

Identity-specific neural responses to three categories of face familiarity (own, friend, stranger) using fast periodic visual stimulation

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ABSTRACT

Previous studies have focused on the modulatory effects of face familiarity on different components of an event-related potential (ERP), but there is controversy in the literature regarding the precise component that reflects the process of identity recognition. This may be partly explained by limits to this waveform analysis approach, as waveforms elicited by the presentation of a face are likely to reflect a variety of different cognitive processes that overlap in time. Using fast periodic visual stimulation and EEG (FPVS-EEG), we directly measured the electrophysiological response reflecting identity-specific recognition after isolating it from responses attributable to low-level visual processing and face-selective processes that are not identity-specific. The observed response therefore provides a robust and objective measure of the recognition of a personally familiar face generated bilaterally in the occipito-temporal region. We tested the magnitude of this identity-specific response to three categories of familiarity: the own-face (high familiarity), a friend's face (moderate familiarity), and a stranger's face (no familiarity). We found the largest response to the participant's own-face, followed by an intermediate response to a highly personally familiar face, and the smallest response to an unfamiliar face. An additional response was observed over the posterior cortical midline for familiar faces only, consistent with theories that familiar identity recognition also triggers post-perceptual semantic processing.

1. Introduction

A face can be categorized at multiple levels of abstraction such as gender, race, and age. However, the critical level in everyday face recognition is the identity level where the face is individuated as a specific identity. According to models of face recognition, face recognition first requires a structural representation of the visual input to be matched to identity-specific, image-invariant perceptual representations in long-term memory (originally termed a "face-recognition unit", or FRU), which subsequently leads to the activation of even more abstract representations storing identity information, such as name and biographical information (Bruce and Young, 1986; Burton et al., 1999a; Burton et al., 2011; Haxby et al., 2000). The identity's image-invariant representation is an important mediating mechanism in recognition because faces undergo constant change due to expression, head movement, and development. Past experience with specific faces demonstrate our reliance on identity-specific perceptual representations in face recognition: familiar faces can be recognized over different and even degraded images, while even small image changes can impair

recognition of unfamiliar faces (e.g., Jenkins et al., 2011; Burton et al., 1999b; Hancock et al., 2000; Watier and Collins, 2009; Ramon et al., 2015).

Yet, despite its critical role in face recognition and large behavioural effects, a reliable neural marker corresponding to the activation of identity-specific representations has not been identified. As temporal resolution of EEG is required to study the neural dynamics of face recognition, previous studies have focused on the modulatory effects of familiarity on different event-related potential (ERP) components elicited by familiar and unfamiliar faces. Recently, a late, occipitotemporal component peaking at 400 ms and lasting until 600 ms post-stimulus has been shown to reliably differentiate between faces of varying familiarity (a "sustained familiarity effect" or "SFE", Wiese et al., 2019). However, as speeded recognition tasks have found that familiar faces can be identified with response times as fast as 260 ms (Besson et al., 2017; see also Barragan-Jason et al., 2015; Ramon et al., 2011), the perceptual representations that trigger these behavioural responses are likely to be accessed at a much earlier latency. These later components are therefore not likely to reflect the stage at which a robust face representation is

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activated.

A component that appears more closely related to memory processes is the N250. The amplitude of this ventral temporal negativity peaks with a latency of 230–330 ms and is enhanced to repeated presentations of face images (Begleiter et al., 1995; Schweinberger et al., 1995; Pfützte et al., 2002; Schweinberger et al., 2004; Neumann and Schweinberger, 2008; Neumann et al., 2011) and identities (Schweinberger et al., 2002; Bindemann et al., 2008). Its relation to perceptual learning is also shown in its sensitivity to newly learned faces (Andrews et al., 2017; Kaufmann et al., 2009; Pierce et al., 2011; Tanaka et al., 2006; Joyce and Kutas, 2005) and newly learned bird species (Scott et al., 2008) that elicit greater negativity at the N250. The N250 has commonly been interpreted to reflect the transient activation of individual face representations elicited by repeated exposure and learning (i.e., the activation of an FRU; c.f. Pfützte et al., 2002; Schweinberger and Burton, 2003; Pierce et al., 2011; Schweinberger and Neumann, 2016); however, it has also been said to more specifically reflect the facilitated access to post-perceptual representations (i.e., the activation of a PIN) due to strengthened input connection from the perceptual face representation rather than a change or activation of the perceptual representation itself (Schweinberger et al., 2002).

At the same time, there is now a large body of research suggesting that identity-sensitive perceptual representations are accessed before 250 ms post-stimulus. The N170 component peaks between 140 and 200 ms in occipitotemporal regions and is the earliest component to distinguish between faces and non-face objects (Bentin et al., 1996; Rossion and Jacques, 2011). Although early studies found no difference in the N170 elicited by famous and non-famous faces (Bentin and Deouell, 2000; Eimer, 2000), a large proportion of studies support the view that this component is sensitive to face familiarity. First, compared to unfamiliar faces, famous faces often do not significantly alter the N170 elicited during passive viewing (Andrews et al., 2017; Gosling and Eimer, 2011; Anaki et al., 2007; Henson et al., 2003; Pfützte et al., 2002; Bentin and Deouell, 2000; Eimer, 2000; but see Jemel et al., 2010), but for a personally familiar face, the N170 is often enhanced (Caharel et al., 2002; Caharel et al., 2005; Herzmann et al., 2004; Wild-Wall et al., 2008; Keyes et al., 2010; Caharel et al., 2014; but see Tanaka et al., 2006; Pierce et al., 2011). This is consistent with the view that personally familiar faces have more robust representations (Tong and Nakayama, 1999; Carbon, 2008) and more efficient global processing (Ramon and Van Belle, 2016; Ramon et al., 2015; Ramon, 2015; Ellis et al., 1979; Caharel et al., 2006). Second, identity adaptation paradigms have demonstrated that the amplitude of the N170 is modulated by face identity (Jacques and Rossion, 2006; Caharel et al., 2009; Caharel et al., 2011; Johnston et al., 2016) and that familiarity may further influence these modulatory effects (Caharel et al., 2011). Similarly, it has been found that the N170 is sensitive to identity priming of familiar but not unfamiliar faces (Jemel et al., 2003). Finally, whole brain analysis of EEG associated with fast and accurate familiarity judgments has shown that face familiarity can be reliably decoded as early as 145 ms post stimulus (Barragan-Jason et al., 2015).

Although the effects of familiarity on the N170 are not consistently observed across all stimulus types and paradigms, collectively, the above findings indicate that identity recognition occurs fast enough to exert modulatory effects within 140–200 ms post-stimulus. Consequently, the N250 might not reflect the identity-specific representation and may instead reflect additional learning or consolidation processes. And yet, the N170 presents the problem of not providing a reliable index of identity-processing. The difficulty in pinning down the precise stage of identity-processing may relate to limitations of the ERP approach of comparing average waveforms. First, the waveforms elicited by the presentation of face are likely to reflect a variety of different cognitive processes that may overlap in time. For example, in the 200–300 ms post-stimulus time window, it has been suggested that the N250 enhancement to repeated faces (i.e., N250r) and the N250 enhancement to familiar or newly learned faces may reflect different learning

mechanisms (c.f. Schweinberger and Neumann, 2016; Kaufmann et al., 2009), or that this negativity reflects a combination of both image-dependent and image-independent processes (Schweinberger et al., 2002). Likewise, the N170 may reflect multiple subprocesses in the occipito-temporal area given that it is sensitive to a range of cognitive factors and shows different response properties to different object categories (Rossion et al., 2003). The discrepancy across studies could therefore be partly due to the signal related to the activation of an identity-specific representation being obscured by other visual and face processing signals in the waveform. Second, many image presentations are needed to increase signal-to-noise ratio in the average ERP waveform, but the components of interest are also sensitive to image repetition (N170: Caharel et al., 2009; Caharel et al., 2014; Kaufmann et al., 2009; N250: Kaufmann et al., 2009; SFE: Wiese et al., 2019). For example, Caharel et al. (2014) found that familiar faces showed an enhanced N170 compared to unfamiliar faces during the first block of testing (2 presentations of each image), but an increase in the N170 to unfamiliar faces in subsequent blocks eliminated this familiarity effect. These modulatory effects might not even be entirely attributable to learning or repetition, since Kauffman et al. (2009) also observed increased N170 and N250 amplitudes to unfamiliar faces over the duration of testing even though each identity was shown only once. This suggests that both ERP components are also likely to reflect general processes engaged by simply performing a face recognition task and highlights the limits of isolating specific processes using this approach.

The aim of the current study was to use frequency-tagging (via fast periodic visual stimulation, or FPVS) to isolate the neurophysiological response which reflects recognition of a specific identity, possibly by means of the activation of an identity-specific perceptual representation in long-term memory. Through neural entrainment, frequency-tagging paradigms can be used to measure specific cognitive processes as neural responses to the stimulus of interest are evoked and quantifiable at the exact frequency of presentation (a steady-state visually-evoked potential; Rossion and Boremanse, 2011; Gentile and Rossion, 2014; for review, see Norcia et al., 2015; Rossion, 2014). The distinct advantage is that signals from processes that overlap in the domain time can be isolated from each other using a dual-frequency paradigm (e.g., Regan and Cartwright, 1970; Tononi et al., 1998; Liu-Shuang et al., 2014; Rossion et al., 2015). This is accomplished by periodically presenting the stimuli of interest within a rapidly presented sequence of other base images. Neural responses associated with processes elicited by both the stimuli of interest and the base images to be entrained and measurable at the general stimulation frequency ($F1$), while the neural responses that are evoked exclusively by the stimuli of interest are only observed at the second, slower frequency at which they occur within the sequence ($F2$). For example, when presented in isolation, a single face image will generate several neural responses that overlap in time and can make it difficult to cleanly separate signals related to low- and mid-level visual processing from the high-level visual categorization processes. However, when inserted within a stream of object images, the responses associated with low-level visual processing and mid-level object perception of the face image are captured at the general stimulation frequency because they are also evoked by the object images, but the responses that are uniquely elicited by the faces are observed only at the face-specific frequency (Rossion et al., 2015). This effectively partials out the low- and mid-level processing signals from the high-level categorization signals.

Compared to an ERP waveform analysis, FPVS avoids the assumption that the only difference between the signal of the two different stimuli is the process of interest and instead seeks to decompose the response signal of a stimulus eliciting the process of interest. It also has the additional benefits of having both a higher signal-to-noise ratio (since noise does not occur periodically, it does not contaminate the periodic signal-of-interest in the predicted frequency bin) and, unlike the practice and expectation effects commonly observed in ERPs (Huang et al., 2017), FPVS responses have been shown to be immune to effects of

expectation and temporal predictability (Quek and Rossion, 2017) despite the temporal repetition of the stimulation. FPVS may therefore be more sensitive to signals that are weak relative to strong general visual response signals.

Based on this logic, we aimed to isolate identity recognition responses by periodically presenting images of a particular identity within base images of different unfamiliar faces and investigate the effect of familiarity on this identity-specific response. Recently, Zimmerman and colleagues (2019) used a similar approach and observed clear identity-specific responses (individual face recognition, or IFR) to famous faces interleaved with unfamiliar faces. They found that, averaged across participants, the celebrity rated as being the most familiar elicited the strongest identity-specific response, and the celebrity rated the least familiar elicited the weakest response. However, in a paradigm where the degree of familiarity for each identity is roughly equal across participants, comparing different levels of familiarity rests on response differences between one single most-familiar face and another single least-familiar face. Response differences could therefore reflect difference in familiarity as well as difference on other dimensions, such as distinctiveness or attractiveness (e.g., head size).

The current research extends these findings and directly compares the effect of familiarity on identity-specific responses by equating the stimuli (face identities) in each of three categories of personal familiarity: the own-face, a personally familiar friend, and an unfamiliar stranger. Exposure to one's own face is usually continuous and consistent; one study found that people spend an average of 41 min per day looking at themselves (Veale and Riley, 2001). By contrast, a visual survey of daily face exposure found that participants spent 12 min of each waking hour looking at other people's faces (Oruc et al., 2019). Assuming a 16-h day, this would amount to 192 min per day looking at other people's faces. The time spent looking at one's own face could therefore account for as much as 18% of the total "face time" (233 min). This exposure has been linked to the processing advantage of one's own-face: The own-face is often recognized faster than less familiar faces, such as friends (Sugiura et al., 2008; Keyes and Brady, 2010; Li, 2011), but not when compared to the recognition of highly familiar others such as parents or romantic partners (Kircher et al., 2001; Wang et al., 2011; Wang and Zheng, 2015), and a meta-analysis indicated that the effect size of the own-face advantage decreases as the own-face is compared to unfamiliar, famous familiar, and personally familiar faces (Bortolon and Raffard, 2018). These findings suggest that own-face recognition is supported by highly robust representations that are attributable to the extensive visual experience acquired for the own-face.

For the current study, participants were recruited in pairs. In the own-face condition, each observer was presented with their own face; in the friend-face condition, each observer was presented with the face of the friend; and in the unfamiliar stranger condition, each observer was presented with the face of another participant who was a stranger to them. Therefore, across the full experiment, the face of each participant was used in each familiarity condition. Because, at the group level, the same test identities were used in each condition, we controlled for any stimulus differences between familiarity conditions arising from test identities, and any response differences observed between conditions could be attributed to the level of observer familiarity with the test stimulus.

Twelve distinct images were used for each identity to ensure that the response generalized across different images of the face. Because personal familiarity is usually based on in-person interactions, we photographed each identity as they engaged in a social interaction with the experimenter to obtain images that capture the person's normal range of facial expression. Since this dimension of facial variability might be very idiosyncratic, our experience with a person's facial gestures may play an important role in how individual faces are represented in memory (Redfern and Benton, 2019). Although they do not capture the appearance variability that arises from changes in external features, age, and

ambient conditions, they provide a different kind of expression variability than is commonly captured in normal photos and selfies. Most importantly, they may reflect a better likeness of the identity as they appear during real-life social interactions.

If representations based on greater visual experience generate a larger neural response, we predicted that the response magnitude to the own-face should be the greatest, followed by the response to the friend-face, and the response to the unfamiliar face should be the lowest. Alternatively, it is possible that identity-specific neural areas recruited during identification do not actually produce graded responses for more familiar faces. In this case, the identity-specific response observed for the friend-face and the own-face should not differ.

2. Materials and methods

2.1. Participants

Twelve participants (mean age = 21.3 ± 2.4 years, all Caucasian females) were recruited through advertisement in the University of Victoria's online psychology participant system and through friends of the experimenters. The experiment was described as a study on best friends, and candidates were requested to apply along with a good friend. Inclusion criteria were that the pairs were friends for a minimum of 6 months with at least weekly face-to-face contact. The sample consisted of six pairs of friends who reported having an average friendship of 2.6 years ($SD = 2.1$, range = 0.75–7) and, at the time of testing, interacted an average of 2.66 times per week ($SD = 1.8$, range = 0.5–6). Participants reported no brain injury or diagnosed learning disability. The experiment and consenting procedures were approved by the human research ethics committee of the University of Victoria.

2.2. Stimuli

Prior to the experimental test session, an experimenter conducted brief interviews with each participant individually that were video-recorded using a Canon EOS Rebel DSLR camera mounted on a tripod. The camera was repositioned throughout the interview to capture video of the seated participant from the front, the right angle, and the left angles. All interviewees sat on the same chair in the same during video recording, so that the background and lighting conditions did not differ across images. Still frame images (6 frontal, 3/4 right, 3/4 left) were randomly selected from the video footage to serve as the image set for each identity (12 images per identity). Using Adobe Lightroom, the images were cropped so that the face occupied roughly 80% of the image with the nose just below centre and then resized to 350×350 pixels. This procedure was applied to the 6 identities who were not experimental participants in the study. The 72 images that were created from these 6 identities served as the image set used for the base stimuli described below (the unfamiliar base faces).

2.3. Procedure

After electrode cap placement, participants were seated at a table in front of a keyboard and LCD monitor. Visual stimulation consisted of four 70 s image sequences for each condition (own, friend, unfamiliar) and was presented using a custom MATLAB script (SinStim; e.g., Jacques et al., 2016) while the EEG was recorded. Breaks of about 1 min were provided between each stimulation sequence, and the condition order was pseudorandomized for each participant. The total testing time was approximately 25 min.

Within each sequence, stimuli were presented at a constant rate of 6 Hz ($F1 =$ the visual-stimulation frequency) via sinusoidal contrast modulation from 0% to 100%. The image sequence was structured so that, depending on the condition, every 7th image was the participant's own face (own), their friend's face (friend), or the unfamiliar identity (stranger), and was drawn randomly from the own/friend/stranger set

of images. All other images were randomly selected from the set of unfamiliar base faces; identity therefore varied at every image cycle. By contrast, the face of the own/friend/stranger appeared with a periodicity of $F1/7 \approx 0.86$ Hz ($F2 =$ the identity-specific frequency).

The presentation of each stimulation sequence was as follows: 1) 2–5 s black fixation cross appeared on a grey background; 2) 2 s image sequence fade-in; 3) 63 s image sequence presentation; 4) 5 s image sequence fade-out; 5) 2 s black fixation cross on grey background (Fig. 1). The fixation cross remained on the screen for the entire duration of the stimulation sequence and was positioned to appear over the centre of the image. Across all face images, this roughly corresponded to the area just above the nose. Displayed on a monitor from a distance of 0.7 m, the stimuli subtended an angle of approximately 7 degrees of visual angle.

To maintain a steady point of fixation and attention during visual stimulation, participants were asked to engage in a fixation colour change detection task during each sequence presentation (e.g., Liu-Shuang et al., 2014). At eight random time points in the sequence, the colour of the fixation cross changed briefly (200 ms) to red. Participants were told that face images would be presented rapidly on the screen with a black fixation cross in the middle of the screen and that their primary task was to press the spacebar on the computer keyboard every time they detected the colour of the cross changed from black to red.

2.4. EEG acquisition

During each stimulation sequence, the electroencephalogram (EEG) was recorded using a montage of 42 electrode sites in accordance to the extended international 10–20 system (Jasper, 1958). Signals were acquired using Ag/AgCl ring electrodes mounted in a nylon electrode cap with an abrasive, conductive gel (EASYCAP GmbH, Herrsching-Breitbrunn, Germany). Signals were amplified by low-noise electrode differential amplifiers with a frequency response of DC 0.017–67.5 Hz (90 dB–octave roll off) and digitized at a rate of 250 samples per second. Digitized signals were recorded to disk using Brain Vision Recorder Software (Brainproducts, Munich, Germany). Impedances were kept below 20 k Ω . The EEG was recorded using the average reference.

2.5. EEG analysis

2.5.1. Preprocessing

All EEG processing steps were carried out using the free software Letswave 6 (<https://github.com/NOCIONS/letswave6>) running on MATLAB (MathWorks). A Butterworth filter with cut-off values of 0.1–120 Hz and a slope of 24 dB/octet was applied to the data. Across participants, the continuously recorded EEG data for each stimulation sequence was segmented to include 2 s before and after the stimulation sequence. Channels which were artifact-prone across multiple trials (less than 5% of channels on average) were re-estimated using linear interpolation of the two nearest channels. Independent component analysis (ICA) was applied to the data for each stimulation sequence and a single component accounting for blink artifacts was removed. All EEG segments were re-referenced to a common average reference.

2.5.2. Frequency-domain analysis

The EEG for each sequence was re-segmented, beginning from sequence onset until approximately 64 s (before stimulus fade-out), to contain an integer number of 0.86 Hz cycles (55 cycles, 16,035 time bins in total \approx 64 s). For every participant, the four segmented sequences within the own, friend, unfamiliar face conditions were averaged in the time-domain to reduce EEG activity that is not phase-locked to the stimulus. A Fast Fourier Transform (FFT) was then applied to the averaged segments to represent the data of each channel as a normalized amplitude spectrum (μ V) in the frequency domain with a frequency resolution of 0.0156 Hz (i.e., 1/64.14 s).

2.5.3. Harmonic selection

As responses are expected to be observed across multiple harmonics of the stimulation frequencies (see Rossion et al., 2015), we determined how many harmonics to include for the response analysis of each stimulation frequency (i.e., $F1, F2$) by pooling all channels and selecting harmonics based on their z-scores from the averaged spectra. The procedure was as follows: 1) Within each condition, individual amplitude spectra were averaged across participants and all channels; 2) For responses at all frequencies of interest (i.e., $F1 = 6$ Hz, $F2 = 0.86$ Hz, and their harmonics), z-scores were computed as the difference between the

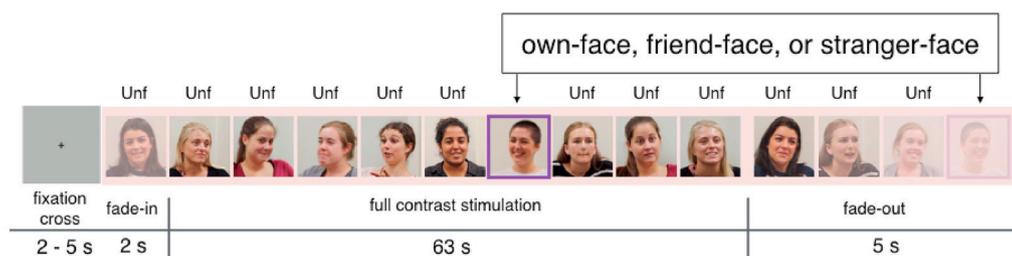


Fig. 1. Visual stimulation sequence.

The visual stimulation sequences consisted of face images contrast modulated at a rate of 6 Hz (each image cycle had a duration of \sim 167 ms). Depending on the condition, every 7th image presented was either the participant's own face, the face of their friend, or the face of an unfamiliar stranger (another subject who was unfamiliar to the participant). The own-, friend-, or stranger-face therefore appeared at a rate of $6 \text{ Hz}/7 = 0.86$ Hz. All other images were selected randomly from a set of faces that were unfamiliar to all participants. During visual stimulation, participants engaged in a fixation cross colour change detection task (not that required them to press the spacebar every time that a fixation cross superimposed in the middle of the screen changed from black to red. Fixation cross changes occurred 8 times at random intervals. Face images are shown here with permission from the participants/models. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

amplitude at the frequency of interest and the mean amplitude of the local baseline divided by the standard deviation of local baseline (local baseline = 20 surrounding frequency bins, excluding the immediately adjacent bins and the bins containing the minimum and maximum response); 3) Using the z-scores as a stopping rule, the range of harmonics to include for each stimulation frequency was constrained to the highest number of consecutively significant harmonics observed in any one condition (e.g., 1F2, 2F2, 3F2, etc., where each $z \geq 3.1$, $p < .001$, 1-tailed, i.e., signal > noise). For visual-stimulation responses, 8 significant harmonics were selected (up to 8F1 = 48 Hz); for identity-specific responses, 10 significant harmonics were selected (up to 11F2 = 9.43 Hz, but excluding 7F2 = 6.00 Hz because it is confounded with the 6 Hz visual-stimulation frequency).

2.5.4. Baseline correction

To visualize the signal-to-noise ratio (SNR) across the frequency spectrum, a baseline-division correction was applied to the amplitude spectra using the same local baseline definition used for the z-score (Fig. 2). For response quantification and scalp topographies, a baseline-subtraction correction was applied instead (Figs. 3 and 4).

2.5.5. Region-of-interest analysis

For each stimulation frequency, responses were quantified as the summed amplitude of the relevant amplitudes (the summed-harmonic responses) and the three channels with the maximum summed-harmonic response were used to define a region-of-interest (ROI). At the visual-stimulation frequency (F1), the channels of maximum

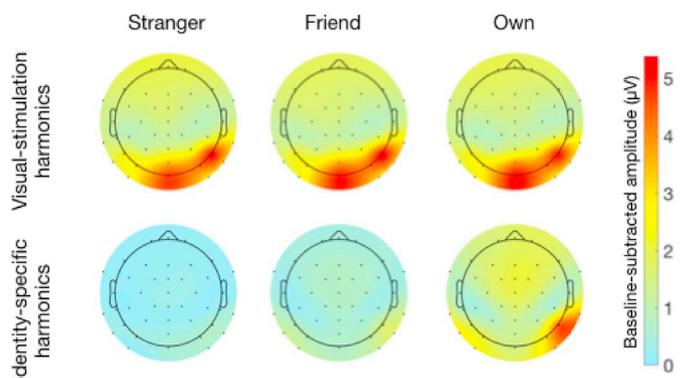


Fig. 3. Scalp topographies of the group-averaged visual-stimulation and identity-specific response in each condition. Summed-harmonic response (baseline-subtracted amplitudes) at the identity-specific and visual stimulation frequency, averaged across all participants.

response were P8, Oz, and PO8, and, with the addition of the left hemisphere homologues PO7 and P7, defined an *occipital region*. At the identity-specific frequency (F2), the channels of maximum response were P10, P8, and TP10, and, with the addition of the left hemisphere homologues P9, P7, and TP9, defined an *occipito-temporal region*. Then, for each condition, the visual-stimulation and identity-specific responses were quantified as the summed-harmonic response averaged across ROI channels. Repeated-measures ANOVA were conducted on baseline-

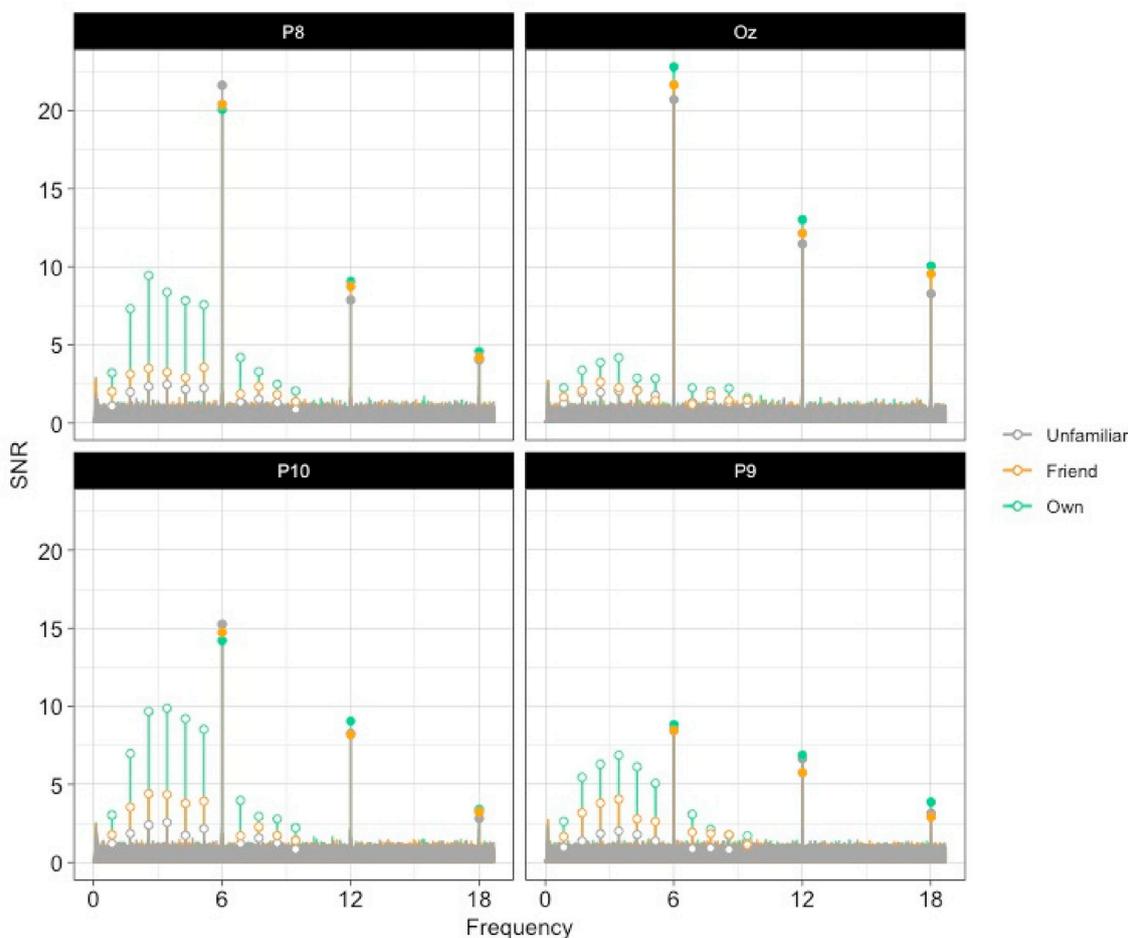


Fig. 2. Signal-to-noise ratio within the frequency spectrum. The EEG amplitude spectra averaged across participants and conditions and represented as the signal-to-noise ratio at the channels of maximum response. At the visual stimulation frequency (6 Hz and its harmonics), SNR was highest in channel P8 and Oz. At the identity-specific frequency (0.86 Hz and its harmonics), SNR was highest in channel P10 (the homologous channel in the left hemisphere, P9, is also shown).

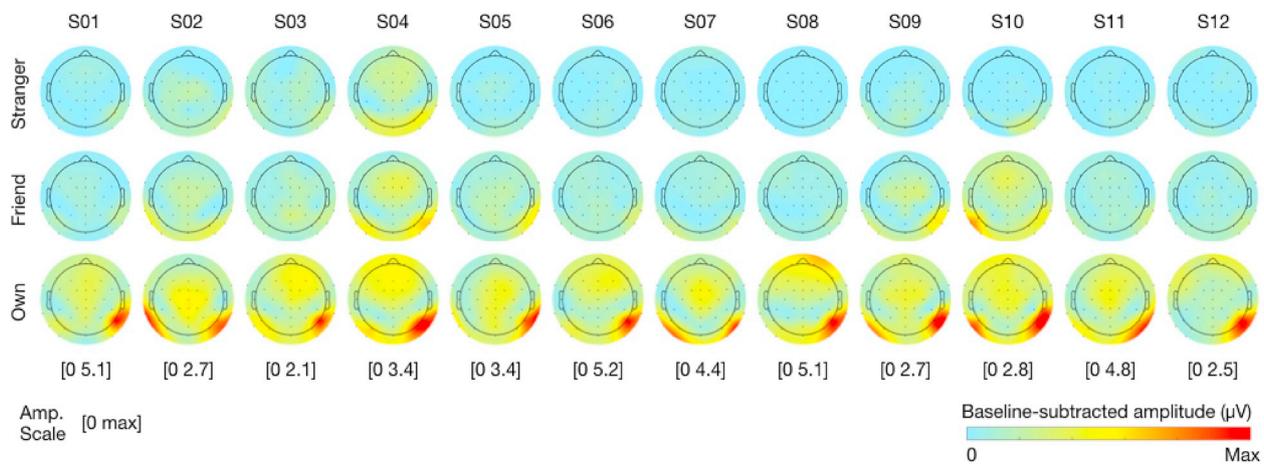


Fig. 4. Scalp topographies of the identity-specific response for each participant and condition. Scalp distribution of each participant's identity-specific response to a stranger (top row), friend (middle row), and their own face (bottom row). The amplitude scale used for each participant is reported at the bottom of each subject's column.

corrected amplitudes for both the visual-stimulation and the identity-specific responses with condition (own, friend, stranger) as a within-subject factor. Mauchly's test for sphericity was performed and a Greenhouse-Geisser correction was applied whenever sphericity was violated. Pairwise comparisons were carried out using paired-sample *t*-tests with a Bonferroni-Holm correction for multiple comparisons.

The lateralization of the identity-specific response was defined based on the magnitude of the left and right channels of the occipito-temporal ROI and expressed as the lateralization index: $(R-L)/(R+L)$.

2.5.6. Harmonic analysis

To examine the neural dynamics of the identity-specific response, we grand-averaged the individual baseline-subtracted spectra for each channel and computed their *z*-scores to compare the topography of significant neural responses of each harmonic. This was done for each condition separately.

3. Results

3.1. Fixation cross task

Response times (RT) were calculated relative to the onset of fixation cross colour change and for responses recorded within 1500 ms of the colour change. Analyses were based on correct RTs. Accuracy for the colour change detection task was close to ceiling in all three conditions (own: $M = 97.0\%$, $SD = 6.7\%$; friend: $M = 95.4\%$, $SD = 15.1\%$; stranger: $M = 94.9\%$, $SD = 10.3\%$; $F < 1$). There was no difference in reaction times across conditions (own: $M = 450$ ms, $SD = 63$ ms; friend: $M = 446$ ms, $SD = 92$ ms; stranger: $M = 448$ ms, $SD = 79$ ms; $F < 1$).

3.2. Frequency domain

The signal-to-noise ratio (SNR) of electrophysiological responses during FPVS are shown in Fig. 2. Clear responses were visible at the visual-stimulation frequency ($1F1 = 6$ Hz) up to the 8th significant harmonic ($8F1 = 48$ Hz). Responses at these frequencies reflect the onset and offset of each visual stimulus in the sequence and therefore the processing that is common to all stimuli. These include responses elicited by low-level properties, such as colour and spatial frequency, but also high-level properties: as each stimulus is the onset of a face, each stimulus would elicit a face categorization response and, as each stimulus is the onset of an identity, each stimulus would elicit a face individuation response. Consistent with this, SNR at 6 Hz and its harmonics was maximal in the medial occipital region (Oz; average SNR of 7.04) as well as the occipito-temporal region (P8; average SNR of 5.38).

Responses at the identity-specific frequency ($1F2 = 0.86$ Hz) were significant up to the 11th significant harmonic ($11F2 = 9.43$ Hz; Fig. 2). Responses at these frequencies are driven by the onset of either the own, friend, or stranger face. However, responses elicited by these face images that are common to responses elicited by unfamiliar face images should be captured at the common presentation rate of 6 Hz and its harmonics (the visual-stimulation frequency). The responses at the identity-specific frequency (and its harmonics) therefore reflect any processing that is unique to the identity of the face images, such as the activation of an identity-specific face representation. As predicted, the SNR at 0.86 Hz and its harmonics was maximal in the occipito-temporal region (P10; average SNR of 3.50).

The scalp topography of the summed-harmonic responses averaged across participants for each condition and stimulation frequency are shown in Fig. 3. Individual differences in the scalp distribution of the summed-harmonic identity-specific response are shown in Fig. 4.

3.3. Identity-specific and visual-stimulation response analysis

For each stimulation frequency, we compared the summed-harmonic response across conditions in the regions-of-interest defined by the channels of maximum response. The identity condition had no effect on the magnitude of the visual-stimulation responses in the occipital region (P8/7, Oz, PO8/O7; own: 1.50 ± 0.81 μ V; friend: 1.49 ± 0.79 μ V; stranger: 1.48 ± 0.74 μ V; $F < 1$). However, there was a main effect of identity on the magnitude of the identity-specific responses in the occipito-temporal region (P10/9, P8/7, TP10/9), $F(2, 22) = 86.12$, $p < .001$, $\eta_p^2 = 0.89$. Pairwise comparisons showed that the response to the friend-face (0.94 ± 0.50 μ V) was significantly greater than the response to the stranger-face (0.31 ± 0.32 μ V; $t(11) = 6.82$, $p = .001$), and the response to the own-face (2.31 ± 1.20 μ V) was significantly greater than both the friend, $t(11) = 8.54$, $p < .001$, and stranger, $t(11) = 10.18$, $p < .001$. In all participants, the magnitude of the identity-specific response in the occipito-temporal region was greater to the friend than the stranger, and the response to the own-face was greatest in magnitude (Fig. 5).

The lateralization index of the identity-specific responses revealed that the occipito-temporal response was right lateralized in all three conditions (own: $M = 0.33$, $SD = 0.22$; friend: $M = 0.21$, $SD = 0.21$; stranger: $M = 0.42$, $SD = 0.40$) and was not significantly different across conditions, $F(2, 22) = 1.63$, $p = .22$ (Fig. 6).

3.4. Harmonic analysis

At the first harmonic of the 6 Hz visual-stimulation frequency, the

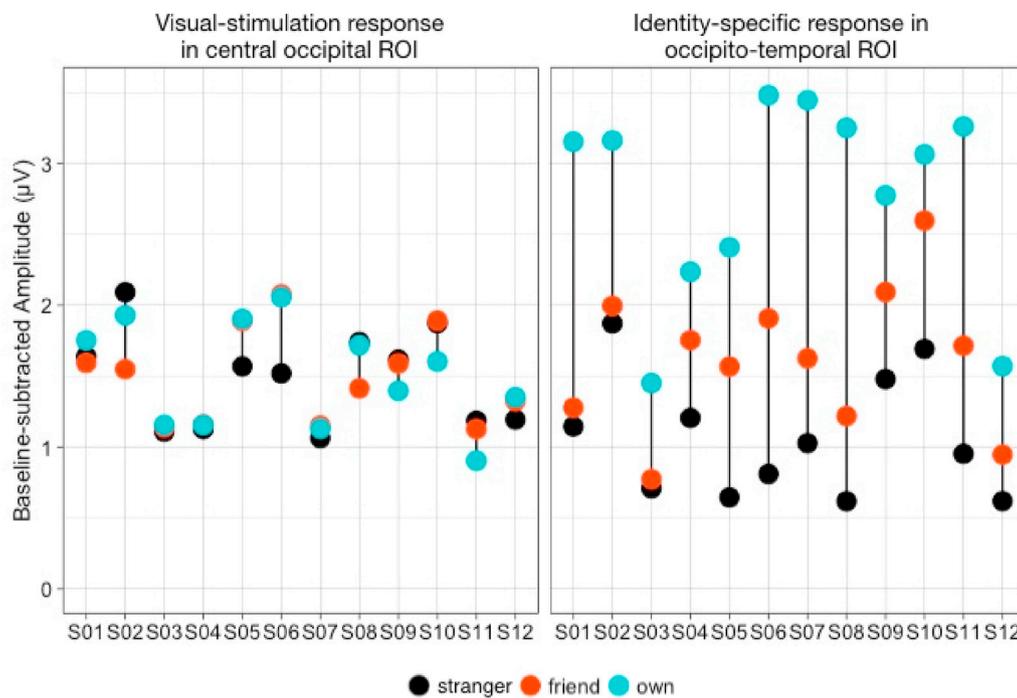


Fig. 5. Summed-harmonic response for the visual-stimulation and identity-specific responses. Visual-stimulation and identity-specific responses for each condition and participant, quantified as the average summed-harmonic response of the channels of maximal response. For the visual-stimulation response, the channels P8, Oz, PO8, P7 and PO7 defined the occipital region of interest. For the identity-specific response, the channels P10, P8, TP10, P9, P7, and TP9 defined the occipito-temporal region of interest.

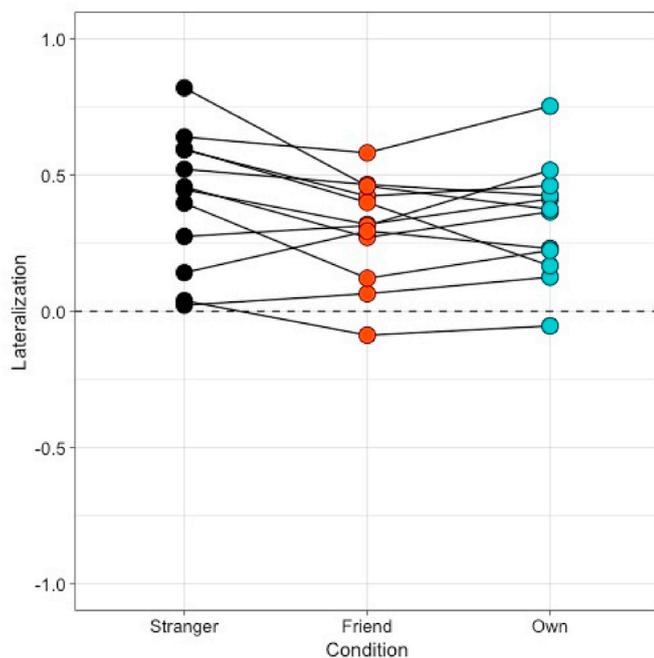


Fig. 6. Lateralization indices for each participant and condition. The lateralization index for identity-specific responses in the occipito-temporal region. Expressed as $(R-L)/(R + L)$, based on magnitude of right and left hemisphere channel responses. Positive values indicate stronger right hemisphere response.

largest response was observed over the right occipito-temporal region. Higher harmonics (e.g., 12 Hz, 18 Hz, up to 48 Hz) were focused on the medial occipital channel Oz (Fig. 7A). For all harmonics of the 0.86 Hz identity-specific frequency (0.86 Hz, 1.72 Hz, up to 9.43 Hz), the largest response was over the right occipito-temporal region (e.g., P10, P8, TP10). However, in the first harmonic (0.86 Hz), an additional response at the centro-parietal channels Pz and POz was observed in response to

the own-face and friend-face, but not to the face of a stranger (Fig. 7B). Importantly, this additional response is dissociable from the occipito-temporal response, since the occipito-temporal response increases in magnitude in subsequent harmonics while the centro-parietal response decreases (Fig. 7B).

Individual responses at this first harmonic (0.86 Hz) were examined by calculating z -scores for each participant. A less conservative threshold of $z > 1.64$ ($p < .05$, one-tailed, signal > noise) was used for the participant-level as the 0.86 Hz response is located in a highly noisy area of the frequency spectrum. Significant responses were observed over the centro-parietal region (POz or Pz) in 8 of 12 participants for the friend condition and in 11 of 12 participants in the own-face condition (Fig. 8). Pairwise comparison of the average amplitude of Pz and POz in the first harmonic (0.86 Hz) revealed a stronger response to the own-face ($0.23 \pm 0.15 \mu V$) compared to the friend-face ($0.08 \pm 0.12 \mu V$; $t(11) = 3.13, p = .01$).

4. Discussion

Using a fast periodic visual stimulation paradigm (e.g., Liu-Shuang et al., 2014; Rossion et al., 2015), we sought to measure the neurophysiological response signals related to image-invariant face identification. This was achieved by periodically presenting either the participant's own face, the face of their friend, or the face of a stranger within a sequence of unfamiliar face images. This presentation technique splits the neural response evoked by the identity of interest (own, friend, or stranger) into two separate response frequencies. Although these specific identities are presented at 0.86 Hz, the low-level visual and general face categorization responses evoked by these images are also evoked by the other unfamiliar face images in the stimulation sequences, and this leads these responses to entrain to and be observed at the 6 Hz visual stimulation frequency. The response that remains observable at the 0.86 Hz identity-specific frequency therefore reflects the isolated response of any population of neurons that are specifically responsive to the own, friend, or stranger face. Compared to previous ERP studies which have been limited to waveform-subtraction analysis to indirectly measure processes specific to familiar faces (e.g., Herzmann et al., 2004; Caharel et al., 2005; Sui et al., 2006; Wild-Wall et al., 2008;

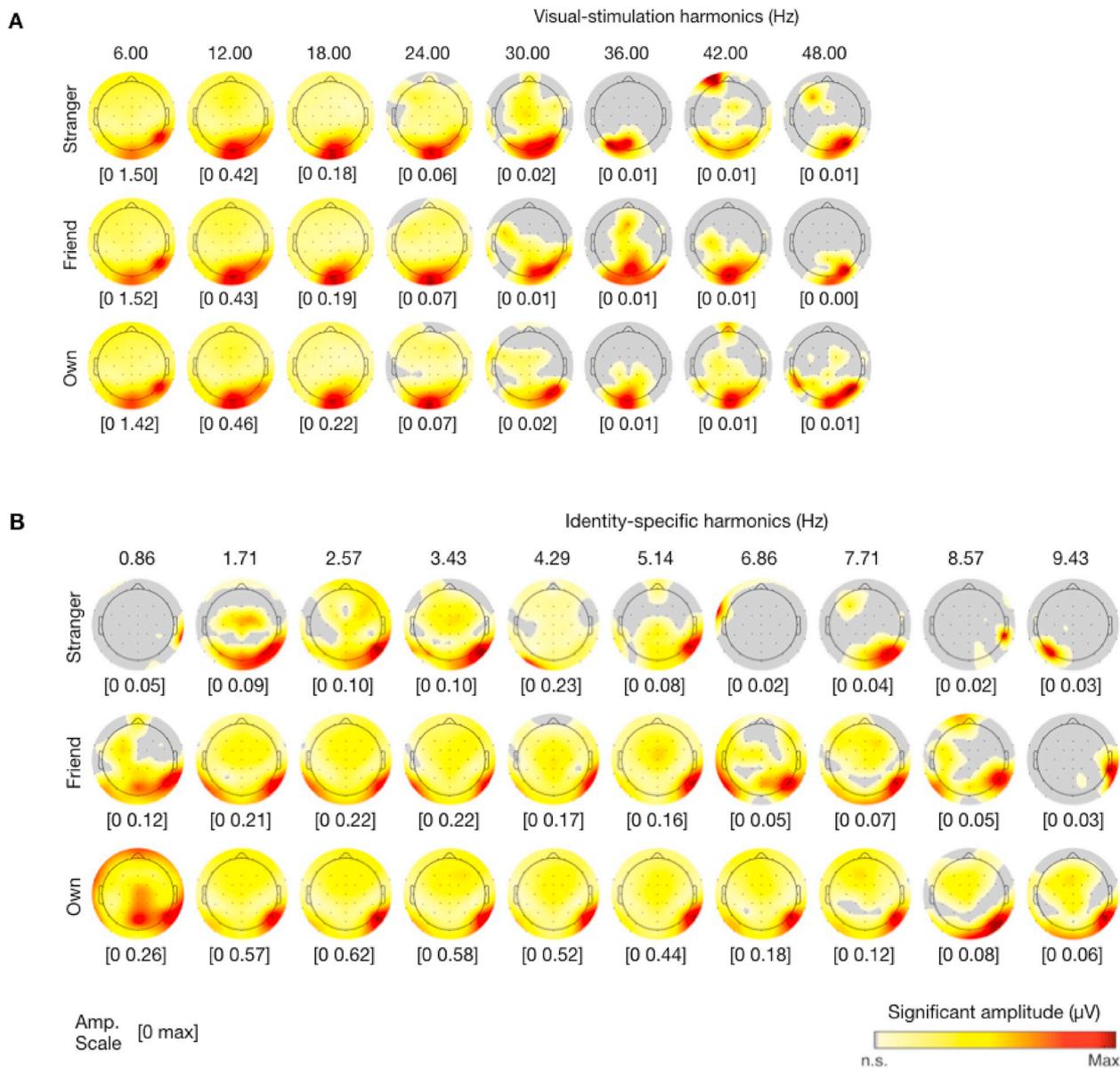


Fig. 7. Scalp topographies of the significant harmonic responses. Scalp topography maps of significant grand-averaged EEG responses (baseline-subtracted) observed for each significant harmonic ($z > 3.1$, $p < .001$, 1-tailed) in each condition (own, friend, and stranger). The amplitude scale used for each harmonic is reported below each map. Grey indicates no significant response. A. Scalp topography of 8 significant visual-stimulation frequency harmonics. B. Scalp topography of 11 significant identity-specific frequency harmonics.

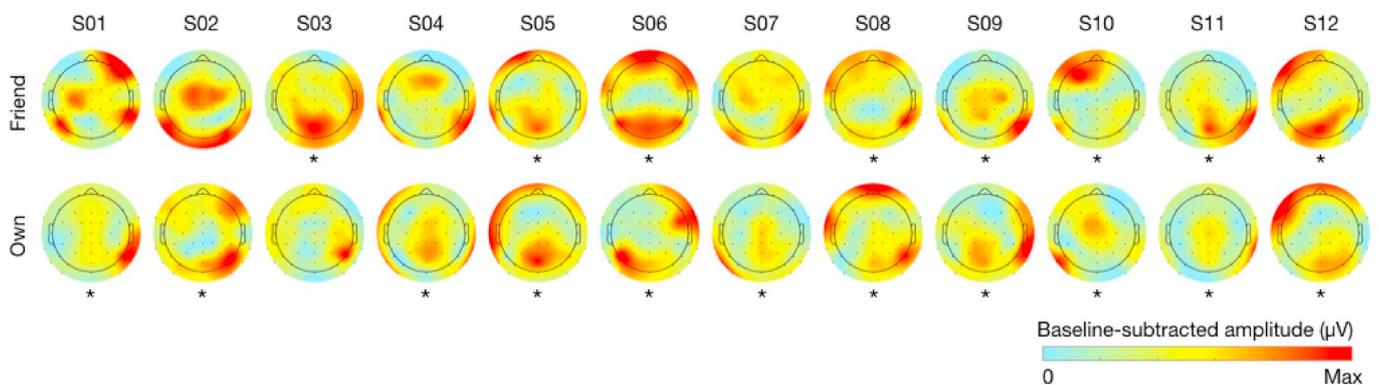


Fig. 8. Scalp topographies of the first harmonic of 0.86 Hz identity-specific response. Subject scalp topography maps of baseline-corrected EEG responses observed at the first harmonic of the identity-specific frequency (0.86 Hz) in the friend- and own-face conditions. Subjects showing a significant response over the centro-parietals channels (POz or Pz, $z > 1.64$, $p < .05$, 1-tailed) are indicated by an asterisk.

Keyes et al., 2010; Caharel et al., 2014; Barragan-Jason et al., 2015; Andrews et al., 2017; Wiese et al., 2019; Alzueta et al., 2019), the fast periodic visual stimulation technique allows identity-specific processes to be measured *directly* because they are parsed from other identity-general processes and *objectively* because they are observed at the exact frequency predicted by the presentation frequency.

The 6 Hz response was maximal over medial-occipital and occipito-temporal regions. This is consistent with the observations made in previous FPVS-EEG studies using sequences of objects (Rossion et al., 2015; Jacques et al., 2016; Retter and Rossion, 2016) and faces (Liu-Shuang et al., 2014; Xu et al., 2017; Dzhelyova et al., 2019) and the prediction that this response reflects low-level visual processing in early visual areas and face-selective processes in high-level visual areas. As predicted, the familiarity condition had no effect on the scalp distribution or the magnitude of this response. The similarity of the general stimulation response across the own-, friend-, and stranger-face conditions indicates that, beyond identity-processing, the overall neural response did not differ across testing conditions. In other words, having seen or potentially expecting to see an image of a familiar face did not have an effect on how images in the test sequences were processed.

By contrast, the 0.86 Hz response that was expected to reflect identity-specific processes was strongest over the right occipito-temporal channels and the magnitude varied according to personal familiarity: responses were greatest to the participant's own face, followed by the friend's face, and were smallest to the stranger's face.

Notably, a stranger's face interleaved in other unfamiliar faces elicited a weaker yet significant response. A smaller response for an unfamiliar face compared to a familiar face is consistent with behavioural studies showing reduced identity recognition of an unfamiliar face across different images (Hancock et al., 2000; Jenkins et al., 2011). However, because images of each identity were taken on the same day, it's possible that part of the signal observed at the 0.86 Hz frequency reflects image regularities due to clothing and external features such as hair.

The topography of the 0.86 Hz identity-specific response was similar across conditions at both the group and individual level (Figs. 3 and 4) and is consistent with the topography of several identity-sensitive ERP components (e.g., Caharel et al., 2014; Gosling and Eimer, 2011; Pierce et al., 2011) and face individuation responses measured with FPVS (Zimmerman et al., 2019; Dzhelyova et al., 2019; Vettori et al., 2018; Dwyer et al., 2019; Xu et al., 2017; Liu-Shuang et al., 2014). We also found that the identity-specific response was right lateralized for all participants and in all conditions (Fig. 4), and that the degree of this lateralization did not differ across categories of familiarity. The fact that lateralization did not change highlights that greater familiarity elicited a stronger response in both the right and left occipito-temporal regions. This is consistent with previous studies showing an increased bilateral response to familiar faces or to the own-face, and even reduced lateralization to more familiar faces (Keyes et al., 2010; Taylor et al., 2009), but that the response remains stronger in the right hemisphere compared to the left (Ma and Han, 2012; Keyes et al., 2010; Taylor et al., 2009; Pierce et al., 2011; Tanaka et al., 2006; Gobbini et al., 2004; Rossion et al., 2003; Sugiura et al., 2008).

When the harmonics of the visual-stimulation and identity-specific response were examined individually, we observed systematic changes in the scalp distribution of the response across harmonics. In the first harmonic of the 6 Hz visual-stimulation response, we observed a right lateral occipito-temporal response, but in the higher harmonics, we observed mostly medial occipital responses. This dissociation of the harmonic scalp topographies is typical of fast periodic presentation of faces and objects (Zimmerman et al., 2019; Xu et al., 2017; Jacques et al., 2016; Gentile and Rossion, 2014; Rossion et al., 2015) and suggests that low-level visual processes reflected by activity in the medial occipital cortex are captured at higher frequencies, while higher-level visual processes (e.g., shape-related processes, face individuation) in the lateral occipital cortex are captured at lower frequencies. This is

consistent with the general finding that the frequency of maximal response decreases when moving up in the ventral visual stream (Hawken et al., 1996; McKeef et al., 2007; Gauthier et al., 2012).

Similarly, we observed a distinct scalp topography in the first harmonic of the 0.86 Hz identity-specific response where there was a strong response over the posterior midline cortex in addition to the right occipito-temporal cortex for familiar faces (own, friend) but not the stranger face. In the same way that low- and high-level visual processes are captured in different harmonics of the general visual-stimulation frequency, it is possible that certain processes elicited by familiar faces are subtended by regions that respond only at very low frequencies (in this case, below 1 Hz) but not at higher frequencies. For example, functional neuroimaging studies show that areas of the cortical midline are sensitive to face familiarity, with the precuneus and posterior cingulate being consistently reported to respond more strongly to personally familiar (Taylor et al., 2008; Gobbini and Haxby, 2007), famous (Avidan and Berhmann, 2009; Eger et al., 2005; Leveroni et al., 2000), and learned faces (Gobbini and Haxby, 2006; Kosaka et al., 2003; Leveroni et al., 2000) relative to unfamiliar faces, with personally familiar faces evoking a larger response compared to famous faces (Gobbini et al., 2004). Additionally, the precuneus has been reported to respond differentially to the own-face compared to less familiar faces (Platek and Kemp, 2009; Devue et al., 2007; Kircher et al., 2000, 2001; Platek et al., 2004; Platek et al., 2006; Sugiura et al., 2000, 2005) and, using pattern-based analyses, the precuneus has also been shown to contain representations useful for the classification of familiar compared to unfamiliar faces (Natu & O'Toole, 2015; di Oleggio Castello et al., 2017), with the dorsal region playing a larger role in identity-specific representations (di Oleggio Castello et al., 2017). Conversely, participants with congenital prosopagnosia fail to show a selective response in the precuneus and posterior cingulate cortex to famous faces compared to unfamiliar faces demonstrated in healthy controls (Avidan and Behrmann, 2009). Functionally, this area is generally linked to the retrieval of long-term episodic and autobiographical memory (Burgess et al., 2001; Ishai et al., 2000; Fletcher et al., 1995; Gorno-Tempini et al., 1998) and, as it is responsive to familiar identity stimuli across sensory modalities (Nakamura et al., 2000; Shah et al., 2001), may reflect post-perceptual person knowledge processing (Gobbini and Haxby, 2006, 2007). In line with the view that recognition of personally familiar individuals entails both visual recognition and semantic retrieval of person knowledge (Gobbini and Haxby, 2007; for review, see Ramon and Gobbini, 2018), it is possible that the posterior midline response reflects post-perceptual person recognition processes while the higher harmonics reflect the perceptual face representations of the familiar face.

A limitation of the current study is that the degree of familiarity might vary between participant pairs (e.g., one pair might be more familiar with each other than another pair) and even within pairs (e.g., one friend might be more familiar with their partner than vice versa). Second, although processing advantages for the own-face have been linked to high visual experience for the own-face compared to other familiar faces (Bortolon and Raffard, 2018), the ratio of exposure to the own-face compared to a personally familiar friend has not been quantified and future work should also attempt to control for variability of familiarity between categories. Finally, the responses observed in both the current study and Zimmerman et al. (2019) may reflect a general face familiarity signal in addition to the identity-specific response which could differentially impact the lateralization of less familiar (famous) or highly familiar faces (Denkova et al., 2006). In future studies, a general face familiarity signal could be inferred by comparing the response to the exact same familiar face identity when interleaved in other familiar faces relative to when it is interleaved in unfamiliar faces.

In conclusion, we used fast periodic visual stimulation to isolate electrophysiological responses reflecting image-invariant identity recognition processes elicited by a personally familiar face from general visual and face individuation processing. These identity-specific

responses were observed bilaterally over the occipito-temporal cortex but were stronger in the right hemisphere and greater in magnitude for more familiar faces. Only familiar faces evoked an additional response in a posterior midline in the first harmonic of the identity-specific response, adding further evidence that this region is involved in personally familiar face processing, even during rapid and implicit recognition.

CRedit authorship contribution statement

Alison Campbell: Conceptualization, Methodology, Software, Formal analysis, Investigation, Resources, Data curation, Writing - original draft, Writing - review & editing, Visualization, Project administration. **Rebecca Louw:** Investigation, Resources, Data curation. **Evelina Michniak:** Investigation, Resources, Data curation. **James W. Tanaka:** Conceptualization, Methodology, Writing - review & editing, Supervision, Funding acquisition.

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References

- Alzueta, E., Melcón, M., Poch, C., Capilla, A., 2019. Is your own face more than a highly familiar face? *Biological Psychology* 142, 100–107. <https://doi.org/10.1016/j.biopsycho.2019.01.018>.
- Anaki, D., Zion-Golumbic, E., Bentin, S., 2007. Electrophysiological neural mechanisms for detection, configural analysis and recognition of faces. *Neuroimage* 37 (4), 1407–1416. <https://doi.org/10.1016/j.neuroimage.2007.05.054>.
- Andrews, S., Burton, A.M., Schweinberger, S.R., Wiese, H., 2017. Event-related potentials reveal the development of stable face representations from natural variability. *Q. J. Exp. Psychol.* 70 (8), 1620–1632. <https://doi.org/10.1080/17470218.2016.1195851>.
- Avidan, G., Behrmann, M., 2009. Functional MRI reveals compromised neural integrity of the face processing network in congenital prosopagnosia. *Curr. Biol.* 19 (13), 1146–1150. <https://doi.org/10.1016/j.cub.2009.04.060>.
- Barragan-Jason, G., Cauchoix, M., Barbeau, E.J., 2015. The neural speed of familiar face recognition. *Neuropsychologia* 75, 390–401. <https://doi.org/10.1016/j.neuropsychologia.2015.06.017>.
- Begleiter, H., Porjesz, B., Wang, W., 1995. Event-related brain potentials differentiate priming and recognition to familiar and unfamiliar faces. *Electroencephalogr. Clin. Neurophysiol.* 94 (1), 41–49.
- Bentin, S., Allison, T., Puce, A., Perez, E., McCarthy, G., 1996. Electrophysiological studies of face perception in humans. *J. Cognit. Neurosci.* 8 (6), 551–565.
- Bentin, S., Deouell, L.Y., 2000. Structural encoding and identification in face processing: ERP evidence for separate mechanisms. *Cogn. Neuropsychol.* 17 (1–3), 35–55. <https://doi.org/10.1080/026432900380472>.
- Besson, G., Barragan-Jason, G., Thorpe, S.J., Fabre-Thorpe, M., Puma, S., Ceccaldi, M., Barbeau, E.J., 2017. From face processing to face recognition: Comparing three different processing levels. *Cognition* 158, 33–43. <https://doi.org/10.1016/j.cognition.2016.10.004>.
- 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 (4), 535–544. [x10.1111/j.1469-8986.2008.00663](https://doi.org/10.1111/j.1469-8986.2008.00663).
- Bortolon, C., Raffard, S., 2018. Self-face advantage over familiar and unfamiliar faces: a three-level meta-analytic approach. *Psychon. Bull. Rev.* 1–14. <https://doi.org/10.3758/s13423-018-1487-9>.
- Burgess, N., Maguire, E.A., Spiers, H.J., O'Keefe, J., 2001. A temporoparietal and prefrontal network for retrieving the spatial context of lifelike events. *Neuroimage* 14 (2), 439–453. <https://doi.org/10.1006/nimg.2001.0806>.
- Burton, A.M., Bruce, V., Hancock, P.J., 1999a. From pixels to people: a model of familiar face recognition. *Cognit. Sci.* 23 (1), 1–31.
- Burton, A.M., Jenkins, R., Schweinberger, S.R., 2011. Mental representations of familiar faces. *Br. J. Psychol.* 102 (4), 943–958. [x10.1111/j.2044-8295.2011.02039](https://doi.org/10.1111/j.2044-8295.2011.02039).
- Burton, A.M., Wilson, S., Cowan, M., Bruce, V., 1999b. Face recognition in poor-quality video: evidence from security surveillance. *Psychol. Sci.* 10 (3), 243–248.
- Bruce, V., Young, A., 1986. Understanding face recognition. *Br. J. Psychol.* 77 (3), 305–327.
- Caharel, S., Poiroux, S., Bernard, C., Thibaut, F., Lalonde, R., Rebai, M., 2002. ERPs associated with familiarity and degree of familiarity during face recognition. *Int. J. Neurosci.* 112 (12), 1499–1512. <https://doi.org/10.1080/00207450290158368>.
- Caharel, S., Courtay, N., Bernard, C., Lalonde, R., Rebai, M., 2005. Familiarity and emotional expression influence an early stage of face processing: an electrophysiological study. *Brain Cognit.* 59 (1), 96–100. <https://doi.org/10.1016/j.bandc.2005.05.005>.
- 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* 47 (3), 639–643. <https://doi.org/10.1016/j.neuropsychologia.2008.11.016>.
- Caharel, S., Fiori, N., Bernard, C., Lalonde, R., Rebai, M., 2006. The effects of inversion and eye displacements of familiar and unknown faces on early and late-stage ERPs. *Int. J. Psychophysiol.* 62 (1), 141–151. <https://doi.org/10.1016/j.ijpsycho.2006.03.002>.
- Caharel, S., Jacques, C., d'Arripe, O., Ramon, M., Rossion, B., 2011. Early electrophysiological correlates of adaptation to personally familiar and unfamiliar faces across viewpoint changes. *Brain Res.* 1387, 85–98. <https://doi.org/10.1016/j.brainres.2011.02.070>.
- Caharel, S., Ramon, M., Rossion, B., 2014. Face familiarity decisions take 200 msec in the human brain: electrophysiological evidence from a go/no-go speeded task. *J. Cognit. Neurosci.* 26 (1), 81–95. <https://doi.org/10.1162/jocn.a.00451>.
- Carbon, C.C., 2008. Famous faces as icons. The illusion of being an expert in the recognition of famous faces. *Perception* 37 (5), 801–806. <https://doi.org/10.1068/p5789>.
- Denkova, E., Botzung, A., Manning, L., 2006. Neural correlates of remembering/knowing famous people: an event-related fMRI study. *Neuropsychologia* 44 (14), 2783–2791. <https://doi.org/10.1016/j.neuropsychologia.2006.05.029>.
- Devue, C., Collette, F., Balteau, E., Degueldre, C., Luxen, A., Maquet, P., Brédart, S., 2007. Here I am: the cortical correlates of visual self-recognition. *Brain Res.* 1143, 169–182. <https://doi.org/10.1016/j.brainres.2007.01.055>.
- di Oleggio Castello, M.V., Halchenko, Y.O., Guntupalli, J.S., Gors, J.D., Gobbini, M.I., 2017. The neural representation of personally familiar and unfamiliar faces in the distributed system for face perception. *Sci. Rep.* 7 (1), 12237. <https://doi.org/10.1038/s41598-017-12559-1>.
- Dwyer, P., Xu, B., Tanaka, J.W., 2019. Investigating the perception of face identity in adults on the autism spectrum using behavioural and electrophysiological measures. *Vis. Res.* 157, 132–141. <https://doi.org/10.1016/j.visres.2018.02.013>.
- Dzhelyova, M., Jacques, C., Dormal, G., Michel, C., Schiltz, C., Rossion, B., 2019. High test-retest reliability of a neural index of rapid automatic discrimination of unfamiliar individual faces. *Vis. Cognit.* 1–15. <https://doi.org/10.1080/13506285.2019.1616639>.
- Eger, E., Schweinberger, S.R., Dolan, R.J., Henson, R.N., 2005. Familiarity enhances invariance of face representations in human ventral visual cortex: fMRI evidence. *Neuroimage* 26 (4), 1128–1139. <https://doi.org/10.1016/j.neuroimage.2005.03.010>.
- Eimer, M., 2000. Event-related brain potentials distinguish processing stages involved in face perception and recognition. *Clin. Neurophysiol.* 111 (4), 694–705. [https://doi.org/10.1016/S1388-2457\(99\)00285-0](https://doi.org/10.1016/S1388-2457(99)00285-0).
- Ellis, H.D., Shepherd, J.W., Davies, G.M., 1979. Identification of familiar and unfamiliar faces from internal and external features: Some implications for theories of face recognition. *Perception* 8 (4), 431–439. <https://doi.org/10.1068/p080431>.
- Fletcher, P.C., Frith, C.D., Baker, S.C., Shallice, T., Frackowiak, R.S., Dolan, R.J., 1995. The mind's eye—precuneus activation in memory-related imagery. *Neuroimage* 2, 195–200. <https://doi.org/10.1006/nimg.1995.1025>.
- Gauthier, B., Eger, E., Hesselmann, G., Giraud, A.L., Kleinschmidt, A., 2012. Temporal tuning properties along the human ventral visual stream. *J. Neurosci.* 32 (41), 14433–14441. <https://doi.org/10.1523/JNEUROSCI.2467-12.2012>.
- Gentile, F., Rossion, B., 2014. Temporal frequency tuning of cortical face-sensitive areas for individual face perception. *Neuroimage* 90, 256–265. <https://doi.org/10.1016/j.neuroimage.2013.11.053>.
- Gobbini, M.I., Haxby, J.V., 2006. Neural response to the visual familiarity of faces. *Brain Res. Bull.* 71 (1–3), 76–82. <https://doi.org/10.1016/j.brainresbull.2006.08.003>.
- Gobbini, M.I., Haxby, J.V., 2007. Neural systems for recognition of familiar faces. *Neuropsychologia* 45 (1), 32–41. <https://doi.org/10.1016/j.neuropsychologia.2006.04.015>.
- Gobbini, M.I., Leibenluft, E., Santiago, N., Haxby, J.V., 2004. Social and emotional attachment in the neural representation of faces. *Neuroimage* 22 (4), 1628–1635. <https://doi.org/10.1016/j.neuroimage.2004.03.049>.
- Gorno-Tempini, M.L., Price, C.J., Josephs, O., Vandenberghe, R., Cappa, S.F., Kapur, N., Tempini, M.L., 1998. The neural systems sustaining face and proper-name processing. *Brain* 121 (11), 2103–2118. <https://doi.org/10.1093/brain/121.11.2103>.
- Gosling, A., Eimer, M., 2011. An event-related brain potential study of explicit face recognition. *Neuropsychologia* 49 (9), 2736–2745. <https://doi.org/10.1016/j.neuropsychologia.2011.05.025>.
- Hancock, P.J., Bruce, V., Burton, A.M., 2000. Recognition of unfamiliar faces. *Trends Cognit. Sci.* 4 (9), 330–337. [https://doi.org/10.1016/S1364-6613\(00\)01519-9](https://doi.org/10.1016/S1364-6613(00)01519-9).
- Hawken, M.J., Shapley, R.M., Grosz, D.H., 1996. Temporal-frequency selectivity in monkey visual cortex. *Vis. Neurosci.* 13 (3), 477–492. <https://doi.org/10.1017/S0952523800008154>.
- Haxby, J.V., Hoffman, E.A., Gobbini, M.I., 2000. The distributed human neural system for face perception. *Trends Cognit. Sci.* 4 (6), 223–233. [https://doi.org/10.1016/S1364-6613\(00\)01482-0](https://doi.org/10.1016/S1364-6613(00)01482-0).
- Henson, R.N., Goshen-Gottstein, Y., Ganel, T., Otten, L.J., Quayle, A., Rugg, M.D., 2003. Electrophysiological and haemodynamic correlates of face perception, recognition and priming. *Cerebr. Cortex* 13 (7), 793–805. <https://doi.org/10.1093/cercor/13.7.793>.
- Herzmann, G., Schweinberger, S.R., Sommer, W., Jentsch, I., 2004. What's special about personally familiar faces? A multimodal approach. *Psychophysiology* 41 (5), 688–701. [x10.1111/j.1469-8986.2004.00196](https://doi.org/10.1111/j.1469-8986.2004.00196).

- Huang, W., Wu, X., Hu, L., Wang, L., Ding, Y., Qu, Z., 2017. Revisiting the earliest electrophysiological correlate of familiar face recognition. *Int. J. Psychophysiol.* 120, 42–53.
- Ishai, A., Ungerleider, L.G., Haxby, J.V., 2000. Distributed neural systems for the generation of visual images. *Neuron* 28, 979–990. [https://doi.org/10.1016/S0896-6273\(00\)00168-9](https://doi.org/10.1016/S0896-6273(00)00168-9).
- Jacques, C., Rossion, B., 2006. The speed of individual face categorization. *Psychol. Sci.* 17 (6), 485–492. <https://doi.org/10.1111/j.1467-9280.2006.01733>.
- Jacques, C., Retter, T.L., Rossion, B., 2016. A single glance at natural face images generate larger and qualitatively different category-selective spatio-temporal signatures than other ecologically-relevant categories in the human brain. *Neuroimage* 137, 21–33. <https://doi.org/10.1016/j.neuroimage.2016.04.045>.
- Jemel, B., Schuller, A.M., Goffaux, V., 2010. Characterizing the spatio-temporal dynamics of the neural events occurring prior to and up to overt recognition of famous faces. *J. Cognit. Neurosci.* 22 (10), 2289–2305. <https://doi.org/10.1162/jocn.2009.21320>.
- Jasper, H.H., 1958. The ten twenty electrode system of the international federation. *Clin. Neurophysiol.* 10, 371–375.
- Jemel, B., Pisani, M., Calabria, M., Crommelinck, M., Bruyer, R., 2003. Is the N170 for faces cognitively penetrable? Evidence from repetition priming of Mooney faces of familiar and unfamiliar persons. *Cognit. Brain Res.* 17 (2), 431–446.
- Jenkins, R., White, D., Van Montfort, X., Burton, A.M., 2011. Variability in photos of the same face. *Cognition* 121 (3), 313–323. <https://doi.org/10.1016/j.cognition.2011.08.001>.
- Johnston, P., Overell, A., Kaufman, J., Robinson, J., Young, A.W., 2016. Expectations about person identity modulate the face-sensitive N170. *Cortex* 85, 54–64. <https://doi.org/10.1016/j.cortex.2016.10.002>.
- Joyce, C.A., Kutas, M., 2005. Event-related potential correlates of long-term memory for briefly presented faces. *J. Cognit. Neurosci.* 17 (5), 757–767. <https://doi.org/10.1162/0898929053747603>.
- Kaufmann, J.M., Schweinberger, S.R., Burton, A.M., 2009. N250 ERP correlates of the acquisition of face representations across different images. *J. Cognit. Neurosci.* 21 (4), 625–641. <https://doi.org/10.1162/jocn.2009.21080>.
- Keyes, H., Brady, N., 2010. Self-face recognition is characterized by “bilateral gain” and by faster, more accurate performance which persists when faces are inverted. *Q. J. Exp. Psychol.* 63 (5), 840–847.
- Keyes, H., Brady, N., Reilly, R.B., Foxe, J.J., 2010. My face or yours? Event-related potential correlates of self-face processing. *Brain Cognit.* 72 (2), 244–254. <https://doi.org/10.1016/j.bandc.2009.09.006>.
- Kircher, T.T., Senior, C., Phillips, M.L., Rabe-Hesketh, S., Benson, P.J., Bullmore, E.T., David, A.S., 2001. Recognizing one’s own face. *Cognition* 78 (1), B1–B15. [https://doi.org/10.1016/S0010-0277\(00\)00104-9](https://doi.org/10.1016/S0010-0277(00)00104-9).
- Kircher, T.T.J., Senior, C., Phillips, M.L., Benson, P.J., Bullmore, E.T., Brammer, M., et al., 2000. Towards a functional neuroanatomy of self processing: effects of faces and words. *Cognition Brain Research* 10, 133–144.
- Kosaka, H., Omori, M., Iidaka, T., Murata, T., Shimoyama, T., Okada, T., Sadato, N., Yonekura, Y., Wada, Y., 2003. Neural substrates participating in acquisition of facial familiarity: an fMRI study. *Neuroimage* 20 (3), 1734–1742. [https://doi.org/10.1016/S1053-8119\(03\)00447-6](https://doi.org/10.1016/S1053-8119(03)00447-6).
- Leveroni, C.L., Seidenberg, M., Mayer, A.R., Mead, L.A., Binder, J.R., Rao, S.M., 2000. Neural systems underlying the recognition of familiar and newly learned faces. *J. Neurosci.* 20 (2), 878–886. <https://doi.org/10.1523/JNEUROSCI.20-02-00878.2000>.
- Li, Y.H., 2011. Self-face Recognition: Perceptual Distinctiveness and Functional Significance. University of California, Los Angeles [Unpublished doctoral dissertation].
- Liu-Shuang, J., Norkia, A.M., Rossion, B., 2014. An objective index of individual face discrimination in the right occipito-temporal cortex by means of fast periodic oddball stimulation. *Neuropsychologia* 52, 57–72. <https://doi.org/10.1016/j.neuropsychologia.2013.10.022>.
- Ma, Y., Han, S., 2012. Functional dissociation of the left and right fusiform gyrus in self-face recognition. *Hum. Brain Mapp.* 33 (10), 2255–2267. <https://doi.org/10.1002/hbm.21356>.
- McKeef, T.J., Remus, D.A., Tong, F., 2007. Temporal limitations in object processing across the human ventral visual pathway. *J. Neurophysiol.* 98 (1), 382–393. <https://doi.org/10.1152/jn.00568.2006>.
- Nakamura, K., Kawashima, R., Sato, N., Nakamura, A., Sugiura, M., Kato, T., et al., 2000. Functional delineation of the human occipito-temporal areas related to face and scene processing. A PET study. *Brain* 123, 1903–1912. <https://doi.org/10.1093/brain/123.9.1903>.
- Natu, V.S., O’Toole, A.J., 2015. Spatiotemporal changes in neural response patterns to faces varying in visual familiarity. *Neuroimage* 108, 151–159. <https://doi.org/10.1016/j.neuroimage.2014.12.027>.
- Neumann, M.F., Mohamed, T.N., Schweinberger, S.R., 2011. Face and object encoding under perceptual load: ERP evidence. *Neuroimage* 54 (4), 3021–3027. <https://doi.org/10.1016/j.neuroimage.2010.10.075>.
- Neumann, M.F., Schweinberger, S.R., 2008. N250r and N400 ERP correlates of immediate famous face repetition are independent of perceptual load. *Brain Res.* 1239, 181–190. <https://doi.org/10.1016/j.brainres.2008.08.039>.
- Norkia, A.M., Appelbaum, L.G., Ales, J.M., Cottareau, B.R., Rossion, B., 2015. The steady-state visual evoked potential in vision research: a review. *J. Vis.* 15 (6) <https://doi.org/10.1167/15.6.4>, 4–4.
- Oruc, I., Shafai, F., Murthy, S., Lages, P., Ton, T., 2019. The adult face-diet: a naturalistic observation study. *Vis. Res.* 157, 222–229. <https://doi.org/10.1016/j.visres.2018.01.001>.
- Pfütze, E.M., Sommer, W., Schweinberger, S.R., 2002. Age-related slowing in face and name recognition: evidence from event-related brain potentials. *Psychol. Aging* 17 (1), 140. <https://doi.org/10.1037/0882-7974.17.1.140>.
- Platek, S.M., Keenan, J.P., Gallup Jr., G.G., Mohamed, F.B., 2004. Where am I? The neurological correlates of self and other. *Cognit. Brain Res.* 19 (2), 114–122. <https://doi.org/10.1016/j.cogbrainres.2003.11.014>.
- Platek, S.M., Kemp, S.M., 2009. Is family special to the brain? An event-related fMRI study of familiar, familial, and self-face recognition. *Neuropsychologia* 47 (3), 849–858. <https://doi.org/10.1016/j.neuropsychologia.2008.12.027>.
- Platek, S.M., Loughead, J.W., Gur, R.C., Busch, S., Ruparel, K., Phend, N., Langleben, D.D., 2006. Neural substrates for functionally discriminating self-face from personally familiar faces. *Hum. Brain Mapp.* 27 (2), 91–98. <https://doi.org/10.1002/hbm.20168>.
- Pierce, L.J., Scott, L., Boddington, S., Droucker, D., Curran, T., Tanaka, J., 2011. The n250 brain potential to personally familiar and newly learned faces and objects. *Front. Hum. Neurosci.* 5, 111. <https://doi.org/10.3389/fnhum.2011.00111>.
- Quek, G.L., Rossion, B., 2017. Category-selective human brain processes elicited in fast periodic visual stimulation streams are immune to temporal predictability. *Neuropsychologia* 104, 182–200.
- Ramon, M., 2015. Perception of global facial geometry is modulated through experience. *PeerJ* 3, e850.
- Ramon, M., Caharel, S., Rossion, B., 2011. The speed of recognition of personally familiar faces. *Perception* 40 (4), 437–449. <https://doi.org/10.1068/p6794>.
- Ramon, M., Gobbi, M.I., 2018. Familiarity matters: a review on prioritized processing of personally familiar faces. *Vis. Cognit.* 26 (3), 179–195. <https://doi.org/10.1080/13506285.2017.1405134>.
- Ramon, M., Van Belle, G., 2016. Real-life experience with personally familiar faces enhances discrimination based on global information. *PeerJ* 4, e1465. <https://doi.org/10.7717/peerj.1465>.
- Ramon, M., Vizioli, L., Liu-Shuang, J., Rossion, B., 2015. Neural microgenesis of personally familiar face recognition. *Proc. Natl. Acad. Sci. Unit. States Am.* 112 (35), E4835–E4844.
- Redfern, A.S., Benton, C.P., 2019. Representation of facial identity includes expression variability. *Vis. Res.* 157, 123–131.
- Regan, D., Cartwright, R.F., 1970. A method of measuring the potentials evoked by simultaneous stimulation of different retinal regions. *Electroencephalogr. Clin. Neurophysiol.* 28 (3), 314–319.
- Retter, T.L., Rossion, B., 2016. Uncovering the neural magnitude and spatio-temporal dynamics of natural image categorization in a fast visual stream. *Neuropsychologia* 91, 9–28. <https://doi.org/10.1016/j.neuropsychologia.2016.07.028>.
- Rossion, B., 2014. Understanding individual face discrimination by means of fast periodic visual stimulation. *Exp. Brain Res.* 232 (6), 1599–1621. <https://doi.org/10.1007/s00221-014-3934-9>.
- Rossion, B., Boremanse, A., 2011. Robust sensitivity to facial identity in the right human occipito-temporal cortex as revealed by steady-state visual-evoked potentials. *J. Vis.* 11 (2) <https://doi.org/10.1167/11.2.16>, 16–16.
- Rossion, B., Jacques, C., 2011. The N170: understanding the time-course of face perception in the human brain. *The Oxford Handbook of ERP Components* 115–142.
- Rossion, B., Joyce, C.A., Cottrell, G.W., Tarr, M.J., 2003a. Early lateralization and orientation tuning for face, word, and object processing in the visual cortex. *Neuroimage* 20 (3), 1609–1624. <https://doi.org/10.1016/j.neuroimage.2003.07.010>.
- Rossion, B., Torfs, K., Jacques, C., Liu-Shuang, J., 2015. Fast periodic presentation of natural images reveals a robust face-selective electrophysiological response in the human brain. *J. Vis.* 15 (1) <https://doi.org/10.1167/15.1.18>, 18–18.
- Rossion, B., Schiltz, C., Crommelinck, M., 2003b. The functionally defined right occipital and fusiform “face areas” discriminate novel from visually familiar faces. *Neuroimage* 19 (3), 877–883. [https://doi.org/10.1016/S1053-8119\(03\)00105-8](https://doi.org/10.1016/S1053-8119(03)00105-8).
- Schweinberger, S.R., Burton, A.M., 2003. Covert recognition and the neural system for face processing. *Cortex* 39 (1), 9–30. [https://doi.org/10.1016/S0010-9452\(08\)70071-6](https://doi.org/10.1016/S0010-9452(08)70071-6).
- Schweinberger, S.R., Huddy, V., Burton, A.M., 2004. N250r: a face-selective brain response to stimulus repetitions. *Neuroreport* 15 (9), 1501–1505. <https://doi.org/10.1097/01.wnr.0000131675.00319.42>.
- Schweinberger, S.R., Neumann, M.F., 2016. Repetition effects in human ERPs to faces. *Cortex* 80, 141–153. <https://doi.org/10.1016/j.cortex.2015.11.001>.
- Schweinberger, S.R., Pickering, E.C., Jentzsch, I., Burton, A.M., Kaufmann, J.M., 2002. Event-related brain potential evidence for a response of inferior temporal cortex to familiar face repetitions. *Cognit. Brain Res.* 14 (3), 398–409. [https://doi.org/10.1016/S0926-6410\(02\)00142-8](https://doi.org/10.1016/S0926-6410(02)00142-8).
- Schweinberger, S.R., Pfütze, E.M., Sommer, W., 1995. Repetition priming and associative priming of face recognition: evidence from event-related potentials. *J. Exp. Psychol. Learn. Mem. Cognit.* 21 (3), 722.
- Scott, L.S., Tanaka, J.W., Scheinberg, D.L., Curran, T., 2008. The role of category learning in the acquisition and retention of perceptual expertise: a behavioral and neurophysiological study. *Brain Res.* 1210, 204–215. <https://doi.org/10.1016/j.brainres.2008.02.054>.
- Shah, N.J., Marshall, J.C., Zafiris, O., Schwab, A., Zilles, K., Markowitsch, H.J., Fink, G.R., 2001. The neural correlates of person familiarity: a functional magnetic resonance imaging study with clinical implications. *Brain* 124 (4), 804–815. <https://doi.org/10.1093/brain/124.4.804>.
- Sugiura, M., Kawashima, R., Nakamura, K., Okada, K., Kato, T., Nakamura, A., Fukuda, H., 2000. Passive and active recognition of one’s own face. *Neuroimage* 11 (1), 36–48. <https://doi.org/10.1006/nimg.1999.0519>.

- Sugiura, M., Sassa, Y., Jeong, H., Horie, K., Sato, S., Kawashima, R., 2008. Face-specific and domain-general characteristics of cortical responses during self-recognition. *Neuroimage* 42 (1), 414–422. <https://doi.org/10.1016/j.neuroimage.2008.03.054>.
- Sugiura, M., Watanabe, J., Maeda, Y., Matsue, Y., Fukuda, H., Kawashima, R., 2005. Cortical mechanisms of visual self-recognition. *Neuroimage* 24 (1), 143–149. <https://doi.org/10.1016/j.neuroimage.2004.07.063>.
- Sui, J., Zhu, Y., Han, S., 2006. Self-face recognition in attended and unattended conditions: an event-related brain potential study. *Cognit. Neurosci. Neuropsychol.* 17 (4), 423–427. <https://doi.org/10.1097/01.wnr.0000203357.65190.61>.
- 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. *J. Cognit. Neurosci.* 18 (9), 1488–1497. <https://doi.org/10.1162/jocn.2006.18.9.1488>.
- Taylor, M.J., Arsalidou, M., Bayless, S.J., Evans, J.W., Barbeau, E.J., 2008. Neural correlates of personally familiar faces: Parents, partner and own faces. *Hum. Brain Mapp.* 30 (7), 2008–2020. <https://doi.org/10.1002/hbm.20646>.
- Tong, F., Nakayama, K., 1999. Robust representations for faces: evidence from visual search. *J. Exp. Psychol. Hum. Percept. Perform.* 25 (4), 1016.
- Tononi, G., Srinivasan, R., Russell, D.P., Edelman, G.M., 1998. Investigating neural correlates of conscious perception by frequency-tagged neuromagnetic responses. *Proc. Natl. Acad. Sci. Unit. States Am.* 95 (6), 3198–3203.
- Veale, D., Riley, S., 2001. Mirror, mirror on the wall, who is the ugliest of them all? The psychopathology of mirror gazing in body dysmorphic disorder. *Behav. Res. Ther.* 39 (12), 1381–1393. [https://doi.org/10.1016/S0005-7967\(00\)00102-9](https://doi.org/10.1016/S0005-7967(00)00102-9).
- Vettori, S., Dzhelyova, M., Jacques, C., Rossion, B., 2018. Reduced neural sensitivity for implicit individual face discrimination in autism. *J. Vis.* 18 (10) <https://doi.org/10.1167/18.10.712>.
- Wang, J., Kitayama, S., Han, S., 2011. Sex difference in the processing of task-relevant and task-irrelevant social information: an event-related potential study of familiar face recognition. *Brain Res.* 1408, 41–51. <https://doi.org/10.1016/j.brainres.2011.05.060>.
- Wang, J., Zheng, Y., 2015. The effect of genuine intimacy between lovers on self-face advantage. *Adv. Psychol.* 5 (12), 753–761.
- Watier, N.N., Collin, C.A., 2009. Effects of familiarity on spatial frequency thresholds for face matching. *Perception* 38 (10), 1497–1507.
- Wiese, H., Tüttenberg, S.C., Ingram, B.T., Chan, C.Y., Gurbuz, Z., Burton, A.M., Young, A.W., 2019. A robust neural index of high face familiarity. *Psychol. Sci.* 30 (2), 261–272. <https://doi.org/10.1177/0956797618813572>.
- Wild-Wall, N., Dimigen, O., Sommer, W., 2008. Interaction of facial expressions and familiarity: ERP evidence. *Biol. Psychol.* 77 (2), 138–149. <https://doi.org/10.1016/j.biopsycho.2007.10.001>.
- Xu, B., Liu-Shuang, J., Rossion, B., Tanaka, J., 2017. Individual differences in face identity processing with fast periodic visual stimulation. *J. Cognit. Neurosci.* 29 (8), 1368–1377. https://doi.org/10.1162/jocn_a.01126.
- Zimmermann, F.G., Yan, X., Rossion, B., 2019. An objective, sensitive and ecologically valid neural measure of rapid human individual face recognition. *Royal Society Open Science* 6 (6), 181904. <https://doi.org/10.1098/rsos.181904>.