



Research Report

Superior neural individuation of mother's than stranger's faces by five months of age

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ABSTRACT

Human adults are better at recognizing different views of a given face as belonging to the same person when that person is familiar rather than unfamiliar. To clarify the developmental origin of this well-established phenomenon, one group of five-month-olds ($N = 22$) was presented with pictures of four different unfamiliar female faces at a fixed rate (6 Hz, 166 msec stimulus onset asynchrony), interrupted every 5th stimulus (1.2 Hz) by either their mother's face (mother oddball condition) or, in different stimulation sequences, a stranger's face (stranger oddball condition). In another group of five-month-olds ($N = 17$), stimulation sequences were reversed such that their mothers' or a given stranger's face were repeated at 6 Hz and interrupted every 5 stimuli by pictures of different female faces (mother standard, stranger standard conditions, respectively). Twelve variable images of each identity served as stimulus material. Besides clear frequency-tagged EEG responses at the 6 Hz stimulation rate over the medial occipital region in all conditions, significant activity at 1.2 Hz and harmonics (2.4 Hz, etc.) was observed in this region, reflecting selective responses to facial identity across changes of views. This effect was strongest when the mother's face was immediately repeated at every stimulation cycle (mother standard). Overall, these observations point to an early developmental advantage of identifying a familiar face presented from different views during immediate stimulus repetition.

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Recognizing people based on their faces (Face Identity Recognition, FIR) is extremely important for social interactions. Despite the complexity of FIR, neurotypical human adults are able to recognize the identity of thousands of faces

on average (Jenkins, Dowsett, & Burton, 2018), rapidly (i.e., at a glance, and within a few hundreds of milliseconds of processing; Hsiao & Cottrell, 2008; Jacques, d'Arripe, & Rossion, 2007; Visconti di Oleggio Castello & Gobbini, 2015) and

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largely automatically (i.e., not under volitional control; Yan, Young, & Andrews, 2017; Zimmermann, Yan, & Rossion, 2019).

Extensive research carried out over the past decades has shown that matching familiar (i.e., faces that have been encoded in long-term memory) faces for their identity across changes of views is much easier than matching pictures of unfamiliar faces. This familiarity effect of FIR has initially been found in old/new recognition tasks (Bruce, 1982), and subsequently using face identity matching tasks across a brief delay or even during simultaneous presentation (e.g., Bruce et al., 1999; Jenkins, White, Van Montfort, & Mike Burton, 2011; Megreya & Burton, 2006).

The FIR advantage for familiar over unfamiliar faces is well established, but its source is unknown and controversial. On the one hand, it has been attributed to high-level visual processes, which would be recruited more – or even only – for familiar faces (Hancock, Bruce, & Burton, 2000; Young & Burton, 2018). On the other hand, this face familiarity effect could be due to the association of common semantic, affective or lexical (i.e., labels) representations for different views of familiar faces rather than to perceptual processes involved in comparing visual representations extracted from these faces (Dixon, Bub, & Arguin, 1998; Rossion, 2018; Schwartz & Yovel, 2016, 2019). In order to better understand the origins of the familiar face advantage in FIR, it may be useful to study its emergence early in ontogeny. During the first year of life, the number of familiar faces is usually quite limited, and the primary caregiver provides a clear example of a highly familiar face. The present study thus investigates familiar and unfamiliar FIR by recording implicit electrophysiological measures to various photographs of a highly familiar (i.e., mother) and an unfamiliar female face in five-month-old infants.

Although the development of the FIR familiar face advantage has not been tested previously, several behavioral and electroencephalographic (EEG) studies have addressed infant recognition of mother's and stranger's faces. Newborn infants prefer their mother over an unfamiliar face when they associate her face with her voice (Coulon, Guellai, & Streri, 2011; Sai, 2005). By six months, electrophysiological responses discriminate the mother's from a stranger female's face (de Haan & Nelson, 1997; Mash, Bornstein, & Arterberry, 2013). Following familiarization, newborns also recognize unfamiliar faces across changes in head orientation or based only on inner/outer facial parts (Turati, Bulf, & Simion, 2008; Turati, Macchi Cassia, Simion, & Leo, 2006). At one month, infants recognize up to four unfamiliar faces and, at three months, they are able to form an average representation of these four faces (de Haan, Johnson, Maurer, & Perrett, 2001). Event-related potential (ERP) repetition effects for repeated identities of unfamiliar faces have been reported at 9 months of age (Peykarjou, Pauen, & Hoehl, 2016). Together, these studies provide evidence that infants less than six months of age are able to discriminate their mother from other faces and to visually recognize single unfamiliar faces.

However, the studies described so far (1) use only 1–2 different images per identity (2) present each image for a relatively long time (e.g., 5–30 s), if they refer to looking times as dependent measure, and (3) rarely control for low-level physical differences between the familiarization and the test

stimuli. Accordingly, they cannot fully evaluate expertise at FIR, a function performed automatically and at a glance in neurotypical adults (Rossion, 2018), and ensure that performance is based on high-level perceptual processes (see Mash et al., 2013, for a demonstration of infant face individuation while controlling for light intensity and spectral power). In electrophysiological studies, faces were presented for at least 500 msec and with long interstimulus intervals, which allows participants to perform multiple fixations on the stimuli and makes it difficult to disentangle the cognitive processes contributing to FIR. Hence, EEG studies presenting individual faces only very briefly, keeping inter-stimulus intervals very short, and showing generalization across low-level physical features of faces presented provide an important extension to this field.

More fundamentally, to our knowledge, studies comparing individuation of familiar and unfamiliar faces across variable views in infancy are lacking. While several ERP (ERP; de Haan & Nelson, 1997; Key, Stone, & Williams, 2009; Swingler, Sweet, & Carver, 2010) and behavioral (e.g., Barrera & Maurer, 1981; Sai, 2005) studies presented both mothers and strangers' faces, they used only one image per identity, and did not test discrimination of these identities from other faces.

In sum, infant studies comparing individuation of familiar and unfamiliar faces by using different views of the same face, short presentation times, and stimuli controlled for low-level physical differences per face category are still lacking. To overcome these limitations, we adapted a Fast Periodic Visual Stimulation (FPVS) oddball design (Liu-Shuang, Norcia, & Rossion, 2014) that has been applied successfully in research on adult face individuation (Damon, Leleu, Rekow, Poncet, & Baudouin, 2020; Zimmermann et al., 2019; for review, see Rossion, Retter, & Liu-Shuang, 2020), and on face categorization in infants (de Heering & Rossion, 2015; Leleu et al., 2020; Peykarjou, Hoehl, Pauen, & Rossion, 2017) to examine FIR in infants.

FPVS is based on the brain's periodic response to periodically presented stimuli (Adrian & Matthews, 1934; Regan, 1966; see Norcia, Appelbaum, Ales, Cottareau, & Rossion, 2015, for review). In the specific design used here, images are presented at a fixed rate (e.g., 6 images per second, 6 Hz), with periodical changes of identity introduced at every 5th position (corresponding to 1.2 Hz). Only if participants (implicitly) detect the identity change introduced periodically, an individuation response at 1.2 Hz and specific harmonics (2.4 Hz, 3.6 Hz, etc.) is elicited in the EEG spectrum. Using this approach, clear frequency-tagged individuation responses have been demonstrated in adult participants for unfamiliar (Liu-Shuang et al., 2014), experimentally familiarized (Verosky, Zoner, Marble, Sammon, & Babarinsa, 2020), famous (Zimmermann et al., 2019), and personally familiar (Campbell, Louw, Michniak, & Tanaka, 2020) faces. This EEG response is a valid marker of FIR (Rossion et al., 2020), objective (i.e., frequency of the expected response pre-determined by the experimenter) and highly reliable even across sessions (Dzhelyova et al., 2019). Since it is largely reduced for inverted faces (Damon et al., 2020; Rossion et al., 2020) and modulated by familiarity with the face category (Campbell et al., 2020; Damon et al., 2020; Verosky et al., 2020), it appears to reflect high-level processes.

In previous studies exploring the effects of familiarity on FPVS face individuation responses, three important aspects have been mixed: the number of different images per target identity, the level of familiarity, and the assignment of target faces to oddball or standard positions. Zimmermann et al. (2019) and Yan, Zimmermann, and Rossion (2020) employed large numbers of images from celebrities, which were presented as oddballs among foreign celebrities unknown to the participants. In contrast, Verosky et al. (2020) experimentally familiarized participants with single images of face targets, which were subsequently employed as standard and oddball images (all images within one sequence equally familiar). Campbell et al. (2020) employed 12 different images of personally familiar faces as oddballs among unfamiliar faces. In all these approaches, strong individuation responses were observed over the right occipito-temporal region of interest (ROI), although the response for familiarized faces was slightly more medial (Verosky et al., 2020). However, it remains an empirical question if and how variations of the design interact with the face individuation response to differentially familiar faces. It can be expected that the oddball is more salient when the same face is presented repeatedly as standard, since the high homogeneity between faces presented at every cycle may lead to stronger individuation responses (Peykarjou et al., 2017; Rossion et al., 2020). In turn, face identity changing at every cycle increases visual heterogeneity and can be expected to increase the base rate response.

Regarding infant face individuation responses, Rossion et al. (2020) mention that 4- to 6-month-old infants did not show successful individuation of cropped unfamiliar faces without external features (i.e., faces without hair/hairline). Whether this result can be attributed to unfamiliarity of the stimuli or other task characteristics remains to be clarified. Another recent study (Barry-Anwar, Hadley, Conte, Keil, & Scott, 2018) found individuation of monkey faces in 6- and 9-month-old infants, but used only one image per identity. Thus, it cannot be excluded that identity-irrelevant aspects such as slight variations in head orientation contributed to this effect (see Rossion et al., 2020). Both previous infant FPVS studies used one face as standard stimulus, with identity changes introduced at every 5th position. The reverse condition (i.e., target face as oddball) was not included.

In the current study, we tested five-month-old infants' ability to individuate mothers' and strangers' faces. Five months were selected as target group because neurophysiological evidence for face recognition has been found at a similar age (de Haan et al., 2001; de Haan & Nelson, 1997). While face recognition has also been reported in younger infants (e.g., Sai, 2005; Turati et al., 2006), these studies employed looking time measures and long presentation times, leaving open the question whether high-level face individuation at a glance can be expected so early. However, even at five months of age, it seems doubtful whether infants are able to individuate unfamiliar faces in an FPVS paradigm. The complexity and difficulty of this approach is much higher than previous studies reporting successful FIR in infancy (de Haan & Nelson, 1997; Rubenstein, Kalakanis, & Langlois, 1999; Sai, 2005), requiring infants to process faces quickly, discriminating the target face from four unfamiliar strangers and generalizing across 12 instances of the target face.

Therefore, individuation is expected to require long-term familiarity with the face and to arise only in the mother's condition.

We employed a mixed design with target identity (mother, familiarized stranger) varying within-subjects, and target position (oddball, standard) varying between-subjects (Fig. 1). Accordingly, in one group of infants, we tested an "oddball" condition where face identity was repeated periodically at every fifth image position. Hence, the target face was presented only rarely (i.e., 20% of images) and the variation of face identity per cycle was high. In another group of infants, we tested a "standard" condition where face identity was repeated at every cycle, with identity changes at oddball positions. Here, the target face was presented often (i.e., 80% of images), and variation of face identity per cycle was lower (every fifth image). In each condition, target identity (mother/familiarized stranger) was varied within-subjects. Before the start of the FPVS presentation of each block, the target face was displayed for 30 s to briefly familiarize the infant with a given face identity. This was done to increase similarity of the present procedure to behavioral work which has demonstrated individuation of unfamiliar faces following a familiarization phase (de Haan et al., 2001; Rubenstein et al., 1999).

All faces were represented by 12 different images, which were created in a standardized fashion, varying in expression (neutral, slight smile, broad smile) and head orientation (0°, 15° right, 15° left). This high amount of within-face variability was employed to diminish the influence of low-level image characteristics on oddball EEG responses.

Based on previous findings, we tested the following hypotheses: (1) The degree of familiarity with the face influences the magnitude of the individuation response. Significant individuation responses are expected only for the mother, but not the familiarized stranger. (2) When the same face is presented repeatedly as standard, due to the high homogeneity between faces presented at every cycle, the oddball is more salient, which should lead to stronger individuation responses (Peykarjou et al., 2017; Rossion et al., 2020). (3) When face identity is repeated at oddball positions, a stronger base rate response is expected because the increased heterogeneity at every stimulation cycle enhances neural responses. (4) With regard to the familiarization phase, we cannot make specific predictions. On the one hand, one could expect infants to look longer at the mothers' face because it is associated with semantic knowledge, including olfactory and auditory information (Leleu et al., 2020; Sai, 2005). On the other hand, one could argue that the stranger's face is more novel and should thus elicit more attention (Fantz, 1964; Mather, 2013). Both effects could also overlap, thus counterbalancing looking times across conditions.

1. Material and methods

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

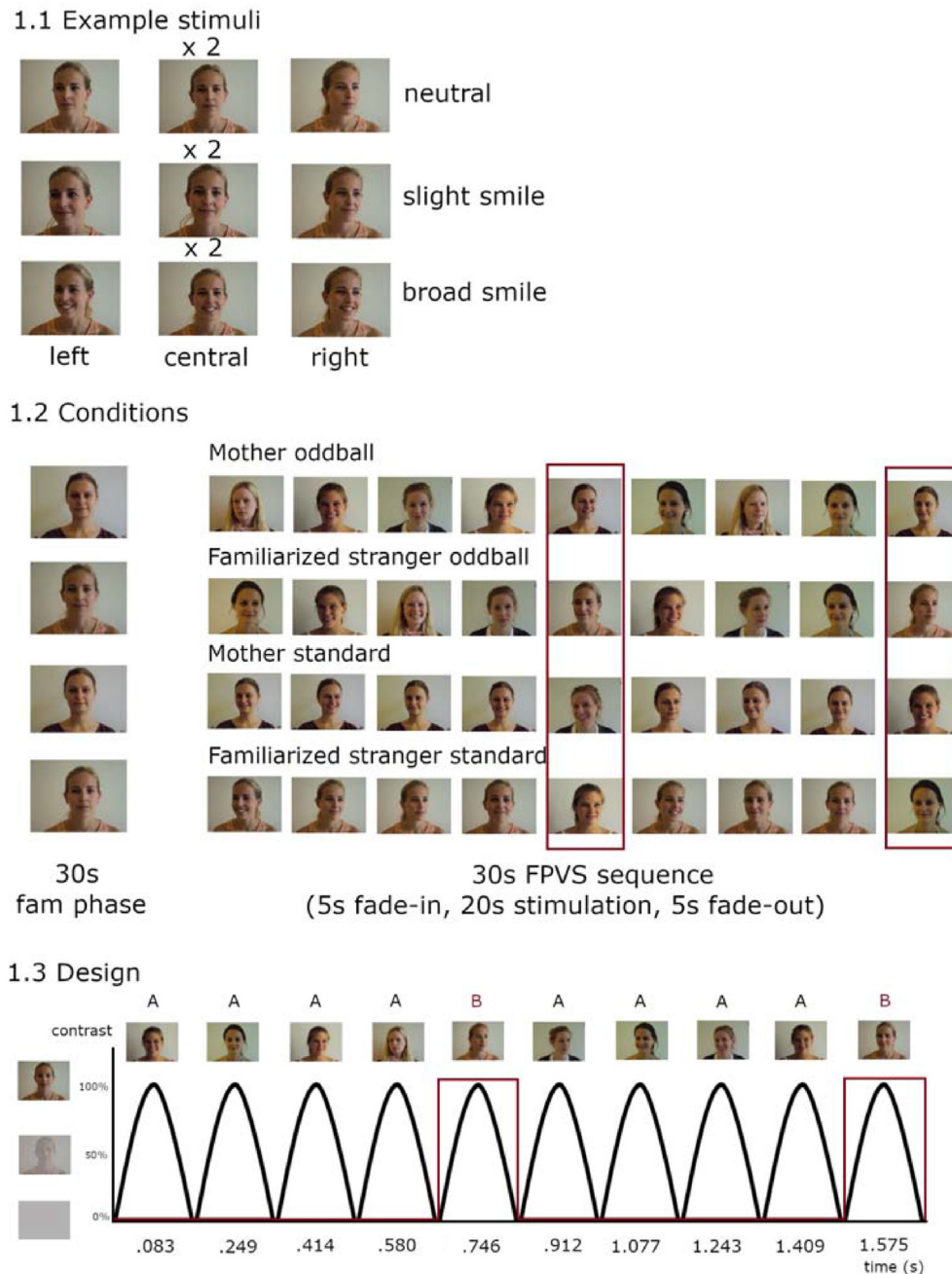


Fig. 1 – Stimuli and design. 1.1 12 images of each face were employed, systematically varied across orientations (central, 15° left, 15° right) and expressions (neutral, slight smile, broad smile). 1.2 Trial structure and conditions. Each trial consisted of a 30 sec familiarization phase and a 30 sec FPVS sequence. One additional frontal neutral image was presented during the 30 sec familiarization phase. During the 30 sec FPVS sequences (5 sec fade-in, 20 sec stimulation, 5 sec fade-out), target identity (mother/familiarized stranger) was varied within-subjects, and condition (target oddball/target standard) was varied between-subjects. 1.3 Paradigm of FPVS sequences. Images were presented by sinusoidal contrast modulation at a rate of 6 cycles per second, corresponding to 6 Hz (1 cycle \approx 170 msec). Identity changes were introduced periodically at every fifth position (6 Hz/5 = 1.2 Hz). Exemplary stimuli shown as we do not have permission to publish all face identities.

1.1. Participants

The final sample consisted of $N = 39$ subjects (18 female) with an average age of five months and seventeen days (age range 5 months, 0 days–5 months, 30 days, $SD = 8$ days). Twenty-two

infants were tested with targets as oddballs, 17 with targets as standards. All infants were born full-term (>37 weeks of gestation) and there was no record of neurological or visual problems. An additional 19 infants were tested but not included in the final analyses due to fussiness ($N = 15$) or bad

data ($N = 4$). Sample size was determined based on previous FPVS studies (de Heering & Rossion, 2015; Leleu et al., 2020; Peykarjou et al., 2017). Recruitment took place in local birth clinics of Heidelberg, a medium-sized German University town. Families visiting the lab were dominantly Caucasian and came from a mixed socio-economic, but mostly higher educational background. In accordance with the terms provided by the local ethics committee of Heidelberg University that approved the general procedure, informed consent was obtained from caretakers prior to the experiment. No part of the study procedures or analyses was preregistered prior to the research being conducted.

1.2. Stimuli

The entire stimulus set consisted of eight different unfamiliar strangers (four in the familiar, four in the unfamiliar face condition, varied within-subjects), two familiarized strangers (varied between-subjects), and thirty-nine mothers (varied between-subjects). In each FPVS sequence, five face identities (4 unfamiliar strangers, 1 target face, i.e., mother or familiarized stranger) were employed, each represented by 12 different images (see Fig. 1 for stimuli and conditions). In the target oddball condition, each face appeared equally often during each sequence (on average 24 times per sequence). Thus, the only difference between unfamiliar strangers and target faces (mother/familiarized stranger) was the fixed order of target faces (every 5th image). When targets were presented as standards, they appeared 80% of the time. Face orientation and expression were varied systematically, with the following specifications: left, central and right orientation (left and right turned by approx. 15°), neutral, slight and broad smile (see Fig. 1 for an example of images used for one identity). For the central orientation, two pictures were taken of each facial expression. For target faces (mother's face, familiarized stranger's face), one additional central neutral image was used during the familiarization phase.

Pictures of the mother's face were obtained when participants visited the lab, preprocessed to match the other images in low-level properties, and inserted into the presentation. All other images were prepared prior to the experiment. All images were taken in a standardized setup and equalized for luminance and contrast within each condition (i.e., all images presented within one sequence were equalized). The same stranger identities were employed across participants, but the identity of unfamiliar strangers differed between mother and familiarized stranger conditions so that infants did not acquire differential familiarity with the faces in successive trials. Exemplary stimuli are shown in the Figures as the conditions of our ethics approval do not permit publication of all images. Stimuli that can be shared can be found on OSF (<https://osf.io/t6q4e/>). For all other stimuli, there is no permission to share them even on request.

1.3. General experimental setting

Participants were invited into a dimly lit and quiet room. Following preparation for EEG recordings, infants were placed on their caregivers' lap in front of a computer monitor (looking distance of approx. 80 cm). Parents were asked not to interact

with their infant during data collection. Infant behavior was recorded on video and brain responses were registered using a BrainProducts actiCap (Gilching, Germany).

1.3.1. General stimulation

The FPVS task was similar to previous studies employing this technique and was implemented using Java (Dzhelyova & Rossion, 2014; Liu-Shuang et al., 2014). Multiple trials (maximum: 12) were presented, each lasting approximately 65 s. Each trial was initiated manually when participants looked attentively at the screen and showed an artefact-free EEG signal and consisted of a familiarization phase during which one frontal-neutral image of this trials' target face was presented (30 s) and then an FPVS flicker sequence with the same identity inserted as target (30 s). The familiarization phase was included to enhance similarity of this procedure to prior studies reporting individuation of strangers in familiarization-preference-for-novelty-tasks (e.g., Pascalis, de Haan, & Nelson, 2002). At the onset of the familiarization, a doorbell-sound was presented to attract infants' attention to the screen, and the target face was presented statically for 30 s.

1.3.2. FPVS sequences

The FPVS sequence started with a uniform gray background (random duration, 5–6 sec), followed by a 5-s fade-in (contrast of images against the background increasing from 0% to 100%), a stimulation sequence of 20 s, and a fade-out of 5 s (30 s total). Fade-in and fade-out phases were introduced to avoid surprise reactions, abrupt eye-movements or blinks.

The complete image set was presented in a random order (first block) before the set was repeated in a second block. Images in each sequence were presented in semi-randomized blocks (randomization ensured that the first image of a block could not be the same as the last image of the previous block). Pixel size of individual images was 779 (width) \times 775 (height), corresponding to approximately 16×16 degrees of visual angle on average. Images changed size ($\pm 5\%$) at every stimulation cycle (maximum/minimum: 90/110%). Triggers were sent via parallel port at the start of each sequence and for each image at onset point (0% contrast).

Images were presented at 6 Hz. At fixed intervals of every fifth image, identity changes were introduced (1.2 Hz; 6 Hz/5). Target faces (i.e., the faces participants were familiarized with prior to the FPVS sequence) varied according to target identity and position. Target identity could either be the mother or a familiarized stranger, varied within-subject. Targets were presented as standard for one part of the sample (s = unfamiliar stranger; t = target: $ttttttttstttts$) and as oddball for the other part of the sample ($ssstssstssstssst...$). Thus, there were four conditions overall: mother standard, familiarized stranger standard, mother oddball, and familiarized stranger oddball. EEG amplitude at the frequency of identity change ($F/5 = 1.2$ Hz) and its harmonics (i.e., $2F/5 = 2.4$ Hz, $3F/5 = 3.6$ Hz...) was used as an index of individuation (Liu-Shuang et al., 2014; Rossion et al., 2020). Each participant took part in two identity conditions, mother target and familiarized stranger target, with target position (standard/oddball) varied between-subjects. Each identity condition was presented in two consecutive trials, and the order of

conditions was semi-randomized between-subjects. Between trials, short breaks were provided if needed. Testing ended when infants became inattentive or fussy and attention could not be redirected to the stimulation. On average, the experiment took about 8 min (including breaks).

1.4. Analysis of looking time during the familiarization phase

Looking duration during the 30 s familiarization phase prior to each FPVS sequence was hand-coded by student assistants to estimate general attention in the different conditions. For this analysis, videos of $N = 49$ participants (25 female) could be included (comprising all participants who provided at least one valid familiarization phase per condition). When infants' looking behavior was not captured on video (e.g., due to movement), data were discarded. 16 videos (33%) were double-coded and provided evidence for a high reliability of coding looking behavior, Cronbach's $\alpha = .961$. Looking time across conditions was compared in a 2 (condition: target oddball, target standard) by 2 (target identity: mother, familiarized stranger) repeated measurements analysis of variance (rmANOVA).

1.5. EEG recordings and analyses

EEG measures were obtained applying a BrainProducts acti-Cap (Gilching, Germany) with 32 active Ag–AgCl electrodes arranged according to the 10–10-system and a right mastoid reference. Sampling rate was set at 250 Hz and the EEG signal was amplified via a BrainAmp amplifier with an input impedance of 10 M Ω and a resolution of .1 μ V per bit. Impedances were considered acceptable if < 20 k Ω .

All EEG processing steps were carried out using Letswave 6 (<http://nocions.webnode.com/letswave>) and Matlab 2012b (The Mathworks) and followed the procedure described previously (e.g., Retter & Rossion, 2016). EEG data was analyzed only for the FPVS sequences. First, data was band-pass filtered at .1–100 Hz using a 4th order Butterworth filter. Filtered data was then segmented 2 s before and after the FPVS sequence, resulting in 32-s segments (–2 sec–32 sec). Next, noisy channels were identified based on visual inspection and the following criteria: 1. Very high amplitudes, 2. Amplitude jumps, 3. Dead channels, 4. Bridged channels. Visual inspection was performed blind to experimental condition. Noisy channels were pooled from 3 to 4 surrounding channels (for a maximum of 3 channels) for each sequence and a common average reference computation was applied to all channels. Sequences with more than 3 bad channels were discarded. Due to noise typical for infant recordings, an average of 1.05 channels ($SD = 1.0$) had to be interpolated per sequence.

Preprocessed data segments were cropped to an integer number of 6 Hz cycles beginning 5 s after onset of the sequence (after fade-in) until 20 s, just before the stimulus fade-out (120 cycles, 5,000 time bins in total = 20 sec). Sequences were averaged in the time-domain for every individual participant. Averaging was performed to increase the signal-to-noise ratio (SNR) by reducing EEG activity non-phase-locked to the stimulus. Then a discrete Fourier Transformation (DFT) was performed via a fast Fourier

Transformation (FFT) algorithm with a Hanning window (over amplitude, providing only the first half of the spectrum and normalizing amplitude). The FFT was applied to these averaged segments to extract amplitude spectra for all channels (square root of sum of squares of the real and imaginary parts divided by the number of data points). Frequency analysis yielded spectra with a high frequency resolution of .05 Hz (1/20 sec).

Channel selection was based on prior work (ERPs: Parise, Handl, & Striano, 2010; Scott & Monesson, 2010; FPVS: Barry-Anwar et al., 2018; Peykarjou et al., 2017), and on visual inspection of grand-averages. For the individuation response, all channels where a significant response was obtained in at least one condition were considered. For the base response, the analysis was focused on its maximum in the occipital area, as this provided primarily a control analysis. The following electrodes were selected for analysis: PO9, PO10, O1, O2, Oz, Iz for the individuation response, O1, O2, Oz for the base response. To measure the magnitude of activity at pre-defined bins of interest, baseline corrected amplitudes were computed by subtracting the average amplitude of 12 surrounding bins (6 on each side, excluding the immediately adjacent bins) from every frequency bin (Peykarjou et al., 2017). SNR spectra were computed by dividing the signal by the amplitude at the 12 neighboring frequency bins and used to display response patterns. In accordance with previous studies, Z-scores were calculated to identify significant harmonics (difference between amplitude at the frequency of interest and mean amplitude of 12 surrounding bins divided by the standard deviation of the 12 surrounding bins). SNR at the base frequency and/or its second harmonic (i.e., 6 and/or 12 Hz) was used as criterion for looking at the screen, and only sequences with an $SNR > 2$ were included, as typical in infant FPVS studies (de Heering & Rossion, 2015; Peykarjou et al., 2017). Overall, 3.02 ($SD = 1.0$) sequences were presented on average, and a mean of 2.50 ($SD = 1.1$) sequences remained after pre-processing for analysis (mother standard: $M = 2.28$, $SD = 1.0$, mother oddball: $M = 2.40$, $SD = .8$, familiarized stranger standard: $M = 2.44$, $SD = 1.2$, familiarized stranger oddball: $M = 3.00$, $SD = 1.2$, no differences between numbers of sequences across conditions, $P > .05$).

To define the range of harmonics for quantification of the response, we first identified all harmonics above noise level at a $P < .05$ (uncorrected) threshold on any posterior (O1, O2, Oz, PO9, PO10, Iz) channel for any of the 4 conditions (Fig. 2). Oddball harmonics 1–9 reached significance and were summed for additional statistical analysis. Responses at the base frequency were significant and summed from 1st to 6th harmonic. This liberal selection of harmonics (i.e., $P < .05$ uncorrected for multiple comparisons) is justified for quantification of the EEG response because missing genuine responses could bias the comparison across conditions, while including a non-significant harmonic response in the quantification is generally not detrimental (i.e., if signal = noise level, it corresponds to adding a zero value to the quantification; Rossion et al., 2020).

Responses were compared across conditions using rmANOVAs for condition (2: target oddball, target standard), target identity (2: mother, familiarized stranger), and electrode. Separate analyses were conducted for the oddball response

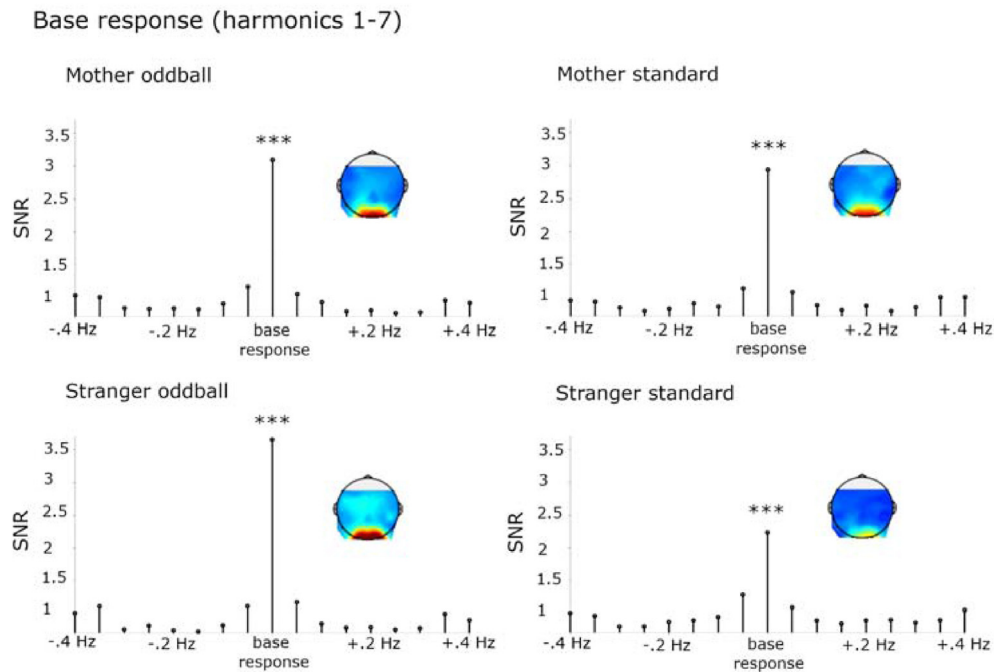


Fig. 2 – Signal-to-noise ratio (SNR) responses across the EEG spectrum. Data has been averaged across posterior electrodes (PO9, PO10, O1, O2, Oz, Iz) and grand-averaged across participants for display. Significant harmonics are marked by * $P < .05$, ** $P < .01$, *** $P < .001$.

across harmonics 1–9 and 2–9 (PO9, PO10, O1, O2, Oz, Iz) and for the base response (O1, O2, Oz). If applicable, Greenhouse–Geisser and Bonferroni corrections were employed.

2. Results

2.1. Looking time during the familiarization phase

There was no difference in mean looking time to the familiarization stimulus between mother's ($M = 18.12$, $SD = 5.9$) and stranger's ($M = 18.72$, $SD = 6.1$) face, $P > .3$. Moreover, looking times did not differ between conditions (target oddball: $M = 18.98$, $SD = 6.2$, target stranger: $M = 17.50$, $SD = 5.6$), $P > .4$.

2.2. Base rate response

Large responses at the base stimulation frequency and its harmonics were observed in all conditions over the medial occipital cortex (see Fig. 5 and Table 1 for illustration of responses across conditions and analyses). Responses were stronger in the mother standard compared to the stranger standard condition, as confirmed by a condition by target identity interaction, $F(1,38) = 4.187$, $P < .05$, $\eta^2 = .013$, followed by a marginal main effect of target identity in the standard condition, $F(1,16) = 3.438$, $P = .081$, $\eta^2 = .061$. In addition, there was a main effect of electrode, $F(2,78) = 4.596$, $P < .05$, $\eta^2 = .025$. Post-hoc tests indicated stronger responses at Oz ($M = 2.07$, $SD = 1.2$) compared to O1 ($M = 1.61$, $SD = 1.2$), $t = -2.987$, $P < .05$. Amplitude at O2 did not differ significantly from the other electrodes (O2 $M = 1.91$, $SD = 1.1$).

2.3. Individuation response

Visually, there were clear responses at 1.2 Hz and harmonics, especially at medial posterior occipital channels, and particularly in the mother standard condition (Fig. 2). In this condition, a very clear response was obtained, with 1.2 Hz and 5 harmonics reaching significance ($P < .05$). In the other conditions, weaker responses were observed, with a particularly low signal in the mother oddball condition. 1.2 Hz failed to reach significance in either of these conditions, but a significant response was obtained in all of them in higher harmonics (mother oddball: 1 harmonic; familiarized stranger standard: 2 harmonics; familiarized stranger oddball: 3 harmonics).

2.3.1. Individuation response summed across harmonics 1–9
In the signal summed across all successively significant harmonics, a strong individuation response was observed only when mother's faces were presented as standards (see Table 1 and Fig. 3). Conversely, the ANOVA revealed a main effect of target identity (mother > familiarized stranger), $F(1,38) = 4.399$, $P < .05$, $\eta^2 = .019$, qualified by a target identity by condition interaction, $F(1,38) = 11.654$, $P < .01$, $\eta^2 = .035$. Looking at the two conditions separately confirmed that the response was increased for mothers compared to familiarized strangers only when targets were presented as standards, $F(1,17) = 11.337$, $P < .01$, $\eta^2 = .135$. When targets were presented as oddballs, no significant difference was observed. No other main effects or interactions were observed.

2.3.2. Individuation response summed across harmonics 2–9
Whereas single harmonics reached significance in all conditions (Fig. 2), this signal was lost in the analysis summed

Table 1 – Baseline corrected amplitude (bca) means and standard deviations (SD), Z-score and signal-to-noise ratio (SNR) ranges for individuation and base rate responses averaged across electrodes (O1, O2, Oz, PO9, PO10, Iz). Bca values represent grand-averages, and Z-scores and SNR ranges represent individual averages. Z-score: values in parenthesis indicate the percentage of participants with a significant ($Z > 1.64$) response.

Response	Target	Condition	Bca mean	Bca SD	Z-score range	SNR range
Individuation response harmonics 1–9	Mother	Target odd	–.08	1.88	–1.40 to 2.35 (9%)	.72–1.36
		Target standard	1.82	2.32	–.36 to 8.30 (65%)	.92–1.98
	Familiarized stranger	Target odd	.32	1.62	–.82 to 2.28 (5%)	.84–1.56
		Target standard	.15	3.00	–1.05 to 5.94 (18%)	.69–1.71
Individuation response harmonics 2–9	Mother	Target odd	.11	.86	–2.53 to 1.67 (5%)	.80–1.27
		Target standard	.76	1.40	–1.2 to 5.55 (59%)	.79–1.88
	Familiarized stranger	Target odd	.43	.91	–.53 to 4.08 (28%)	.94–1.76
		Target standard	.50	1.21	–.41 to 9.79 (24%)	–.95 to 1.97
Base response harmonics 1–6	Mother	Target odd	2.06	1.19	2.77–32.15 (100%)	1.47–7.95
		Target standard	1.78	1.26	2.12–38.43 (100%)	1.21–5.61
	Familiarized stranger	Target odd	2.16	1.18	1.97–37.93 (100%)	1.37–8.84
		Target standard	1.36	.94	1.68–32.99 (100%)	1.26–5.07

Signal-to-noise ratio (SNR)

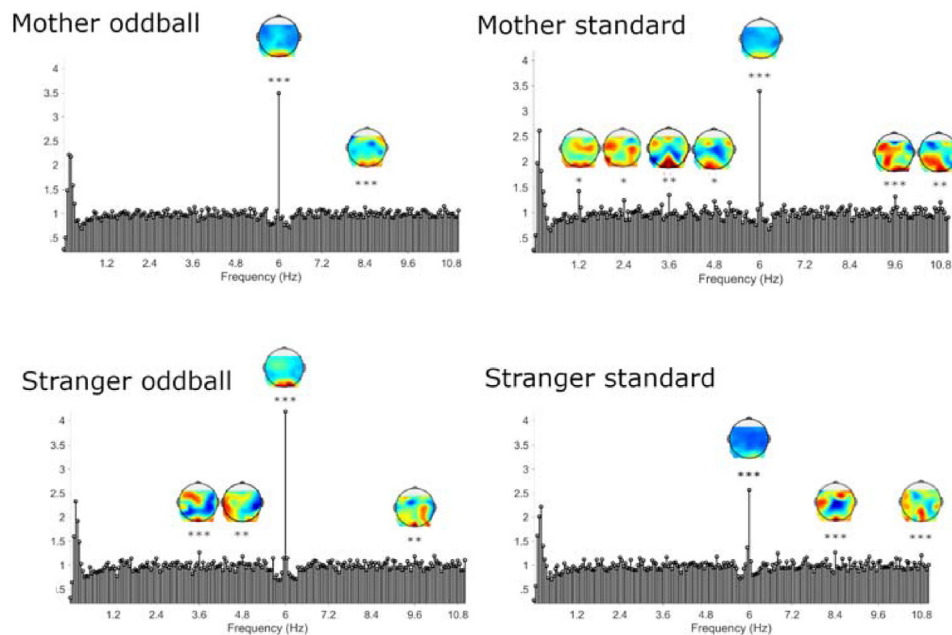


Fig. 3 – SNR spectra of individuation response summed across harmonics 1–9. Data has been averaged across electrodes (PO9, PO10, O1, O2, Oz, Iz) and grand-averaged across participants for display. A significant individuation response was observed only in the mother standard condition, $P < .01$.**

across harmonics 1–9 in three conditions. This seems to be due to a disproportionate noise contamination in the first harmonic (i.e., at a low EEG frequency), which may have masked genuine individuation responses in the weaker conditions (see [Supplemental Fig. S1](#); 1.2 Hz not significant except for the mother standard condition). Thus, to provide a balanced view of the data, we ran additional analyses excluding the first harmonic, i.e., summing harmonics 2–9. Here, a significant individuation response was observed in all conditions except for mother target oddball ([Fig. 4](#)), showing that infants individuated faces not only in the mother

standard condition, but also in conditions where the familiarized stranger served as target.

3. Discussion

The current study indicates that five-month-old infants individuate faces, especially when the face identity is highly familiar (i.e., their mother's face) and appears at every stimulation cycle. To our knowledge, this is the first study reporting a proficient human FIR in the first year of life across

Individuation response (harmonics 1-9)

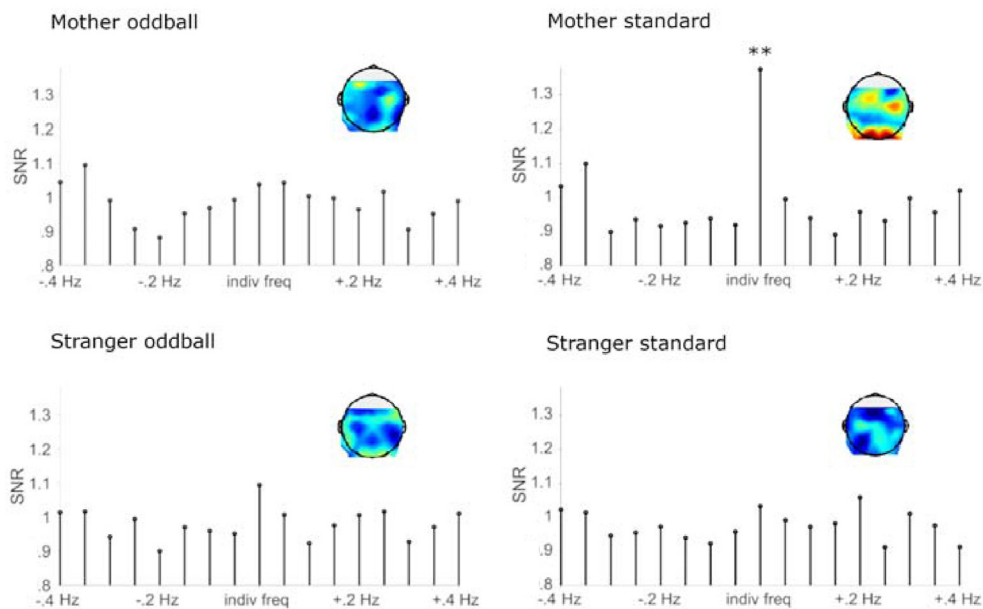


Fig. 4 – SNR of individuation response summed across harmonics 2–9. Data has been averaged across electrodes (PO9, PO10, O1, O2, Oz, Iz) and grand-averaged across participants for display. When the first harmonic was not considered in the analysis, a significant individuation response was observed again in the mother standard condition, $**P < .01$, but also in the familiarized stranger standard and familiarized stranger oddball conditions, $*P < .05$.

Individuation response (harmonics 2-9)

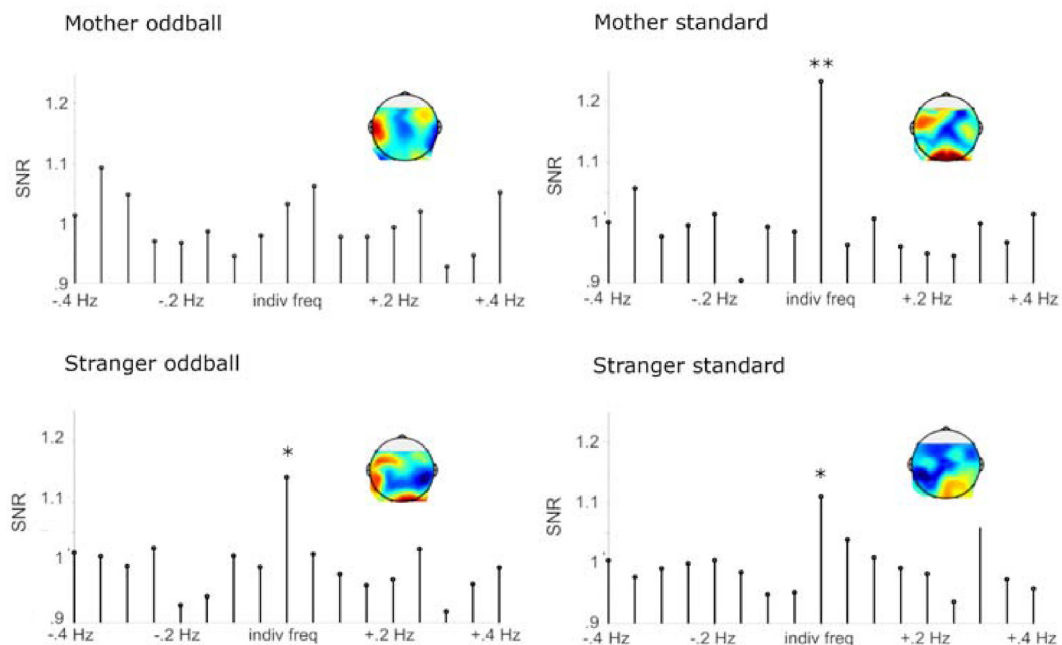


Fig. 5 – SNR of base response summed across harmonics 1–6. Data has been averaged across electrodes (O1, O2, Oz) and grand-averaged across participants for display. A highly significant base response was observed in all conditions, $***P < .001$.

head orientations and facial expressions at a high speed of presentation (i.e., one fixation/face).

When the mother's face was presented as standard, a strong response to periodically presented stranger oddballs

was observed. This finding could be either due to strong visual adaptation for the mothers' face and release from adaptation for the unfamiliar face oddball stimuli appearing at 1.2 Hz. Alternatively, this response could be due to a systematically

elevated response to the mother's face and a periodic decrease in response amplitude when strangers' faces appear.

Indeed, in the main analysis, an individuation response was observed only in the mother standard condition. This proficient FIR may be attributed to infants' familiarity with their mother's face, but specifics of stimuli and design may also have contributed to this finding. Substantial efforts were made to decrease low-level image contributions to individuation by standardizing the photo setup, equalizing brightness and contrast for each image set, and employing a large number of different images. However, due to the challenge of preparing stimuli with participants being present, uncropped images including external features of the face and the upper body until the neckline were employed. Indeed, several studies report an outer face processing advantage in infancy (Bartrip, Morton, & De Schonen, 2001; Turati et al., 2006). While these cues may certainly contribute to the individuation response, they cannot explain the advantage for mother face standards observed here, in particular when comparing to the stranger's face condition (Figs. 2 and 3).

The FIR for mother standards likely reflects infants' prior experience and more proficient representation of the mother's face, and a potential precursor of the FIR advantage for familiar over unfamiliar faces (Bruce, 1982; Jenkins & Burton, 2011). Whereas language is unlikely to play a role in this early advantage in preverbal infants, broad multimodal semantic associations may have contributed to it during learning, for example by strengthening representations for familiar faces through other cues that are present simultaneously, such as the voice or body odor (Leleu et al., 2020; Sai, 2005). The effect of these multimodal cues on familiar face individuation and identity acquisition should be examined in future studies.

Interestingly, when the mother's face was presented as oddball among unfamiliar strangers, no individuation response was obtained, in contrast to robust responses found in adult studies for famous (Yan et al., 2020; Zimmermann et al., 2019) but also personally familiar faces (Campbell et al., 2020). Inspection of individual harmonics revealed a significant response in this condition only at 8.4 Hz, but in the summed signal, this response was not detectable. In comparison, a more pronounced response was observed for familiarized stranger oddballs, but only in the additional analysis on harmonics 2–9. This additional analysis was run to provide a balanced view of the data and capture the individuation response observed in higher harmonics in the familiarized stranger conditions (Fig. 2). However, since this analysis was performed post-hoc, replication studies are needed. A conservative account is that infants were able to individuate familiarized strangers in the present study, albeit to a lesser extent than the mothers.

The unexpected pattern of results with a individuation responses across a range of harmonics for strangers, but not mothers presented as oddballs, can be explained in several ways. The frequent appearance of unfamiliar faces, interrupted by the familiar face, may have induced infants to focus more strongly on individuating strangers than on identifying their mother and, in turn, may have decreased oddball responses. Alternatively, differences in discriminability/generalizability of stimuli may have influenced the pattern of results. As the identity of mothers varied between all

participants, but the stranger target was the same across participants, it cannot be excluded that the stranger target, by chance, was more easily discernible compared to the other unfamiliar faces. Future studies should further elucidate how infants individuate faces with different stimulus sets and task settings, and whether a familiarization phase is necessary to induce individuation.

In addition to familiarity effects on individuation responses, participants also responded more strongly to the general visual stimulation when their mother was presented as standard. Rather than responding more strongly to sequences with targets presented as oddballs, the base response was modulated by target identity. This finding may reflect increased attention (e.g., Müller et al., 1998; review in Norcia et al., 2015) elicited by the mother or the alternating presentation of mothers and unfamiliar strangers, and further indicates that infants respond differently to mothers and strangers.

Prior adult studies (Campbell et al., 2020; Verosky et al., 2020; Zimmermann et al., 2019) varied aspects of the design (e.g., number of different images per target identity, assignment of target faces to oddball or standard positions) that are likely to influence the strength of individuation responses for familiar(ized) faces. The current study carefully controlled these aspects and provides evidence that the level of familiarity (long-term/short-term) and the assignment of faces to oddball or standard positions may influence the pattern of individuation observed in infants. Although the proportion of target faces relative to unfamiliar faces (4:1 in target standard vs 1:1 in target oddball) had an effect on the pattern of individuation responses, individuation was also observed in the target oddball condition, where target stimuli appeared with the same ratio as unfamiliar strangers. Thus, individuation responses cannot be attributed to the ratio of target and stranger faces alone.

In non-human primates, no advantage in individual face matching for familiar faces has been observed when images of conspecific faces were employed (Micheletta et al., 2015; Rossion & Taubert, 2019), suggesting that the advantage in humans is promoted by additional language-related semantic processes activated by familiar faces (e.g., labels, Dixon et al., 1998; Schwartz & Yovel, 2016). However, the current study demonstrates a FIR advantage for familiar faces in preverbal infants. The short presentation times and interruption of processing by immediate presentation of the next stimulus in this paradigm, together with the predominant activation over the visual cortex, render enhanced perceptual processing the most likely source of this familiar face advantage. However, future work should evaluate whether affective and semantic processes induced by the mother's face also contribute to this effect.

In addition, it remains unclear whether the individuation response observed here is face-specific or would be also observed for non-face objects. Given the importance and salience of the mother's face which is unequalled in the object domain, a similar familiarity effect does not seem likely, but more research would be needed to answer this question. Moreover, the spatial distribution of face individuation early in life should be investigated in future research.

Previous studies mostly presented infants with single images of target faces and used looking-time (Coulon et al., 2011; Sai, 2005) or ERP methods (de Haan & Nelson, 1997; Peykarjou

et al., 2016), requiring relatively long presentation times (e.g., 10–80 s in looking-time studies, 5–1.5 s in ERP studies). While these studies showed that infants are able to recognize faces, the proficiency of this ability remained largely unexplored. In particular, it remained obscure whether infants show signatures of the adult face individuation response such as a high processing speed and generalization across images. The present study revealed that infants individuate their mothers' face across a range of emotional expressions and orientations, despite short presentation times (~170 msec per image) and following only a brief familiarization phase (30 s). In addition, a weaker but significant individuation response was also observed for strangers following a brief familiarization. The current study thus demonstrates that, even under challenging circumstances, five-month-old infants proficiently individuate familiar faces.

Data and code availability

The conditions of our ethics approval do not permit public sharing or archiving of anonymized study data. Readers seeking access to the data should contact the corresponding author (stefanie.peykarjou@psychologie.uni-heidelberg.de). Access will be granted to named individuals in accordance with ethical procedures governing the reuse of sensitive data.

Specifically, informed consent will need to be obtained from participants' parents and requestors must complete a formal data sharing agreement.

Author notes

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Author contributions

St.P., B.R., S.P.: Conceptualization; St.P., M.L., E.B.: Investigation; St.P.: Formal analysis; St.P., M.L., E.B., B.R., S.P.: Writing.

Declaration of competing interest

None.

Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.cortex.2022.07.011>.

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