in Tanaka et al. (2006) experiment, because all faces were presented in a front view. Initial evidence for view-independent learning of unfamiliar faces comes from a study by Kaufmann et al. (2009). These authors observed an N250 component to faces of unfamiliar individuals that were previously encountered in a video clip, and found that this component increased across repeated presentations of different exemplars of the same face during the test phase (see also Schulz, Kaufmann, Walther, & Schweinberger, 2012, who found an N250 component to different images of previously learned unfamiliar faces).

If familiar and unfamiliar face recognition are differentially affected by changes in view between initial exposure and subsequent test (Bruce, 1982), acquiring familiarity with novel faces through repeated exposure should reduce this type of viewdependence: Early during learning, when faces are still essentially unfamiliar, successful face recognition might depend on an exact physical match between face images of the same individual. In the course of learning, face recognition may gradually become more view-independent. One possibility to account for such a transition from view-dependence to view-independence in unfamiliar face recognition is to assume that abstract image-independent structural descriptions of facial identity become available in the course of face learning, in line with the proposed dichotomy of pictorial versus structural representations for unfamiliar versus familiar faces (e.g., Burton & Jenkins, 2011). Another possibility is that multiple low-level visual images of the same face are stored and become associated during learning, and that view-independence emerges as a result of a match between the currently seen face and one of these stored images (Longmore, Liu, & Young, 2008). For example, the observation that impairments in recognizing photographs of unfamiliar faces that are presented from a different viewpoint or under different illumination conditions remain present even when these faces were encountered repeatedly during training (Longmore et al., 2008) suggests that face learning does not necessarily change the reliance of face recognition on multiple low-level pictorial codes. The question whether the recognition of faces is based on image-independent or view-based representations is reminiscent of analogous theoretical debates in the object recognition literature. Some authors (e.g., Biederman & Bar, 1999) have claimed that object recognition is based on largely viewindependent structural descriptions of volumetric object features, while others (e.g., Tarr, 1995) have argued for multiple imagebased representations of different views of the same object (see also Hayward, 2012, for a recent evaluation of this debate).

The aim of the current experiment was to use the N250r component as an electrophysiological marker of face recognition to investigate whether and when the recognition of unfamiliar faces becomes view-independent in the course of face learning. Image pairs of computer-generated unfamiliar faces were presented in rapid succession at fixation. On half of all trials, the two images showed the same person, while two different individuals were shown on the other half. Participants performed an identitymatching task, and reported on each trial whether the same or two different individuals were presented. Face images could be presented either in a front view or in a side view, and the critical manipulation was whether the two images in each pair were shown in the same view (front-front or side-side) or in two different views (front-side or side-front; see Fig. 1). To avoid identical retinal stimulation by successive images on trials where both faces showed the same identity and the same view, the second face image in each pair was always larger than the first. Both images were presented for 200 ms, and were separated by a 200 ms interstimulus interval (ISI). The fact that this interval was shorter than in most previous N250r experiments allowed us to track the rapid encoding and activation of visual memory traces for individual unfamiliar faces independently of more timeconsuming visual transformations (i.e., mental rotation) in working memory, or semantic recoding of the first image. An ISI of 200 ms is long enough to ensure that face matching processes are based on comparisons between on-line visual percepts and working memory representations, and not on a direct match between two simultaneously available percepts (Brockmole, Wang, & Irwin, 2002; Dalvit & Eimer, 2011).

If memory traces of individual unfamiliar faces are formed rapidly and are then immediately accessible to face recognition, a reliable N250r component should be observed on trials where the same face is repeated in the same view as compared to trials where two different faces are shown in the same view, reflecting a successful match between a visual representation of the second face and a memory trace of the first face. The critical question was whether this component would also be triggered on view-change trials. If unfamiliar face recognition, as reflected by the N250r component, is strictly view-dependent in the sense that it depends on a physical match between two successive images of the same individual face, the N250r should be absent on view-change trials. However, if face learning results in the gradual emergence of viewindependent face recognition, acquiring familiarity with individual faces through repeated exposure may be mirrored by a systematic change in the view-dependence of the N250r component in the course of the experiment: Initially, this component should be found solely for view-repetition trials, but not for view-change trials. During a later phase of the experiment, an N250r could also emerge for view-change trials, demonstrating a transition from strict view-dependence to view-independence of unfamiliar face recognition as a result of learning.

2. Method

2.1. Participants

Twelve paid volunteers (six females, mean age 24 years) were tested. Data from two further participants were excluded due to an insufficient number of artifactfree EEG trials (less than 60% of all trials left after artifact rejection). All participants were right-handed, had normal or corrected-to-normal vision, and gave written informed consent prior to testing.

2.2. Stimuli and procedure

The stimulus set consisted of 12 unfamiliar faces (six female and six male faces) created using FaceGen Modeller 3.4 (Singular Inversions Inc., Toronto). Faces were full-colour images, and were shown either in a front view or in a left-facing side view at an angle of approximately 35° (see Fig. 1 for examples). All images were cropped into an oval shape using Adobe Photoshop 6.0 (Adobe Systems Inc.). In order to avoid identical stimulation of the same retinal area on trials where two physically identical faces were presented in rapid succession, the visual angle subtended by the face presented in the first position ($5.2^{\circ} \times 3.4^{\circ}$) was always smaller than the angle subtended by the second face ($5.7^{\circ} \times 4.6^{\circ}$). The combination of 12 different identities, two different views, and two different sizes resulted in a total of 48 face images. All face stimuli were presented centrally on a CRT monitor against a dark grey background (4.0 cd/m²), at a viewing distance of 100 cm, using L-prime software (Psychology Software Tools, Pittsburgh, PA). Their average luminance was 20.1 cd/m².

On each trial, two faces were presented in rapid succession for 200 ms each, separated by a 200 ms interstimulus interval (see Fig. 1). The intertrial interval was 1500 ms. Each block contained 80 trials. Each face pair was equally likely to show the same or two different individuals, and the same or two different face views. These two factors were varied orthogonally, with 20 trials per block for each combination of identity (same identity versus different identity) and view (view repetition versus view change). On different identity trials, a face of one of the eleven individuals that were not shown in the first position was chosen randomly and with equal probability as the second face image to be shown on that trial. The view of the second face of each pair (front or side view) remained constant within each block, and was changed across successive blocks. Six participants started with a block where the second face was always presented in a front view, and the other six started with a side-view block.

Eight experimental blocks were run, with self-paced breaks between blocks, and a longer break after block 4. Participants performed an identity-matching task. They were instructed to respond with a left-hand button press on trials where a face pair showed the same individual (regardless of whether their view was the same or different), and with a right-hand button press when two different individuals were shown. The experiment lasted about 25 min. It was preceded by two training blocks of 40 trials (10 trials for each combination of identity and view). In one training block, the second face was presented in a front view. In the other, it was presented in a side view. All participants exceeded a criterion level of 80% accuracy in both training blocks. No feedback about response accuracy was provided during these blocks.

2.3. EEG recording and data analysis

EEG was DC-recorded with a BrainAmps DC amplifier (upper cut-off frequency 40 Hz, 500 Hz sampling rating) and Ag–AgCI electrodes mounted on an elastic cap from 23 scalp sites Fpz, F7, F3, Fz, F4, F8, FC5, FC6, T7, C3, Cz, C4, T8, CP5, CP6, P7, P3, Pz, P4, P8, PO7, PO8, and Oz, according to the extended international 10–20 system. Horizontal electrooculogram (HEOG) was recorded bipolarly from the outer canthi of both eyes. An electrode placed on the left earlobe served as reference for online recording, and EEG was re-referenced off-line to the average of the left and right earlobe. Electrode impedances were kept below 5 k Ω . No additional off-line filters



Fig. 1. Top panel: temporal parameters of stimulus presentation on each trial. Bottom panel: examples of different face stimulus sequences. On each trial, the identity of the two faces could either be repeated or changed (same identity versus different identity trials), and their view could either be the same (front–front or side–side; view-repetition trials) or different (front–side or side–front; view-change trials).

were applied. EEG was epoched offline from 50 ms before to 400 ms after the onset of the second face of each pair. For each EEG epoch, amplitude values were computed relative to a baseline with a duration of 100 ms (ranging from 50 ms before to 50 ms after the onset of the second face stimulus). EEG epochs with activity exceeding \pm 30 µV in the HEOG channel (reflecting horizontal eye movements) or \pm 60 µV at Fpz (indicating eye blinks or vertical eye movements) were excluded from analysis, as were epochs with voltages exceeding \pm 80 µV at any other electrode. On average, 18% of all trials had to be excluded. For all trial conditions, a minimum of 60 trials was included in each individual average waveform. Following artifact rejection, EEG waveforms were averaged separately for each combination of the factors identity (same versus different identity) and view (view repetition versus view change).

Mean amplitude values were computed at posterior electrodes P7/8 for the N170 time interval (160–190 ms after the onset of the second face) and for the N250r time interval (210–260 ms after the onset of the second face). Repeated-measures analyses of variance (ANOVAs) were performed for the factors identity, view, and hemisphere (left versus right: P7 versus P8). To assess the impact of face learning, N250r components were also analyzed separately for the first half (blocks 1–4) and second half (blocks 5–8) of the experiment. These analyses included the additional factor half (first half versus second half). Separate N250r analyses were also conducted for view change trials in blocks 1 and 2, 3 and 4, 5 and 6, and 7 and 8.

3. Results

3.1. Behaviour

Participants correctly matched facial identities on 92% of all trials. Accuracy was higher on view-repetition as compared to view-change trials (95% versus 90%; F(1,11)=20.6; p < .01), and did not differ between the first half (blocks 1–4) and the second half (blocks 5–8) of the experiment (F < 1). False Alarms (i.e., same-identity judgments on trials where faces of two different individuals were shown) occurred on 5% of all trials. They tended to be more frequent on view-change trials than on view-repetition trials (7.6% versus 2.8%; t(11)=2.1; p=.06). Participants missed same-

identity face pairs (i.e., incorrectly classified them as showing two different individuals) on 10% of these trials. These errors were more frequent on view-change trials than on view-repetition trials (12.5% versus 8.3%; t(11)=2.5; p < .05).

Mean correct RT was 526 ms. Responses were faster on trials where both facial identity and face view were repeated (462 ms) than on trials with a view change, an identity change, or a change of both attributes (531 ms, 552 ms, and 563 ms, respectively). This was reflected by main effects of identity (F(1,11) = 24.3; p < .001), view (F(1,11) = 58.5; p < .001), and an interaction between both factors (F(1,11) = 14.3; p < .01). RTs were faster in the second half of the experiment than in the first half (512 ms versus 543 ms; F(1,11) = 5.4; p < .05). An additional analysis of response latencies for successive pairs of blocks revealed that RTs were faster in blocks 3 and 4 (531 ms) relative to blocks 1 and 2 (554 ms), and faster in blocks 5 and 6 (508 ms) relative to blocks 3 and 4 (both p < .05). RTs in blocks 5 and 6 and blocks 7 and 8 (515 ms) did not differ reliably. A three-way interaction between identity, view, and half approached significance for RTs (F(1,11) = 4.2; p < .07): On view-change trials, same-identity responses were significantly faster than different-identity responses in the second half of the experiment (513 ms versus 553 ms; F(1,11) = 2.3; p < .05), but not in the first half (550 ms versus 574 ms; F(1,11) = 1.2; p = .24).

3.2. ERP markers of unfamiliar face recognition: All blocks

Fig. 2 (top panel) shows ERPs triggered on same identity and different identity trials at lateral occipital electrodes P7/8 in the 400 ms interval after the onset of the second face, separately for view-repetition and view-change trials, averaged across all eight experimental blocks. The N170 component was not differentially modulated on same identity versus different identity trials, and



Fig. 2. Top panel: Grand-averaged ERPs measured at lateral posterior electrodes P7 and P8 in the 400 ms interval after the onset of the second stimulus in a face pair, for same identity trials (solid lines) and different identity trials (dashed lines), and averaged across all eight experimental blocks. ERPs are shown separately for view-repetition and view-change trials. Bottom panel: Topographic maps constructed by spherical spline interpolation (Perrin, Pernier, Bertrand, & Echallier, 1989), obtained by subtracting ERP mean amplitudes in the N250r time window (210–260 ms post-stimulus) on different identity trials from mean amplitudes on same identity trials, shown separately for view-repetition and view-change trials. Enhanced negative amplitudes in identity repetitions are shown in blue, enhanced positivities in red. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

+1μV

-1 µV

this was confirmed by the absence of a significant main effect of identity on N170 mean amplitudes (F(1,11)=3.2; p > .10) and peak latencies (F < 1) at P7/8 in the 160–190 ms post-stimulus time window. Clear N250r components were elicited on same identity trials, and this was the case not just when the two faces showed the same view, but also on view-change trials. Scalp topographies of ERP amplitude differences between same and different identity trials obtained in the N250r time window (210–260 ms after the

onset of the second face) are shown in Fig. 2 (bottom panel), separately for view-repetition and view-change trials. These maps show bilateral negativities over posterior electrodes (N250r components) that were accompanied by an anterior positivity in the same latency range.

A highly significant main effect of identity was present in the N250r time window (210–260 ms; F(1,11)=12.1; p < .01), reflecting the presence of N250r components. An identity × hemisphere



Fig. 3. Grand-averaged ERPs measured on view-repetition and view-change trials at lateral posterior electrodes P7 and P8 in the 400 ms interval after the onset of the second stimulus in a face pair, for same identity trials (solid lines) and different identity trials (dashed lines). ERPs are shown separately for the first half (blocks 1–4) and the second half (blocks 5–8) of the experiment.

interaction (F(1,11)=7.0; p < .03) was due to the fact that the N250r tended to be larger over the right hemisphere. However, follow-up analyses confirmed the presence of a reliable N250r both at right-hemisphere electrode P8 (F(1,11)=19.5; p < .01) and left-hemisphere electrode P7 (F(1,11)=6.1; p < .04). Even though the N250r was numerically larger on view-repetition trials as compared to view-change trials (see Fig. 2), the interaction between identity

and view only approached significance (F(1,11)=3.9; p < .08). To confirm the presence of the N250r not just for trials where both faces showed the same view, but also for trials where their view changed, separate analyses were conducted for both types of trials. These analyses demonstrated that reliable N250r components were elicited on view-repetition trials (F(1,11)=10.3; p < .01) as well as on view-change trials (F(1,11)=8.7; p < .02).

3.3. Impact of face learning on the view-dependence of face recognition

Fig. 3 shows ERPs triggered at P7 and P8 on same identity and different identity trials, separately for view-repetition trials (top panels) and view-change trials (bottom panels). To demonstrate the effects of face learning on the N250r component, ERPs measured in blocks 1–4 (first half of the experiment) and in blocks 5–8 (second half) are shown separately. When both faces in each pair showed the same view, N250r components were already present in the first half of the experiment, and these were very similar to the N250r observed in the second half (Fig. 3, top panels). A very different pattern was found for view-change trials. Here, N250r components were absent during the first half of the experiment, and only emerged during the last four blocks (Fig. 3, bottom panels).

These observations were confirmed by statistical analyses of ERP mean amplitudes measured in the N250r time window at P7 and P8. A main effect of identity (F(1,11)=13.2; p < .005) was accompanied by an interaction between identity and half F(1,11) =6.2; p < .04), and by a three-way interaction (identity \times view \times half: *F*(1,11)=6.6; *p* < .03). This was further assessed in separate analyses for view-repetition and view-change trials. For view-repetition trials, there was a main effect of identity (F (1,11) = 10.5; p < .01), but no interaction between identity and half (F < 1), confirming that the N250r on these trials was essentially unchanged between the first and second half of the experiment. Reliable N250r components were indeed present not only in blocks 5–8 (F(1,11) = 11.4; p < .01), but already in blocks 1–4 (F(1,11) = 8.2; p < .02). A very different pattern was observed for view-change trials. Here, a main effect of identity (F(1,11)=9.5;p < .02) was accompanied by a significant interaction between identity and half (F(1,11) = 7.6; p < .02). Follow-up analyses demonstrated that the N250r was absent on view-change trials in the first half of the experiment (F < 1), but emerged strongly during the second half (F(1,11) = 14.0; p < .005). The same pattern was also evident when analyses were conducted separately for each experimental half. An interaction between identity and view for the first four blocks (F(1,11) = 9.6; p < .02), reflected the presence of the N250r on view-repetition trials, and its absence on view-change trials. In blocks 5-8, no such interaction was obtained (F < 1), demonstrating that the N250r was now elicited in a viewindependent fashion both on view-repetition and on view-change trials.

As can be seen in Fig. 3 (bottom panels), the N250r component observed on view-change trials in the second half of the experiment was more sustained than the N250r on view-repetition trials in either half. This difference was assessed in analyses of ERP mean amplitudes measured at P7/8 in a 260–310 ms post-stimulus time window. For view-repetition trials, there was no main effect of identity and no identity × half interaction (both F < 1), demonstrating that the N250r had already disappeared during this time window. In contrast, there was a significant identity × half interaction for view-change trials (F(1,11)=5.7; p < .05). Follow-up analyses confirmed that the N250r was reliably present during this 260–310 ms interval in blocks 5–8 (F(1,11)=6.6; p < .05), but was absent during the first experimental half (F < 1).

To track the time course of face learning on the N250r component on view-change trials in more detail, Fig. 4 (top panel) shows N250r amplitudes at right-hemisphere electrode P8 on these trials (obtained by subtracting ERPs on same identity trials from ERPs on different identity trials in the N250r time window), separately for blocks 1/2, 3/4, 5/6, and 7/8. No N250r is present in either blocks 1 and 2 or in blocks 3 and 4 (both t(11) < 1). In contrast, reliable N250r components were elicited in blocks 5 and 6 (t(11)=5.2; p < .001) as well as in blocks 7 and 8 (t(11)=3.2;



Fig. 4. Top panel: N250r mean amplitudes obtained at right-hemisphere electrode P8 on view-change trials, obtained by subtracting ERPs on same identity trials from ERPs on different identity trials, separately for experimental blocks 1 and 2, blocks 3 and 4, blocks 5 and 6, and blocks 7 and 8. Bottom panel: Grand-averaged ERPs measured on view-change trials at P7/8 in block 5 of the experiment for same identity trials (solid lines) and different identity trials (dashed lines).

Same Identity Different Identity

p < .01). These results suggest that a view-independent N250r component first emerged in experimental block 5, and this was further confirmed by computing averaged ERP waveforms for view-change trials separately for this block only. Fig. 4 (bottom panel) shows ERPs for same and different identity trials measured in block 5. In spite of the limited signal-to-noise ratio of these waveforms, an N250r component to identity repetitions is clearly visible over both hemispheres. This was confirmed by a statistical analysis conducted for view-change trials in block 5 only, which revealed a reliable main effect of identity in the N250r time window (F(1,11)=6.5; p < .03).

4. Discussion

The recognition of familiar face images is less affected by view changes and other pictorial differences than the recognition of unfamiliar faces (Bruce, 1982). The aim of the present experiment was to use the N250r component as an electrophysiological marker of face recognition to study whether and how increased familiarity with individual unfamiliar faces through repeated exposure affects the view-dependence of unfamiliar face recognition. On each trial, two face images of the same or two different individuals were presented in rapid succession, and these faces were shown in the same or two different views.

N170 amplitudes were not differentially modulated on same identity trials as compared to different identity trials, in line with previous findings that this component is not sensitive to facial identity (Eimer, 2000a; Bentin & Deouell, 2000; but see also Caharel, d'Arripe, Ramon, Jacques, & Rossion, 2009). In contrast, the subsequent N250r component was reliably triggered by unfamiliar face repetitions. This component showed the typical scalp distribution, with a posterior negativity accompanied by an anterior positivity in the same time range (see Fig. 2). These findings confirm previous reports that N250r components can be observed for repetitions of unfamiliar faces (Pfütze et al., 2002: Itier & Taylor, 2004). The fact that an N250r was triggered when two faces of the same individual were presented within 400 ms of each other demonstrates that information about the identity of an unfamiliar face is extracted very rapidly, and that the resulting visual memory traces are immediately available to be matched with on-line visual representations of individual faces. In an earlier study (Trenner, Schweinberger, Jentzsch, & Sommer, 2004), N250r components to repeated famous faces were found with even shorter ISIs (17 ms). However, this effect is likely to reflect a match between two simultaneous perceptual face representations rather than visual face memory (see Brockmole et al., 2002; Dalvit & Eimer, 2011, for the transition from percept-percept to memorypercept interactions as a function of ISI). In contrast, the ISI of 200 ms that was used in the present study was sufficiently long to prevent direct perceptual interactions between the two face images, and to ensure that N250r components reflect the presence of rapidly generated visual memory representations for individual faces.

Our central aim was to find out whether unfamiliar face recognition processes are strictly view-dependent or are also triggered when two successive face images show the same individual in two different views, and whether this changes in the course of face learning. To answer these questions, we measured N250r components on trials where two successively presented faces of the same individual were shown in different views. Analyses of ERP data across all experimental blocks suggested that the N250r component was largely view-independent: An N250r was reliably present on view-change trials, and its scalp distribution was very similar to the pattern observed for viewrepetition trials (see Fig. 2). Although N250r amplitudes were numerically reduced on view-change relative to view-repetition trials, the interaction between identity and view failed to reach statistical significance, suggesting that N250r components of similar size were triggered on these two types of trials. These observations are analogous to previous demonstrations that the N250r in response to repeated famous faces is image-independent (Bindemann et al., 2008), and suggest that even unfamiliar face recognition is not strictly view-dependent. N250r components to repetitions of unfamiliar faces which were presented in two different views have been observed in one previous experiment (Caharel et al., 2009). However, even though the blank interval separating the two faces was similar to the interval used in the present study, the first face remained on the screen for much longer (about 3 s) in Caharel et al. (2009) experiment, which suggests that face identity matching processes may have been supported by preparatory transformations of visual working memory representations, such as mental rotation.

When N250r components were analyzed separately for the first and second experimental half, it became obvious that face learning was the critical factor behind the apparent view-independence of unfamiliar face recognition. In blocks 1–4, an N250r was triggered by repetitions of identical faces on view-repetition trials, while this component was entirely absent on view-change trials (Figs. 3 and 4). This is exactly the pattern that would be expected if the underlying face matching processes were based solely on strictly view-dependent

pictorial codes. In marked contrast, N250r components were elicited in the second half of the experiment (blocks 5-8) on view-repetition trials as well as on view-change trials. This transition from viewdependence to view-independence of facial identity matching in the course of the experiment is remarkable, because it suggests that acquired familiarity with novel faces through repeated exposure triggers a qualitative change in the mechanisms of face recognition. During the first few encounters with individual unfamiliar faces, only a strictly view-dependent pictorial representation was available to the face matching operations that determine facial identity. Once these faces had become more familiar, face recognition operated in a more flexible fashion, and generalized across the two different views of an individual face. These observations are in line with the results of a previous study with famous faces (Schweinberger et al., 2002b), where larger N250r components were found for repetitions of the same image than for repetitions of different images of the same individual, suggesting that view-dependent and view-independent representations both contribute to the N250r. Although reliable N250r components were elicited both on view-repetition trials (throughout the experiment) and on view-change trials (in blocks 5–8 only), there was one notable difference between these two types of trials (see Fig. 3): The N250r was more sustained on view-change trials, and remained reliably present during the 260-310 ms post-stimulus interval, where it had already disappeared on view-repetition trials. The sustained presence of the N250r on view-change trials beyond 300 ms may reflect the increased difficulty of matching the identity of two face images with different views as compared to matching same-view images.

How many encounters with an individual unfamiliar face are required before face recognition becomes view-independent? This may depend on the distinctiveness of individual unfamiliar faces in a specific stimulus set. The computer-generated faces employed in the present study were generally quite similar to each other (see Fig. 1), and view-independence only emerged in blocks 5-8 after each individual face had been encountered approximately 25 times in each of the two views during the first part of the experiment. It is possible that view-independence might develop more rapidly when naturalistic face photographs are used, or when face learning is based on dynamic video clips instead of static images (e.g., Kaufmann et al., 2009). To determine the point in time when a view-independent N250r component first emerged more precisely, we analyzed ERPs obtained on view-change trials separately for pairs of experimental blocks (Fig. 4, top panel). While this component was entirely absent in blocks 1 and 2 as well as during blocks 3 and 4, it emerged in experimental block 5, where it was reliably present over both hemispheres (Fig. 4, bottom panel). In other words, view-independent face recognition emerged rapidly at the beginning of the second half of the experiment. The fact that blocks 1-4 and 5-8 were separated by a longer break might point to an important role of face memory consolidation processes. This will need to be investigated in future studies.

The absence of the N250r component on view-change trials in the first four blocks indicates that the underlying identitysensitive face matching processes were not triggered during this phase of the experiment when two successively presented faces of the same individual were shown in different views. This raises the question of how participants were able to perform the identitymatching task at all on these trials. It is likely that identity judgments were based primarily on generic low-level visual cues provided by individual face stimuli, such as their overall shape or distinctive surface features (e.g., colour and pigmentation patterns). Because the front and side views of the same individual shared some of these low-level visual properties, this featurebased matching strategy was readily available. The fact that accuracy was already high in the first experimental half indicates that the current identity-matching task was relatively easy, and certainly less challenging than previous behavioural tests of unfamiliar face recognition, such as tasks where a target face has to be identified among a set of candidate face photographs (Bruce et al., 1999, 2001). This is the likely reason why only modest behavioural evidence for face learning was obtained in this experiment. The observation that RTs became incrementally faster up to block 5 before reaching a stable level in the second half of the experiment and the fact that same-identity judgments on view-change trials were reliably faster than different-identity judgments only in this second half both suggest that face recognition was facilitated by view-independent codes once faces had become more familiar. If face matching on view-change trials in the first half of the experiment was based on local visual features. the absence of an N250r on these trials indicates that this component is not simply generated by any successful visual match between two successive face images, regardless of its nature, but only when this match is based on more global-configural information about facial identity.

The current findings demonstrate that unfamiliar face recognition, as reflected by the N250r component, becomes view-independent once novel faces become more familiar through repeated exposure. What is the basis for this view-independence that emerges during face learning? One possibility is that the repeated presentation of individual faces results in the generation of structural codes for facial identity. According to Bruce and Young (1986), structural codes are abstract generalized descriptions of those invariant aspects of an individual face that are required to distinguish it from other faces. The availability of image-independent structural codes is assumed to be responsible for the efficiency of familiar face recognition across different image transformations, including changes in view (Hancock et al., 2000). The emergence of the N250r component on viewchange trials in the second half of this experiment might thus reflect the availability of abstract structural descriptions of facial identity. According to an alternative account (Longmore et al., 2008), viewindependent face recognition might be mediated by a set of stored pictorial representations of the same face for different views and other image transformations. In this scenario, the presence of a viewindependent N250r component in the second half of this experiment might reflect associative links between two view-specific and previously independent pictorial representations of the same face (front view and side view) that become established during face learning. Once such associations are formed, visual face memory can be activated by either view, and N250r components will therefore become view-independent, as was observed in blocks 5-8 of the current study. Both accounts are compatible with the results of the present study, where view-independent face recognition mechanisms were defined as mechanisms that are triggered both when faces are presented in the same or in two different views. To obtain evidence that unfamiliar face recognition is genuinely view-invariant, it would be informative to measure the N250r component for novel views of individual faces that were previously only encountered in other views. If unfamiliar face learning gives rise to abstract imageindependent structural codes of facial identity, N250r components should show full view-invariance, and should immediately generalize to these novel views. If face learning is image-based and operates on the basis of associations between stored pictorial representations, the N250r will initially be absent for novel views of previously seen faces, and should only emerge once these views have been encountered repeatedly.

In summary, the present study has provided new electrophysiological evidence that face learning has a strong impact on the processes that underlie unfamiliar face recognition. The recognition of novel faces initially operates in a strictly view-dependent fashion, but becomes more view-independent once the same individual faces have been encountered repeatedly. This transition could either reflect the build-up of associative links between sets of pictorial representations of the same face, or the emergence of genuinely image-independent structural codes of facial identity.

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References

- Begleiter, H., Porjesz, B., & Wang, W. Y. (1995). Event-related brain potentials differentiate priming and recognition to familiar and unfamiliar faces. *Electroencephalography and Clinical Neurophysiology*, 94, 41–49.
- Bentin, S., & Deouell, L. (2000). Structural encoding and identification in face processing: ERP evidence for separate mechanisms. Cognitive Neuropsychology, 17, 35–54.
- Biederman, I., & Bar, M. (1999). One-shot viewpoint invariance in matching novel objects. Vision Research, 39, 2885–2899.
- Bindemann, M., Burton, A. M., Leuthold, H., & Schweinberger, S. R. (2008). Brain potential correlates of face recognition: geometric distortions and the N250r brain response to stimulus repetitions. *Psychophysiology*, 45, 535–544.
- Brockmole, J. R., Wang, R. F., & Irwin, D. E. (2002). Temporal integration between visual images and visual percepts. *Journal of Experimental Psychology: Human Perception and Performance*, 28, 315–334.
- Bruce, V. (1982). Changing faces: visual and non-visual coding processes in face recognition. British Journal of Psychology, 73, 105–116.
- Bruce, V., Henderson, Z., Greenwood, K., Hancock, P. J. B., Burton, A. M., & Miller, P. (1999). Verification of face identities from images captured on video. *Journal of Experimental Psychology: Applied*, 5, 339–360.
- Bruce, V., Henderson, Z., Newman, C., & Burton, A. M. (2001). Matching identities of familiar and unfamiliar faces caught on CCTV images. *Journal of Experimental Psychology: Applied*, 7, 207–218.
- Bruce, V., & Young, A. (1986). Understanding face recognition. British Journal of Psychology, 77, 305–327.
- Burton, A. M., & Jenkins, R. (2011). Unfamiliar face perception. In: A. J. Calder, G. Rhodes, M. H. Johnson, & J. V. Haxby (Eds.), *The Oxford handbook of face perception* (pp. 287–306). New York: Oxford University Press.
- Burton, A. M., White, D., & McNeill, A. (2010). The Glasgow face matching test. Behavior Research Methods, 42, 286–291.
- Caharel, S., d'Arripe, O., Ramon, M., Jacques, C., & Rossion, B. (2009). Early adaptation to repeated unfamiliar faces across viewpoint changes in the right hemisphere: evidence from the N170 ERP component. *Neuropsychologia*, 45, 639–643.
- Cooper, T. J., Harvey, M., Lavidor, M., & Schweinberger, S. R. (2007). Hemispheric asymmetries and abstractive priming of famous faces: evidence from reaction times and event-related brain potentials. *Neuropsychologia*, 45, 2910–2921.
- Dalvit, S., & Eimer, M. (2011). Mechanisms of percept-percept and image-percept integration in vision: behavioral and electrophysiological evidence. *Journal of Experimental Psychology: Human Perception and Performance*, 37, 1–11.
- Dörr, P., Herzmann, G., & Sommer, W. (2011). Multiple contributions to priming effects for familiar faces: analyses with backward marking and event-related potentials. *British Journal of Psychology*, 102, 765–782.
- Eimer, M. (2000a). Event-related brain potentials distinguish processing stages involved in face perception and recognition. *Clinical Neurophysiology*, 111, 694–705.
- Eimer, M. (2000b). The face-specific N170 component reflects late stages in the structural encoding of faces. *NeuroReport*, *11*, 2319–2324.
- Ellis, A. W., Young, A. W., & Flude, B. M. (1990). Repetition priming and face processing: priming occurs within the system that responds to the identity of a face. *Quarterly Journal of Experimental Psychology*, 42A, 495–512.
- Ellis, A. W., Young, A. W., Flude, B. M., & Hay, D. C. (1987). Repetition priming of face recognition. Quarterly Journal of Experimental Psychology, 39A, 193–210.
- Ewbank, M. P., & Andrews, T. J. (2008). Differential sensitivity for viewpoint between familiar and unfamiliar faces in human visual cortex. *NeuroImage*, 40, 1857–1870.
- Gosling, A., & Eimer, M. (2011). An event-related brain potential study of explicit face recognition. *Neuropsychologia*, 49, 2736–2745.
- Goshen-Gottstein, Y., & Ganel, Y. (2000). Repetition priming for familiar and unfamiliar faces in a sex-judgment task: evidence for a common route for the processing of sex and identity. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 26,* 1198–1214.
- Hancock, P. J. B., Bruce, V., & Burton, A. M. (2000). Recognition of unfamiliar faces. Trends in Cognitive Sciences, 4, 223–233.
- Hayward, W. G. (2012). Whatever happened to object-centered representations? Perception, 41, 1153–1162.
- Herzmann, G., Schweinberger, S. R., Sommer, W., & Jentzsch, I. (2004). What's special about personally familiar faces? A multimodal approach. *Psychophysiology*, 41, 688–701.
- Itier, R. J., & Taylor, M. J. (2004). Effects of repetition learning on upright, inverted and contrast-reversed face processing using ERPs. *NeuroImage*, 21, 1518–1532.

- Kanwisher, N., McDermott, J., & Chun, M. M. (1997). The fusiform face area: A module in human extrastriate cortex specialized for face perception. *Journal of Neuroscience*, 17, 4302–4311.
- Kaufmann, J. M., Schweinberger, S. R., & Burton, A. M. (2009). N250 ERP correlates of the acquisition of face representations across different images. *Journal of Cognitive Neuroscience*, 21, 625–641.
- Longmore, C. A., Liu, C. H., & Young, A. W. (2008). Learning faces from photographs. Journal of Experimental Psychology: Human Perception and Performance, 34, 77–100.
- Malone, D. R., Morris, H. H., Kay, M. C., & Levin, H. S. (1982). Prosopagnosia: a double dissociation between the recognition of familiar and unfamiliar faces. *Journal of Neurology, Neurosurgery and Psychiatry*, 45, 820–822.
- Martin, D., & Greer, J. (2011). Getting to know you: from view-dependent to viewinvariant repetition priming for unfamiliar faces. *Quarterly Journal of Experimental Psychology*, 64, 217–223.
- Natu, V., & O'Toole, A. J. (2011). The neural processing of familiar and unfamiliar faces: a review and synopsis. *British Journal of Psychology*, 102, 726–747.
- Perrin, F., Pernier, J., Bertrand, O., & Echallier, J. F. (1989). Spherical splines for scalp potential and current density mapping. *Electroencephalography and Clinical Neurophysiology*, 72, 184–187.
- Pfütze, E.-M., Sommer, W., & Schweinberger, S. R. (2002). Age-related slowing in face and name recognition: evidence from event-related brain potentials. *Psychology and Aging*, 17, 140–160.
- Pourtois, G., Schwartz, S., Mohamed, L. S., Lazeyras, F., & Vuilleumier, P. (2005a). View-independent coding of face identity in frontal and temporal cortices in modulated by familiarity: an event-related fMRI study. *NeuroImage*, 24, 1212–1224.
- Pourtois, G., Schwartz, S., Seghier, M. L., Lazeyras, F., & Vuilleumier, P. (2005b). Portraits or people? Distinct representations of face identity in the human visual vortex. *Journal of Cognitive Neuroscience*, 17, 1043–1057.
- Rossion, B., Gauthier, I., Tarr, M. J., Despland, P., Bruyer, R., Linotte, S., et al. (2000). he N170 occipito-temporal component is delayed and enhanced to inverted

faces but not to inverted objects: an electrophysiological account of facespecific processes in the human brain. *NeuroReport*, 11, 69–74.

- Schulz, C., Kaufmann, J. M., Walther, L., & Schweinberger, S. R. (2012). Effects of anticaricaturing vs. caricaturing and their neural correlates elucidate a role of shape for face learning. *Neuropsychologia*, 50, 2426–2434.
- Schweinberger, S. R., & Burton, A. M. (2003). Covert recognition and the neural system for face processing. *Cortex*, 39, 9–30.
- Schweinberger, S. R., Huddy, V., & Burton, A. M. (2004). N250r—a face-selective brain response to stimulus repetitions. *NeuroReport*, 15, 1501–1505.
- Schweinberger, S. R., Pfütze, E.-M., & Sommer, W. (1995). Repetition priming and associative priming of face recognition: evidence from event-related potentials. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 21*, 722–736.
- Schweinberger, S. R., Pickering, E. C., Burton, A. M., & Kaufmann, J. M. (2002a). Human brain potential correlates of repetition priming in face and name recognition. *Neuropsychologia*, 40, 2057–2073.
- Schweinberger, S. R., Pickering, E. C., Jentzsch, I., Burton, A. M., & Kaufmann, J. M. (2002b). Event-related brain potential evidence for a response of inferior temporal cortex to familiar face repetitions. *Cognitive Brain Research*, 14, 398–409.
- Tanaka, J. W., Curran, T., Porterfield, A. L., & Collins, D. (2006). Activation of preexisting and acquired face representations: the N250 event-related potential as an index of face familiarity. *Journal of Cognitive Neuroscience*, 18, 1488–1497.
- Tarr, M. J. (1995). Rotating objects to recognize them: a case study of the role of viewpoint dependency in the recognition of three-dimensional objects. *Psychonomic Bulletin & Review*, 2, 55–82.
- Trenner, M. U., Schweinberger, S. R., Jentzsch, I., & Sommer, W. (2004). Face repetition effects in direct and indirect tasks: an event-related brain potentials study. *Cognitive Brain Research*, 21, 388–400.