



# Sibling experience prevents neural tuning to adult faces in 10-month-old infants

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## ARTICLE INFO

### Keywords:

Face processing  
Age bias  
ERPs  
Perceptual experiences  
Infancy

## ABSTRACT

Early facial experience provided by the infant's social environment is known to shape face processing abilities, which narrow during the first year of life towards adult human faces of the most frequently encountered ethnic groups. Here we explored the hypothesis that natural variability in facial input may delay neural commitment to face processing by testing the impact of early natural experience with siblings on infants' brain responses. Event-Related Potentials (ERPs) evoked by upright and inverted adult and child faces were compared in two groups of 10-month-old infants with ( $N = 21$ ) and without ( $N = 22$ ) a child sibling. In first-born infants, P1 ERP component showed specificity to upright adult faces that carried over to the subsequent N290 and P400 components. In infants with siblings no inversion effects were observed. Results are discussed in the context of evidence from the language domain, showing that neural commitment to phonetic contrasts emerges later in bilinguals than in monolinguals, and that this delay facilitates subsequent learning of previously unencountered sounds of new languages.

## 1. Introduction

Faces are among the most salient and frequent visual stimuli in our everyday environment. As adults, we are experts at processing facial signals that convey social information about other individuals, such as identity (Bruce and Young, 1986), age (Anastasi and Rhodes, 2005), gender (Lewin & Herlitz, 2002), ethnicity (Pascalis et al., 2002), and emotional state (Erwin et al., 1992). This expertise is mediated by an extensive network of neural regions along the ventral visual pathway that shows greater activation in the processing of faces compared to other visual stimuli (Haxby et al., 2000). This cortical specialization for face perception gradually emerges across childhood and young adulthood (see reviews by Haist and Anzures, 2017 and Kadosh and Johnson, 2007), and has its roots in the attentional bias towards face-like stimuli that infants show right after birth (Johnson et al., 1991; Macchi Cassia et al., 2004; Valenza et al., 1996). Various evidence suggests that this early bias interacts with the statistical properties of the infants' visual environment to shape neural circuits through experience-expectant processes (Greenough et al., 1987). Indeed, there is mounting evidence

that infants' visual experience during the first six months of life is strongly biased towards faces, as faces are the target of infants' gaze for a large part of their waking time (e.g., Jayaraman et al., 2017; Sugden et al., 2014). This massive exposure to faces drives the development of a specialized neural system for face processing from an early age (e.g., Gomez et al., 2017; Guy et al., 2016; Macchi Cassia et al., 2006).

Event-related potentials (ERPs) elicited by visual stimuli have been extensively used to track the developmental trajectory of neural specialization for face processing. Due to their non-invasive nature, they are an optimal tool to measure functional brain activation in infants and children. Indeed, ERP studies with children have shown that by the age of 4 years faces elicit two components, the P1 and the N170, that show a pattern of topographical distribution and face-sensitivity similar to that observed in adulthood (e.g., Kuefner et al., 2010; Itier and Taylor, 2004). Although the degree to which the processes reflected in the P1 are specific to faces remains debated in the literature (e.g., Itier and Taylor, 2002; Rossion and Caharel, 2011), the P1 has often been reported to be sensitive to faces (versus non-face objects, Kuefner et al., 2010) and face manipulations (e.g., face inversion, Taylor et al., 2004;

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face age: Melinder et al., 2010; Peykarjou et al., 2013) in young children. Indeed, using magnetoencephalography, Liu et al. (2011) investigated the sequence of cognitive and neural processes underlying the processing of faces in adult participants, suggesting the existence of an initial stage of face categorization occurring as early as 100 ms (i.e., M100) after stimulus onset, which would be followed by a later occurring identification stage (i.e., M170).

Albeit frequently observed in studies looking at face processing in infants (e.g., Balas et al., 2011; Halit et al., 2003; de Haan and Nelson, 1999; Peykarjou and Hoehl, 2013; Scott and Monesson, 2010), the P1 has been rarely reported and analyzed (e.g., Macchi Cassia et al., 2006; Peykarjou et al., 2014). Rather, most of the studies investigating the electrophysiological responses to faces (versus non-face visual objects) in infancy focused the examination on two ERP components that share some of the face-specific qualities associated with the adult N170: the N290 and the P400 (de Haan et al., 2003; Halit et al., 2003). The N290 is a negative peak occurring 290–350 ms after stimulus onset over medial occipital sites (de Haan et al., 2003; Halit et al., 2003). In 3-month-old infants, the N290 is more pronounced in response to faces than matched visual noise over right occipital channels (Halit et al., 2004), and shows inversion effects for faces and not for cars (Peykarjou and Hoehl, 2013). The P400 is a later occurring positive wave, more laterally distributed (de Haan et al., 2002; Halit et al., 2003), that is larger for upright than for inverted faces (de Haan et al., 2003) in 6-month-old infants. The role of the P400 in infants' face processing is still not well understood. Although some studies reported it to peak earlier for faces than toys (de Haan and Nelson, 1999; McCleery et al., 2009), others failed to find face-specific latency effects, and rather reported larger amplitude for toys than for faces (Guy et al., 2016). Similarly, although in some studies with infants (Key et al., 2009; Scott et al., 2006) and children (Carver et al., 2003; Dawson et al., 2002) the P400 showed sensitivity to stimulus familiarity, other studies failed to report familiarity effects at the level of this component (de Haan and Nelson, 1999; Luyster et al., 2014).

Recent ERP studies using the fast-periodic visual stimulation (FPVS) paradigm confirmed that discrimination of faces from non-face objects is lateralized in the right hemisphere at least from the age of 4 months (de Heering and Rossion, 2015; Farzin et al., 2012; but see Lochy et al., *in press*, for contrasting evidence in preschool-age children). Moreover, the topographical distribution of occipital and occipitotemporal activation during individual-level discrimination of monkey faces becomes progressively right lateralized between 6 and 9 months of age (Barry-Anwar et al., 2018). Together, these results indicate that right lateralized face-selective neural networks are in place early in life, and they are recruited to support identity discrimination by the end of the first year of life.

As infants gain extensive experience with faces within their individual social environment, their face-sensitive neural responses become increasingly selective to specific characteristics of facial stimuli, like species, ethnicity and age. Recent attempts to characterize the nature of the perceptual input received by infants within their social environment have shown that the majority of their facial experience is with individuals who share the same demographic characteristics as their primary caregiver, namely individuals of the same gender, ethnicity, and age group as the primary caregiver (Rennels and Davis, 2008; Sugden et al., 2014). This biased experience drives infants to build a perceptual representation that progressively adapts to include diagnostic attributes of the more familiar face categories.

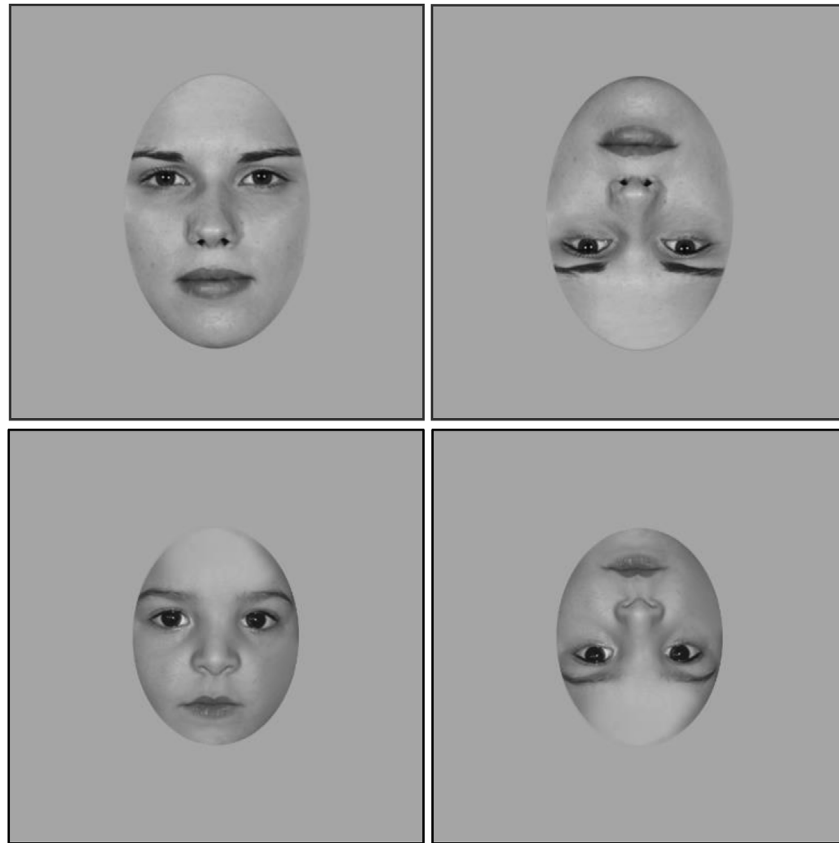
Accordingly, between 3 and 12 months of age the N290 and the P400 increase their specificity to upright human faces, as their sensitivity to stimulus inversion becomes selective to human as opposed to monkey faces (de Haan et al., 2003; Halit et al., 2003). Using a rapid repetition ERP paradigm, Peykarjou et al. (2014) showed that, at 9 months, human and monkey faces are treated as belonging to a common superordinate category at the level of the early occurring P1 component, but they are subsequently differentiated at the level of the

N290. Similarly, by comparing ERP responses evoked in 9-month-old infants by own- and other-race faces, Balas and colleagues (Balas et al., 2011) found that the N290 differentiated between more familiar (i.e., own-race) and less familiar (i.e., other-race) face categories. Evidence of emerging neural specialization for adult human faces also comes from the only existing infant study comparing brain responses evoked by faces of different ages: adult faces, but not infant faces, induced increased right-lateralized hemodynamic responses in temporal areas of 9-month-old infants (Kobayashi et al., 2018). Taken together, these findings indicate that, by the end of the first year of life, the infant brain has developed a certain degree of specialization for those face types that are more frequently experienced.

This neural specialization occurs along with the attunement of infants' perceptual sensitivity towards these categories resulting in a process known as perceptual narrowing (see review by Maurer and Werker, 2014). At 10–12 months, infants use more expert visual exploration strategies to process faces of familiar categories in comparison to other face types (Ferguson et al., 2009; Gaither et al., 2012; Liu et al., 2011). Within the same time window infants' sensitivity to perceptual differences among individual faces tunes to human faces (versus monkey faces: Pascalis et al., 2002; Simpson et al., 2011), adult faces (versus infant faces: Kobayashi et al., 2018; Macchi Cassia et al., 2014; versus child faces: Proietti et al., 2018), and faces of the ethnicity that is more represented in their social environment (Kelly et al., 2007; Anzures et al., 2013). Indeed, when the natural statistics of facial experience are artificially altered by delivering laboratory-training with other-race faces (Anzures et al., 2012; Heron-Delaney et al., 2011) or monkey faces (Pascalis et al., 2005; Scott and Monesson, 2009) between 6 and 9 months, or immediately after this period, the ability to discriminate individuals belonging to these face types is maintained. Furthermore, neural sensitivity to stimulus inversion develops for those faces as well as for more familiar face categories (Scott and Monesson, 2010).

More evidence confirms that the natural statistics of facial experience drives the attunement of infants' perceptual discrimination abilities. For instance, when infants are massively exposed to multiple face age categories (i.e., adult and non-adult faces) right from birth, the trajectory of perceptual narrowing towards adult faces changes. Both Caucasian (Macchi Cassia et al., 2014) and Asian (Kobayashi et al., 2018) 3-month-old infants can differentiate equally well among individual adult and infant own-race faces, whereas 9-month-old infants maintain this ability for adult faces but not anymore for infant faces. Critically though, at 9 months the ability to distinguish among child faces depends on sibling experience: infants with a child sibling show successful discrimination whereas first-born infants do not (Proietti et al., 2018). These findings show that perceptual experience provided by everyday contact with an older sibling right from birth allows for the development of a face representation whose tuning properties suit child faces as well as adult faces.

This line of research shows how infants' perceptual discrimination abilities are sensitive to variations in the natural statistics of their early facial experience. Nevertheless, there is still no evidence of how these same variations modulate infants' brain responses. Insights into this topic come from an ERP study investigating neural activations in response to adult and newborn faces in 3-year-old children with and without a younger sibling (Peykarjou, Westerlund, Macchi Cassia et al., 2009). Results showed that sibling experience modulated children's processing of both adult and infant faces. That is, age of sibling at test correlated negatively with P1 amplitude, suggesting an influence of sibling's age on early neural responses to faces. Assuming that in children, like in adults (e.g., Rossion et al., 1999), smaller amplitudes reflect ease of processing, the authors concluded that longer experience with the sibling's face may have progressively broadened children's face representation, resulting in more efficient processing of different face ages in children with siblings than in singletons. Although these findings can inform us about the effects of sibling experience on children's



**Fig. 1.** Exemplary stimuli of the four stimulus categories used in the study: Adult Upright (AdUp), Adult Inverted (AdInv), Child Upright (ChUp), Child Inverted (ChInv). Stimuli were presented in color.

face representation and its neural underpinnings, there is currently no evidence showing that exposure to a sibling's face from birth is capable of tuning face-specific electrocortical responses in infancy.

The present study investigates this issue by testing the influence of sibling experience on the specificity of 10-month-old infants' brain responses to upright adult faces. The susceptibility of face-specific ERP components to the detrimental effects of stimulus inversion is commonly taken as an index of neural specialization for face processing (Rossion et al., 2003). Accordingly, developmental studies have shown that by 6 months of age the sensitivity of the infant N290 and P400 components to stimulus inversion becomes selective to human as opposed to monkey faces (de Haan et al., 2003; Halit et al., 2003). In light of this evidence we expected that, following continuous experience with adult caregivers, infants without siblings would show neural specialization for adult faces, as evidenced by selective or larger inversion effect for these faces compared to child faces. In contrast, we expected to observe a comparable face inversion effect for adult and child faces in infants with siblings, who acquired massive experience with the face of their sibling as well as their caregivers.

## 2. Method

### 2.1. Participants

Forty-three 10-month-old infants (18 males,  $M$  age = 307 days,  $SD$  = 23 days) were included in the final sample; they were all Caucasian, healthy and full-term. Infants were assigned to one of two groups based on the absence or presence of at least one older sibling, so that the no-sibling group was composed of 22 infants, and the sibling group was composed of 21 infants. An additional 61 infants were tested but excluded from the final sample because of fussiness ( $N$  = 11) or excessive eye or body movements that resulted in recording artifacts

( $N$  = 50; see Supplementary Material 1). The attrition rate in the current study was comparable to that from other infant face processing ERP studies, especially considering the fully factorial within-subject design of our study. Indeed, it was consistent with that reported in other ERP studies with infants over 6 months of age (e.g., DeBoer et al., 2005) using purely visual stimulation (e.g., Righi et al., 2014; see also Stets et al., 2012). At the end of the testing session, parents filled a questionnaire with general demographic enquiries, and specific questions aimed at assessing if, in the past 10 months, their infants have had contact with children aged between 2 and 6 years. Infants in the no-sibling group had no more than 10 h of experience per week with children within this age range, with an average exposure time of 1 h per week (range = 0–10 h). Average exposure time for infants in the sibling group did not differ from that of the first-born infants ( $M$  = 1.4 h per week; range = 0–15 h;  $p$  = .41). Within the sibling group, 19 infants had 1 older sibling, and 2 infants had two older siblings. The mean age of the youngest among the older siblings at the time of the participants' birth was 4.3 years (range = 2.3–7.1). All infants except 6 spent at least 60% ( $M$  = 78%, range = 60%–95%) of their waking hours with a female adult (the mother or a caregiver), while 6 infants had equal exposure (50%) to male and female caregivers. Participants were recruited via a written invitation that was sent to parents based on birth records provided by neighboring cities, and parents gave their written informed consent. The study was explained to the parents and written consent for their infants' participation was obtained. The protocol was carried out in accordance with the ethical standards of the Declaration of Helsinki (BMJ 1991; 302: 1194) and approved by the Ethics Committee of the University of \*\*\* (omitted for blind purposes).

### 2.2. Stimuli

Stimulus material consisted of color photographs of 10 adult and 10

child Caucasian faces, all displaying a full-frontal neutral expression. The age of the adult faces ranged between 20 and 30 years, while age of the child faces ranged between 3 and 6 years, so that it matched with the age of the siblings at the time of the participants' birth. Because the majority of infants included in the sample had more daily exposure to female than male faces, adult face gender was kept constant, with all faces being female. No efforts were made to keep gender constant for child faces in light of biometric and morphometric studies suggesting that stable interindividual patterns of sexual dimorphism in facial morphology are not yet apparent during early childhood (Bulygina et al., 2006; Farkas et al., 1988). In addition to that, the cropping of the stimuli into an oval shape to mask external features (e.g. hair, ears and neck), made gender-diagnostic information unavailable in our child face stimuli. Using the software Adobe Photoshop, all face images were equalized for luminance, which did not differ between adult and child faces,  $t(18) = 0.48, p = .638$ . Faces within each age category (i.e., adult and child faces) were cropped to be the same size, and were pasted on a gray background; to reflect the natural differences in the size and shape of real adult and child faces, adult faces were slightly taller and larger than child face stimuli (Fig. 1). When viewed from approximately 60 cm, adult faces subtended  $15.19^\circ$  of visual angle vertically and  $10.22^\circ$  of visual angle horizontally, and child faces subtended visual angles of  $12.23^\circ \times 9.27^\circ$ . Each face was presented in both the upright and inverted orientation, with inverted stimuli being created by rotating each upright face by  $180^\circ$ .

### 2.3. Apparatus and procedure

After application of the sensor net, infants passively viewed the stimuli while seated on their parent's lap at a distance of approximately 60 cm from a 24-inches monitor in a dimly lit, audiometric and electrically shielded cabin. The parent was blind to the hypothesis of the study, and was instructed to remain silent and avoid visual contact with the infant while keeping him or her aligned to the monitor's midline. A digital video-camera mounted above the monitor and centered on the infant's face fed into a TV monitor and a digital video recorder, both located outside the testing cabin. The TV monitor allowed for observation of the infant at all times during the testing session, and the video-recorded images of the infant's face allowed offline coding of looking times.

A  $2 \times 2$  within-participants design was used, so that each infant was exposed to four trial types corresponding to the four experimental conditions: face age (adult, child)  $\times$  orientation (upright, inverted).

Stimuli were presented using E-Prime software v2.0 (Psychology Software Tools Inc., Pittsburgh, PA). A trial consisted of 1000 ms stimulus presentation followed by an inter-stimulus interval which varied randomly in duration between 800 and 1200 ms. Whenever necessary between trials the experimenter presented a looming fixation point to reorient the infant's attention to the screen. Trials were presented in blocks, with face age alternated between blocks and orientation presented with equal probability and in random order within each block with the constraint that the same orientation was not repeated more than three times in succession; the age of the faces presented in the first block was counterbalanced across participants. Infants were presented with a maximum of 6 blocks of 40 trials each, during which each unique image in the adult and child face sets was presented twice in each orientation. Stimuli presentation continued until the infant became too fussy or bored to attend, with a maximum of 60 trials for each experimental condition. The average number of total trials viewed by the infants was 197.

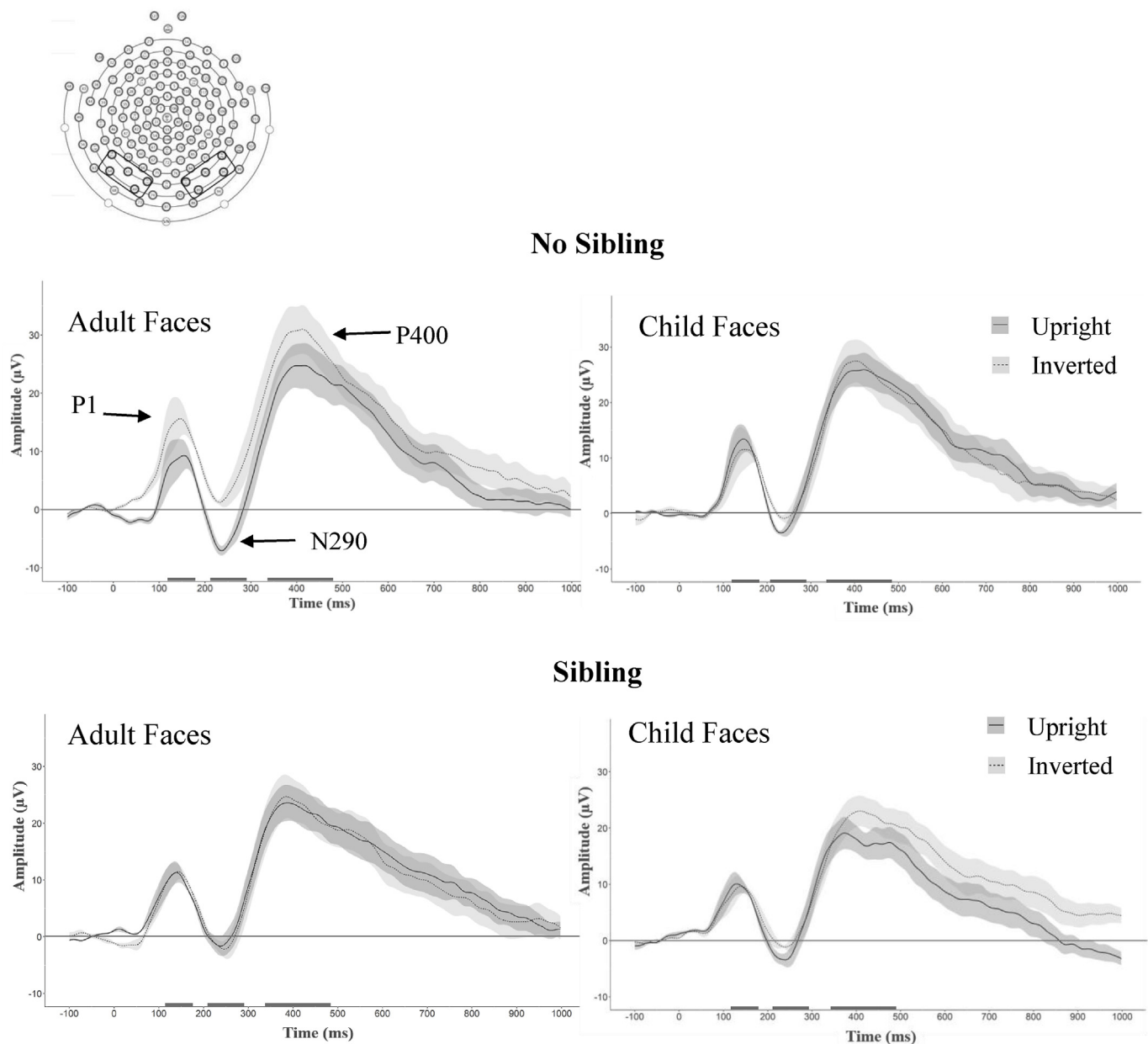
### 2.4. ERP recording and data analysis

The electroencephalogram (EEG) was recorded continuously using a Geodesic 128-electrode HydroCel Geodesic Sensor Net (Electrical Geodesic Inc., Eugene, OR), amplified using an EGI NetAmps 300

amplifier, and referenced online to the vertex electrode (Cz). Data were sampled at 500 Hz, with an online band-pass filter of 0.1–100 Hz. Impedances were checked prior to the beginning of recording and considered acceptable if lower than  $50 \text{ k}\Omega$ . EEG data were further processed offline using NetStation v4.6.4 (Eugene, OR). A band-pass filter of 0.3–30 Hz was applied, and the continuous signal was time-locked to target onset and segmented into epochs from 100 ms before stimulus onset to 1000 ms past stimulus onset. Data were corrected to the baseline using the average voltage of the 100 ms prior to stimulus onset, and re-referenced to the algebraic mean of all channels. An automatic artifact rejection was applied on segmented data whenever the signal exceeded  $\pm 200 \mu\text{V}$  at any electrode in a sliding window of 80 ms. Data were further checked through visual inspection for eye-movements, eye-blinks and other body movement artifacts not detected by the automated algorithm. Trials were excluded if more than eighteen bad channels were detected. Of the remaining trials, individual bad channels were replaced using spherical spline interpolation. Individual subject averages for each of the four conditions (AdUp, AdInv, ChUp, ChInv) were computed separately for each channel across all trials, and then re-referenced to the average reference. Infants in the no-sibling group and those in the sibling group viewed an average of 50 and 49 trials per condition, respectively. Similar to other infant visual ERP studies (e.g., Peykarjou and Hoehl, 2013; 2013; 2014), an inclusion criterion of 10 good trials for each stimulus category was adopted to include participants in the final sample (see also Stets et al., 2012). The mean number of trials contributing to the average ERP across participants and conditions was 18 for the no-sibling group (AdUp: 16,  $SD = 6$ ; AdInv = 17,  $SD = 7$ ; ChUp = 18,  $SD = 6$ ; ChInv = 17,  $SD = 7$ ) and 17 for the sibling group (AdUp = 17,  $SD = 7$ ; AdInv = 16,  $SD = 6$ ; ChUp = 17,  $SD = 7$ ; ChInv = 17,  $SD = 7$ ). A similar number of trials contributed to the final analysis for each condition in each participants' group,  $F(3,123) = 1.05, p = .37$ .

Inspection of the grand-averaged waveforms revealed three well-defined components, P1, N290, and P400, that were subsequently analyzed by averaging electrodes within occipital-temporal regions of the left (58, 64, 65, 69, 70) and right (96, 95, 90, 83, 89) hemisphere (Fig. 2). These electrode sites were chosen based on visual inspection of the component topography and correspond to electrode clusters in which the components of interest have been recorded in previous studies (e.g., Scott and Monesson, 2010; Peykarjou et al., 2014). Time windows for analyses were chosen based on previous infant ERP reports of the three components, and on an examination of the peak of each component across participants: P1, 120–180 ms; N290, 210–290 ms; P400, 330–480 ms (e.g., Vogel et al., 2012; Peykarjou et al., 2014). We are aware that peak amplitude measures are typically more sensitive to spurious fluctuations in latency compared to mean amplitude measures (Luck, 2005). However, visual inspection of the waveforms revealed that potential amplitude differences at the level of the N290 may be driven by differences at the preceding P1 component, and, similarly, differences at the level of the P400 may be driven by differences at the preceding N290. Therefore, we opted for extracting peak amplitude values for each component, which allowed us to obtain peak-to-trough adjusted measures (analyses on mean amplitude values are reported in Supplementary Material 2). Peak amplitude ( $\mu\text{V}$ ) was identified as the maximum value (positive or negative) within the given time window, and peak latency (ms) was identified as the time at which the most positive or negative peak occurred. To take into account P1 variations, we obtained peak-to-trough adjusted amplitude measures (Picton et al., 2000) by computing the difference between the maximum negative amplitude of the N290 and the maximum positive amplitude of the P1, and between the maximum positive amplitude of the P400 and the maximum negative amplitude of the N290 (see Kuefner et al., 2010 and Peykarjou et al., 2014 for a similar procedure applied to infant ERP data). In addition to the analyses on P1, N290, and P400, analyses on peak amplitude and latency of the Nc (350–630 ms), an attention-related ERP component visible in our data over fronto-central sites (left:





**Fig. 2.** Grand-averaged ERP waveforms of adult and child faces for infants in the no-sibling group ( $N = 22$ ) and for infants in the sibling group ( $N = 21$ ). Upright stimuli are depicted with solid black lines, while Inverted stimuli with dashed gray lines. The x-axis represents time in milliseconds (ms), and the y-axis represents amplitude in microvolts ( $\mu V$ ). The topographic map shows the electrodes included in the left (58, 64, 65, 69, 70) and right (96, 95, 90, 83, 89) clusters used to obtain peak amplitude and peak latency measures for each of the three analyzed ERP components (P1, N290, and P400).

13, 20, 24, 29; right: 112, 118, 124, 111) were carried out. However, those analyses did not yield any significant results (all  $ps > .105$ ), so they are not discussed further. We note briefly that, for all components, analyses on mean amplitude, calculated by averaging all data points within the given time window, confirmed the results obtained on peak response. Results of these analyses are reported in Supplementary Material 2.

In order to test our hypothesis that stimulus inversion would differentially affect infants' ERPs for adult and child faces as a function of sibling experience, we ran two mixed-design Analyses of Variance (ANOVAs), one for each dependent variable (i.e., peak latency and peak amplitude), for each of the identified ERP components. The ANOVAs included the between-participants factor sibling group (no-sibling, sibling) and the within-participants factors face age (adult, child), orientation (upright, inverted) and hemisphere (left, right). Significant

interactions were followed-up through paired-sample  $t$ -tests, and Bonferroni correction was applied to correct for multiple comparisons. Analyses on amplitude values were conducted using both uncorrected values of each ERP component and adjusted difference scores computed as described in the previous paragraph. The analyses on corrected amplitude values for the N290 and the P400 are reported in the Result section, while results for uncorrected values are reported in the Supplementary Material 2.

### 3. Results

Fig. 2 shows the grand-averaged waveforms from the left and right posterior temporal recording sites for upright and inverted adult and child faces for infants in the no-sibling group and those in the sibling group. Means and standard deviations of peak latencies and adjusted

**Table 1**

Means (Standard Deviations) of Peak Latency Values (ms) for the P1, N290, and P400 Components for Infants in the No-Sibling Group and for those in the Sibling Group.

		Peak Latency		
		P1	N290	P400
No-Sibling	AdUp	148.62 (12.37)	245.09 (13.77)	414.25 (27.40)
	AdInv	149.35 (10.75)	243.09 (18.75)	409.86 (28.20)
	ChUp	149.44 (13.86)	242.02 (18.97)	417.09 (31.26)
	ChInv	153.78 (13.41)	245.49 (18.51)	416.38 (30.57)
Sibling	AdUp	142.60 (12.37)	241.24 (20.77)	403.70 (36.15)
	AdInv	147.53 (12.65)	244.95 (18.50)	402.67 (38.69)
	ChUp	142.16 (13.90)	238.19 (14.95)	414.29 (31.86)
	ChInv	147.43 (15.25)	245.14 (18.61)	423.63 (33.83)

**Table 2**

Means (Standard Deviations) of adjusted Peak Amplitude Values ( $\mu\text{V}$ ) for Infants in the No-Sibling Group and for those in the Sibling Group.

		Peak Amplitude	
		N290-P1	P400-N290
No-Sibling	AdUp	−23.74 (7.17)	39.44 (10.81)
	AdInv	−22.44 (11.05)	38.57 (12.20)
	ChUp	−25.40 (8.38)	37.95 (10.32)
	ChInv	−21.46 (9.96)	36.95 (11.49)
Sibling	AdUp	−20.47 (7.49)	33.74 (8.22)
	AdInv	−21.11 (9.43)	34.22 (8.09)
	ChUp	−20.14 (8.51)	30.26 (9.50)
	ChInv	−18.91 (8.87)	32.85 (8.79)

peak amplitudes of the P1, N290 and P400 are reported in Table 1 and Table 2, respectively.

### 3.1. P1 component

P1 latency showed sensitivity to stimulus orientation in that it was longer for inverted faces ( $M = 149.52$  ms;  $SD = 11.60$  ms) than for upright faces ( $M = 145.71$  ms;  $SD = 12.32$  ms),  $F(1,41) = 10.27$ ,  $p = .003$ ,  $\eta_p^2 = 0.20$ , irrespective of face age and sibling experience. All other effects, including the Face age main effect ( $p = .40$ ), did not reach significance ( $ps > .06$ ).

The ANOVA on P1 amplitude revealed a main effect of hemisphere,  $F(1,41) = 6.67$ ,  $p = .013$ ,  $\eta_p^2 = 0.14$ , showing that the P1 was of larger amplitude over the right ( $M = 16.48 \mu\text{V}$ ;  $SD = 6.68 \mu\text{V}$ ) than the left channels ( $M = 14.38 \mu\text{V}$ ;  $SD = 5.65 \mu\text{V}$ ), regardless of stimulus type. The Face age main effect was nonsignificant ( $p = .54$ ). Rather, there was a Face age  $\times$  Orientation interaction,  $F(1,41) = 8.74$ ;  $p = .005$ ,  $\eta_p^2 = 0.18$ , which was qualified by a significant three-way interaction involving face age, orientation and sibling group,  $F(1,41) = 7.04$ ,  $p = .011$ ,  $\eta_p^2 = 0.15$ . Bonferroni corrected  $t$ -tests revealed that, in the no-sibling group, P1 amplitude was larger for inverted adult faces than for upright adult faces,  $t(21) = -4.18$ ,  $p < .001$ , Cohen's  $d_z = 0.89$ , and for upright child faces than for upright adult faces,  $t(21) = -3.44$ ,  $p = .002$ , Cohen's  $d_z = 0.73$  (Fig. 3). No differences across age nor orientation conditions attained significance for infants in the sibling group ( $ps > .26$ ).

### 3.2. N290 component

The ANOVA on N290 latency revealed a spurious Face Age  $\times$  Hemisphere  $\times$  Sibling group interaction,  $F(1,41) = 7.92$ ,  $p = .007$ ,  $\eta_p^2 = 0.16$ , for which all post-hoc comparisons were nonsignificant (all  $ps > .096$ ). Specifically, there were no significant differences in N290 latency in response to adult versus child faces in singletons ( $ps > .15$ ) nor in infants with siblings ( $ps > .10$ ).

In the ANOVA on corrected amplitude values, no interactions were observed ( $ps > .10$ ). Rather, there was a significant main effect of hemisphere,  $F(1,41) = 6.49$ ,  $p = .015$ ,  $\eta_p^2 = 0.14$ , with enhanced N290 amplitude on the right recording sites ( $M = -22.90 \mu\text{V}$ ;  $SD = 8.70 \mu\text{V}$ ) compared to the left sites ( $M = -20.51 \mu\text{V}$ ;  $SD = 7.78 \mu\text{V}$ ). The Face age main effect was also nonsignificant ( $p = .57$ ).

### 3.3. P400 component

A Face age main effect,  $F(1,41) = 6.66$ ,  $p = .014$ ,  $\eta_p^2 = 0.14$ , revealed that P400 latency differentiated between adult and child faces, peaking earlier in response to adult faces ( $M = 407.62$  ms;  $SD = 29.39$  ms) than to child faces ( $M = 417.84$  ms;  $SD = 28.45$  ms), regardless of stimulus orientation and sibling experience. All other effects failed to reach statistical significance (all  $ps > .17$ ).

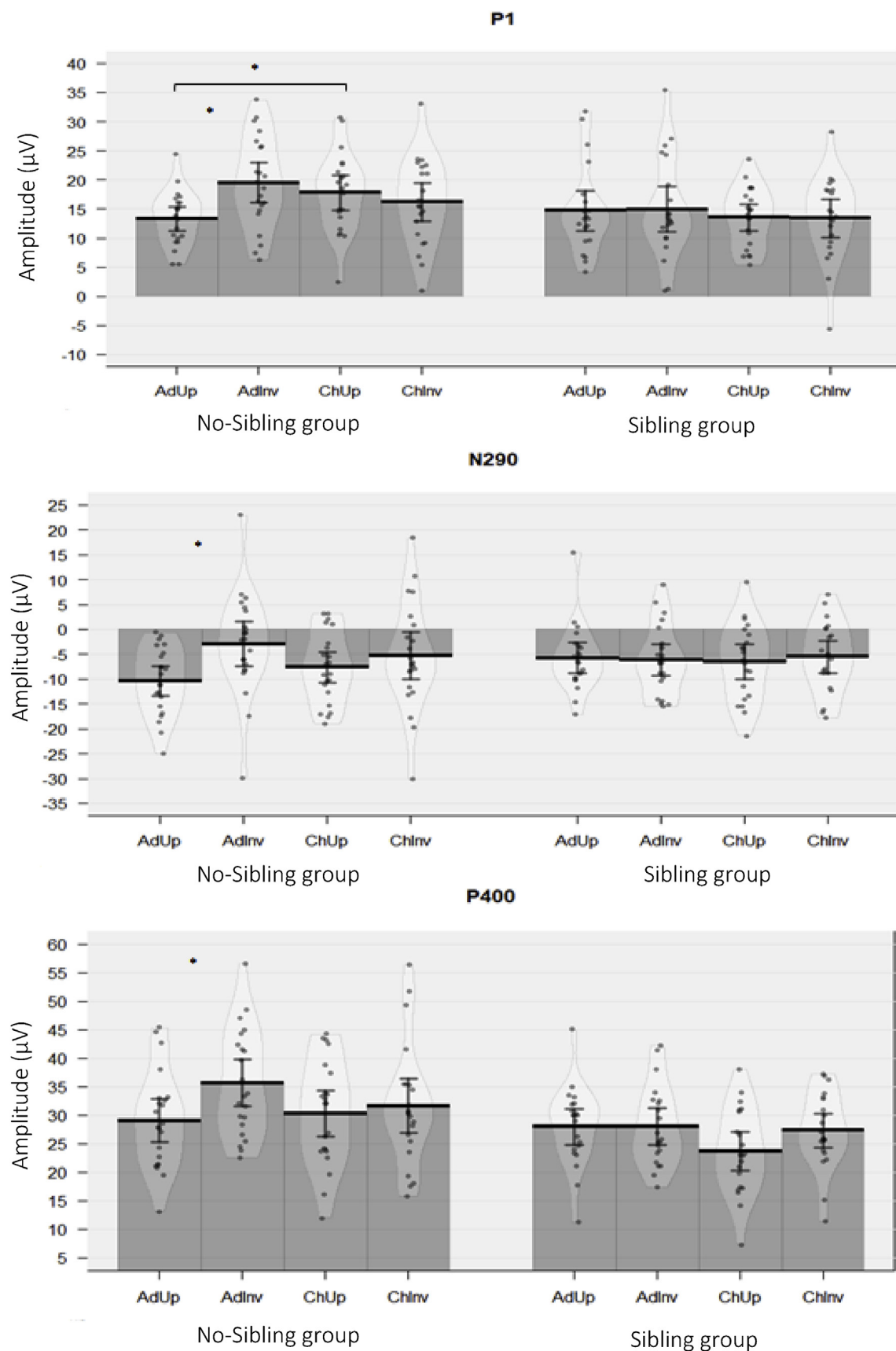
In the analyses on uncorrected amplitude values, Orientation,  $F(1,41) = 6.31$ ,  $p = .016$ ,  $\eta_p^2 = 0.13$ , and Face Age,  $F(1,41) = 8.75$ ,  $p = .005$ ,  $\eta_p^2 = 0.18$ , main effects revealed that P400 amplitude was enhanced for inverted ( $M = 30.68 \mu\text{V}$ ;  $SD = 8.26 \mu\text{V}$ ) relative to upright faces ( $M = 27.76 \mu\text{V}$ ;  $SD = 6.17 \mu\text{V}$ ),  $F(1,41) = 6.31$ ,  $p = .016$ ,  $\eta_p^2 = 0.13$ , and for adult faces ( $M = 30.20 \mu\text{V}$ ;  $SD = 6.83 \mu\text{V}$ ) relative to child faces ( $M = 28.24 \mu\text{V}$ ;  $SD = 7.63 \mu\text{V}$ ). However, these main effects were both qualified by a significant Face age  $\times$  Orientation  $\times$  Sibling group interaction,  $F(1,41) = 6.44$ ,  $p = .015$ ,  $\eta_p^2 = 0.14$ , showing that amplitude values were larger in response to inverted than to upright adult faces,  $t(21) = -2.98$ ,  $p = .009$ , Cohen's  $d_z = 0.59$ , in the no-sibling group (Fig. 3). No other comparison attained statistical significance ( $ps > .12$ ), and no differences across age nor orientation conditions attained significance for infants in the sibling group ( $ps > .06$ ). Analyses on adjusted amplitude values revealed a Face age main effect,  $F(1,41) = 8.94$ ;  $p = .005$ ,  $\eta_p^2 = 0.18$ , with larger amplitude for adult faces ( $M = 36.94 \mu\text{V}$ ;  $SD = 9.47 \mu\text{V}$ ) than for child faces ( $M = 34.50 \mu\text{V}$ ;  $SD = 9.95 \mu\text{V}$ ). No other significant main effect or interactions were observed ( $ps > .14$ ).

## 4. Discussion

Here, we investigated how infants' experience with faces in their everyday social environment modulates face-sensitive electrocortical responses. To this end, we examined ERP responses to adult and child upright and inverted faces in 10-month-old infants with and without older siblings. Three components were observed and analyzed: the P1, the N290, and the P400. A fourth component, the Nc, was also analyzed but did not prove sensitive to our experimental manipulations, and thus is not discussed further.

Overall, both stimulus inversion and face age affected infants' ERP responses. Inverted faces, irrespective of face age, elicited longer P1 latency, and were differentiated from upright faces at the level of both the N290 and the P400, whose amplitudes were modulated in opposite directions. Critically though, the presence of a significant Face age  $\times$  Orientation  $\times$  Sibling interaction for the amplitude of all the three components showed that the effect of stimulus orientation varied for adult and child faces as a function of sibling experience. Indeed, an inversion effect was present for adult faces but not for child faces in infants without siblings, while absent for both face ages in infants with siblings.

More specifically, in infants without siblings, the amplitude of the P1 was significantly larger for inverted than upright adult faces, but not child faces, thus showing a selective inversion effect for adult faces only. In the unadjusted analyses, this selective inversion effect carried over to the subsequent N290 and P400 components (see Supplementary Material 2). Moreover, in the no-sibling group, P1 amplitude was also enhanced for child relative to adult faces in the upright, but not inverted, orientation. This finding indicates that the P1 was sensitive to the diagnostic features of facial age, and not to the difference in low-



**Fig. 3.** Peak amplitude values for the P1, N290, and P400 components for infants in the no-sibling and those in the sibling group plotted as a function of face age and orientation. Bar graphs include mean (black lines) and 95% Confidence Interval (gray lines) as well as individual data points. \* indicates significant differences ( $p < .05$ ).

level visual properties (e.g., physical size, local contrast, energy distribution) of the two face categories, which were equalized for luminance and contrast (see Method section). When considering adjusted analyses, the selective inversion effect did not carry over to the N290 nor the P400, but an overall age effect, not specific to the upright orientation nor to one particular infants' group, remained visible at the level of the P400. Once more, considering that the time window chosen to analyze the P400 started at 330 ms after stimulus onset, it is unlikely that this nonspecific age effect reflected the processing of low-level cues of stimuli. Unlike first-born infants, infants with older siblings showed no effects of orientation or age for latency or amplitude of any of the three analyzed components. Therefore, our original hypothesis that there would be an inversion effect for both adult and child faces in infants with siblings was not confirmed.

Overall, these results show that sibling experience modulates the selectivity of infants' electrophysiological responses to upright adult faces at the earliest stages of processing. Indeed, both the effects of stimulus inversion and face age were statistically significant already at the level of the P1, which was clearly visible and quite prominent in our data. As already mentioned, although the P1 has been reported to be sensitive to faces (versus non-face objects, Kuefner et al., 2010) and face manipulations (e.g., face inversion, Taylor et al., 2004; face age: Melinder et al., 2010; Peykarjou et al., 2013) in young children, it has been only occasionally analyzed in infant face processing studies (e.g., Macchi Cassia et al., 2006; Peykarjou et al., 2014). Most importantly, face age was not manipulated as a critical dimension in any of these studies. The P1 in our data was more prominent over right compared to left occipital sites. Although claiming right-lateralization of face processing effects at the P1 in the absence of a ROI that includes medial electrodes sites would be unwarranted, this laterality effect is similar to that reported in 5-year-old children (Kuefner et al., 2010). Moreover, the inversion effects that we observed on the latency and amplitude of the P1 are in line with earlier demonstrations of P1 sensitivity to face orientation in 3- (Peykarjou et al., 2013), 4- (Taylor et al., 2004), and 5-year-old (Melinder et al., 2010) children. Lastly, the age effect for upright faces on the amplitude of the P1 in our first-born infants is in line with previous evidence of P1 sensitivity to face age coming from studies looking at processing of adult and non-adult faces in children (Melinder et al., 2010; Peykarjou et al., 2013).

In adults, the P1 is known to be susceptible to low-level visual characteristics inherent to faces (Rossion and Caharel, 2011; Rossion and Jacques, 2008). However, we believe there are at least three findings that make it unlikely that differences in low-level visual cues of the stimuli, alone, were responsible for the observed P1 amplitude effects in our data. First, the face age effect on P1 amplitude was selective to upright faces; second, the inversion effect on P1 amplitude was selective to adult faces; third, the two above mentioned selective effects were present in infants without siblings but absent in infants with siblings. Together, these findings extend earlier evidence from children (Peykarjou et al., 2013) by showing that, in infants as well, the P1 is sensitive to both the age and orientation of faces, and also to the amount of differential experience with specific face age groups.

Indeed, it is in first-born infants only that the inversion effect for P1 amplitude was specific to adult faces. Although the orientation main effect for P1 latency indicates that these infants showed sensitivity to stimulus inversion for child faces as well, the presence of an orientation by age interaction for the amplitude of the P1 is in line with behavioral demonstrations of perceptual tuning to upright adult (vs. non-adult) faces in 9-month-old infants (Macchi Cassia et al., 2014; Proietti et al., 2018). This finding indicates that perceptual attunement is accompanied by neural specialization for the processing of this familiar face category. This pattern of results resembles the one obtained by previous behavioral and ERP studies showing enhanced perceptual and neural sensitivity to human versus monkey faces (e.g., Halit et al., 2003; Pascalis et al., 2002), and to faces of the ethnic group that is more represented in the infants' social environment (Balas et al., 2011; Kelly

et al., 2007). Our results show that not only the species and ethnicity, but also the age of the faces surrounding the infant, most frequently the caregivers (Sugden et al., 2014), is coded and represented in the infant's brain.

In most of these earlier ERP studies perceptual attunement to a specific face category, as evidenced by stimulus orientation effects, was reported at the level of the N290 and/or P400 components. Importantly, albeit observed, the P1 was not analyzed in any of these earlier investigations, leaving open the question of whether the absolute values of the N290 and/or P400 parameters would show significant modulations even when corrected for the preceding component. Regardless, the finding that, in our study, face age and orientation effects were visible at the level of P1 in infants without siblings may reflect the influence of top-down attentional modulation, which could facilitate the processing of upright adult faces. Indeed, the P1 has been reported to be sensitive to top-down modulation and stimulus saliency in children and adults (Taylor, 2002), and its amplitude has been proposed to vary as a function of attentional engagement to different face ages in children (Peykarjou and Hoehl, 2013). In light of this evidence, the face age and inversion effects on the amplitude of the P1 in infants from the no-sibling group in the current study may reflect differences in attentional engagement towards the two face types. We speculate that the presented female adult faces might have maximally engaged first born infants' attention based on their resemblance to the demographic characteristics of the primary caregiver (the mother in our sample), and other individuals that share the demographics characteristics of the caregiver (see Sugden et al., 2014).

A concurrent explanation of the discrepancies in the results between the present and previous studies is methodological. To the best of our knowledge our study is the first to adopt a fully factorial within-subject design with infants to test ERP modulations induced by face orientation and an additional face manipulation (i.e., face age in the current study). In previous studies looking at orientation and other-species effects, orientation was chosen as the within-subjects variable whereas face species was manipulated between participants (de Haan et al., 2003; Halit et al., 2003). Although we do not have specific predictions about how this difference in the studies' design may have affected results, it is possible that top-down attentional modulation on the P1 favoring the processing of upright adult faces were strengthened in our participants by the concurrent, within-subjects, presentation of multiple face types, which may have enhanced the perceived saliency of upright adult faces.

Overall, the finding that sibling experience significantly impacted the age and orientation effects in our data adds an important piece of evidence to prior work in support of the claim that the emergence of neural specialization for face processing is shaped by the natural statistics of the infant's social environment.

The most critical finding of the current study is the absence of inversion and age effects on the P1 and subsequent components in the group of infants with older siblings. Behavioral studies have shown that consistent exposure to at least one child face, through the presence of an older sibling in the infant's household, is capable of maintaining initial sensitivity to perceptual differences among individual child faces (Proietti et al., 2018). Our results indicate that such perceptual sensitivity is not associated to neural sensitivity to upright child faces, as no inversion effect was observed for child faces in infants with siblings. More crucially, the inversion effect in these infants was absent even for adult faces, suggesting that sibling experience hindered the tuning of face-specific neural circuitries towards upright adult faces.

The finding of non-selective neural activation associated to experience with multiple face ages resonates well with evidence from the language domain, and specifically from research on the development of speech processing in bilingual infants. Electrophysiological evidence suggests that the pattern of changes in bilinguals' brain responses to speech across the first year of life differs from the pattern shown by infants exposed to only one native language (e.g., Petitto et al., 2012). Although selective neural discrimination for native phonetic contrasts



develops by the end of the first year of life in both monolinguals and bilingual infants, at 6–9 months of age only monolinguals show discriminatory response to phonetic contrasts of different languages (Rivera-Gaxiola et al., 2005), while bilinguals show no contrast discrimination for any of the languages to which they are exposed (i.e., English and Spanish) (Garcia-Sierra et al., 2011; Ramirez, Ramirez, Clarke, Taulu, & Kuhl, 2011). Moreover, there is behavioral evidence that, while Catalan monolingual infants discriminate vowel contrasts used in Catalan at the age of 8 months, it takes four more months of language exposure for Spanish-Catalan bilinguals to become able, by the age of 12 months, to perform this same discrimination (Bosch and Sebastián-Gallés, 2003; see also Sebastián-Gallés and Bosch, 2009).

These differences in the developmental pattern of contrast discrimination skills for monolingual and bilingual infants is taken as evidence that exposure to multiple perceptual categories during the first year of life leads to a delay in the process of neural commitment to the acoustic properties of the native language/s (Byers-Heinlein & Fennell, 2014; Kuhl, 2010). This is further supported by evidence showing that the protracted process of establishing native phonological system in bilinguals facilitates subsequent word learning in additional languages. Indeed, unlike their monolingual peers, bilinguals at 18–20 months can learn object labels based on pitch contours (Graf Estes and Hay, 2015) and click consonants (Singh, 2018) that are not used to differentiate words in either of their native languages.

The finding that bilingual infants do not discriminate any phonetic contrast at the age when their monolingual peers show phonetic contrasts discrimination for different languages parallels our observation that infants with siblings fail to show inversion effects for any face type (not adult nor child faces) at the age when their singleton peers show inversion effect for adult faces. This may suggest that same principles that drives neural commitment to phonetic contrasts are relevant for the development of neural commitment to face processing, as the time-window in which perceptual narrowing have been shown to occur overlaps greatly across the language and face processing domains (see Maurer and Werker, 2014; Pascalis et al., 2017).

Greater variability in facial input provided by the presence of older siblings in the infant's household may delay the tuning of neural circuitries to adult faces in infants with siblings, leaving these infants not yet neurally tuned to any specific face age type at 10 months. Such delayed neural tuning could also be influenced by attentional and motivational factors that may differentiate singletons and infants with siblings. Recent evidence suggests that the developmental time course of face processing behavior is influenced by transitions in age-appropriate developmental tasks, which constrain the computational goals of the perceptual system (Picci and Scherf, 2016; Scherf and Scott, 2012). During the first year of life, the task of building an attachment relationship with the caregivers affects infant's motivation to attend to adult (female) faces, which have a unique status within the infant's perceptual environment. It is possible to speculate that, in second-born infants, the drive to build an attachment relationship with the older sibling, which follows a similar developmental trajectory as attachment relationship with caregivers (e.g., Dunn, 1983), may push infants' attentional and processing resources away from adult faces, and towards child faces, thus affecting the timing of the narrowing of neural responses towards adult faces. By this reasoning, neural specialization for adult faces in infants with siblings would be expected to emerge at a later point in time in comparison to first-born infants. This hypothesis could be tested in future studies that may use the same stimulus and methods as in the current investigation with infants older than 10 months. We would expect to observe no difference in neural responses to stimulus inversion for adult faces as a function of sibling experience in these older infants, and a generalized inversion effect for both adult and child faces in the presence of sibling experience.

In conclusion, the current study provides the first evidence that natural variations in the amount of differential experience with adult and non-adult faces during the first year of life affects infants' neural

responses. Although 10 months of experience with adult caregivers are sufficient to induce neural specialization for the processing of adult faces, experience with multiple face ages within the same time frame is associated with non-selective neural activation, suggesting that variability in facial input may delay neural commitment to face processing. These findings provide the first demonstration that sibling experience affects the development of neural specialization for face processing, and offer an important contribution to the understanding of the role of early perceptual experiences in shaping cortical specialization for faces.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.neuropsychologia.2019.03.010>.

## References

- Anastasi, J.S., Rhodes, M.G., 2005. An own-age bias in face recognition for children and older adults. *Psychon. Bull. Rev.* 12 (6), 1043–1047. <https://doi.org/10.3758/BF03206441>.
- Anzures, G., Wheeler, A., Quinn, P.C., Pascalis, O., Slater, A.M., Heron-Delaney, M., ... Lee, K., 2012. Brief daily exposures to Asian females reverses perceptual narrowing for Asian faces in Caucasian infants. *J. Exp. Child Psychol.* 112, 484–495. <https://doi.org/10.1016/j.jecp.2012.04.005>.
- Anzures, G., Quinn, P.C., Pascalis, O., Slater, A.M., Tanaka, J.W., Lee, K., 2013. Developmental origins of the other-race effect. *Curr. Dir. Psychol. Sci.* 22, 173–178. <https://doi.org/10.1177/0963721412474459>.
- Balas, B., Westerlund, A., Hung, K., Nelson, C.A., 2011. Shape, color and the other-race effect in the infant brain. *Dev. Sci.* 14, 892–900. <https://doi.org/10.1111/j.1467-7687.2011.01039>.
- Barry-Anwar, R., Hadley, H., Conte, S., Keil, A., Scott, L.S., 2018. The developmental time course and topographic distribution of individual-level monkey face discrimination in the infant brain. *Neuropsychologia* 108, 25–31. <https://doi.org/10.1016/j.neuropsychologia.2017.11.019>.
- Bruce, V., Young, A., 1986. Understanding face recognition. *Br. J. Psychol.* 77 (3), 305–327. <https://doi.org/10.1111/j.2044-8295.1986.tb02199.x>.
- Byers-Heinlein, K., Fennell, C.T., 2014. Perceptual narrowing in the context of increased variation: insights from bilingual infants. *Dev. Psychobiol.* 56, 274–291. <https://doi.org/10.1002/dev.21167>.
- Bosch, L., Sebastián-Gallés, N., 2003. Simultaneous bilingualism and the perception of a language-specific vowel contrast in the first year of life. *Lang. Speech* 46 (2–3), 217–243. <https://doi.org/10.1177/00238309030460020801>.
- Bulygina, E., Mitteroecker, P., Aiello, L., 2006. Ontogeny of facial dimorphism and patterns of individual development within one human population. *Am. J. Phys. Anthropol.* 131, 432–443. <https://doi.org/10.1002/ajpa.20317>.
- Carver, L.J., Dawson, G., Panagiotides, H., Meltzoff, A.N., McPartland, J., Gray, J., Munson, J., 2003. Age-related differences in neural correlates of face recognition during the toddler and preschool years. *Dev. Psychobiol.* 42 (2), 148–159. <https://doi.org/10.1002/dev.10078>.
- Dawson, G., Carver, L., Meltzoff, A.N., Panagiotides, H., McPartland, J., Webb, S.J., 2002. Neural correlates of face and object recognition in young children with autism spectrum disorder, developmental delay, and typical development. *Child Dev.* 73 (3), 700–717. <https://doi.org/10.1111/1467-8624.00433>.
- de Haan, M., Nelson, C.A., 1999. Brain activity differentiates face and object processing in 6-month-old infants. *Dev. Psychol.* 35, 1113–1121. <https://doi.org/10.1037/0012-1649.35.4.1113>.
- de Haan, M., Pascalis, O., Johnson, M.H., 2002. Specialization of neural mechanisms underlying face recognition in human infants. *J. Cogn. Neurosci.* 14, 199–209. <https://doi.org/10.1162/089892902317236849>.
- de Haan, M., Johnson, M.H., Halit, H., 2003. Development of face-sensitive event-related potentials during infancy: a review. *Int. J. Psychophysiol.* 51, 45–58. [https://doi.org/10.1016/S0167-8760\(03\)00152-1](https://doi.org/10.1016/S0167-8760(03)00152-1).
- de Heering, A., Rossion, B., 2015. Rapid categorization of natural face images in the infant right hemisphere. *eLife* 4, 1–14. <https://doi.org/10.7554/eLife.06564.001>.
- DeBoer, T., Scott, L.S., Nelson, C.A., 2005. Event-related potentials in developmental populations. In: Todd, Handy (Ed.), *Methodological Handbook for Research Using Event-Related Potentials*. The MIT Press, Cambridge, MA, pp. 263–297.
- Dunn, J., 1983. Sibling relationships in early childhood. *Child Dev* 787–811.
- Erwin, R.J., Gur, R.C., Gur, R.E., Skolnick, B., Mawhinney-Hee, M., Smailis, J., 1992. Facial emotion discrimination: I. Task construction and behavioral findings in normal subjects. *Psychiatr. Res.* 42 (3), 231–240. [https://doi.org/10.1016/0165-1781\(92\)90115-J](https://doi.org/10.1016/0165-1781(92)90115-J).
- Farkas, L.G., Ngim, R.C., Lee, S.T., 1988. The fourth dimension of the face: a preliminary report of growth potential in the face of the Chinese population of Singapore. *Ann. Acad. Med. Singapore* 17, 319–327.
- Farzin, F., Hou, C., Norcia, A.M., 2012. Piecing it together: infants' neural responses to face and object structure. *J. Vis.* 12 <https://doi.org/10.1167/12.13.6>. 6–6.
- Ferguson, K.T., Kulkofsky, S., Cashion, C.H., Casasola, M., 2009. The development of specialized processing of own-race faces in infancy. *Infancy* 14, 263–284. <https://doi.org/10.1080/15250000902839369>.

- Gaither, S.E., Pauker, K., Johnson, S.P., 2012. Biracial and monoracial infant own-race face perception: an eye tracking study. *Dev. Sci.* 15, 775–782. <https://doi.org/10.1111/j.1467-7687.2012.01170.x>.
- García-Sierra, A., Rivera-Gaxiola, M., Percaccio, C.R., Conboy, B.T., Romo, H., Klarman, L., et al., 2011. Bilingual language learning: an ERP study relating early brain responses to speech, language input, and later word production. *J. Phonet.* 39, 546–557. <https://doi.org/10.1016/j.wocn.2011.07.002>.
- Gomez, J., Barnett, M.A., Natsu, V., Mezer, A., Palomero-Gallagher, N., Weiner, K.S., et al., 2017. Microstructural proliferation in human cortex is coupled with the development of face processing. *Science* 355 (6320), 68–71. <https://doi.org/10.1126/science.aag0311>.
- Graf Estes, K., Hay, J.F., 2015. Flexibility in bilingual infants' word learning. *Child Dev.* 86 (5), 1371–1385. <https://doi.org/10.1111/cdev.12392>.
- Greenough, W.T., Black, J.E., Wallace, C.S., 1987. Experience and brain development. *Child Dev.* 539–559. <https://doi.org/10.2307/1130197>.
- Guy, M.W., Zieber, N., Richards, J.E., 2016. The cortical development of specialized face processing in infancy. *Child Dev.* 87 (5), 1581–1600. <https://doi.org/10.1111/cdev.12543>.
- Haist, F., Anzures, G., 2017. Functional development of the brain's face-processing system. *Wiley Interdisciplinary Reviews: Cogn. Sci.* 8, 1–12. <https://doi.org/10.1002/wcs.1002/wcs>.
- Halit, H., De Haan, M., Johnson, M.H., 2003. Cortical specialisation for face processing: face-sensitive event-related potential components in 3- and 12-month-old infants. *Neuroimage* 19, 1180–1193. [https://doi.org/10.1016/S1053-8119\(03\)00076-4](https://doi.org/10.1016/S1053-8119(03)00076-4).
- Halit, H., Csibra, G., Volein, A., Johnson, M.H., 2004. Face-sensitive cortical processing in early infancy. *J. Child Psychol. Psychiatry Allied Discip.* 45, 1228–1234. <https://doi.org/10.1111/j.1469-7610.2004.00321.x>.
- Haxby, J.V., Hoffman, E.A., Gobbini, M.I., 2000. The distributed human neural system for face perception. *Trends Cognit. Sci.* 4, 223–233. [https://doi.org/10.1016/S1364-6613\(00\)01482-0](https://doi.org/10.1016/S1364-6613(00)01482-0).
- Heron-Delaney, M., Anzures, G., Herbert, J.S., Quinn, P.C., Slater, A.M., Tanaka, J.W., Lee, K., Pascalis, O., 2011. Perceptual training prevents the emergence of the other race effect during infancy. *PLoS One* 6, e19858. <https://doi.org/10.1371/journal.pone.0019858>.
- Itier, R.J., Taylor, M.J., 2002. Inversion and contrast reversal affect both encoding and recognition of faces: a repetition study using ERPs. *Neuroimage* 15, 353–372. <https://doi.org/10.1006/nimg.2001.0982>.
- Itier, R.J., Taylor, M.J., 2004. Face recognition and configural processing: a developmental ERP study using upright, inverted and contrast-reversed faces. *J. Cogn. Neurosci.* 16, 1–15. <https://doi.org/10.1162/089992904322926818>.
- Jayaraman, S., Fausey, C.M., Smith, L.B., 2017. Why are faces denser in the visual experiences of younger than older infants? *Dev. Psychol.* 53 (1), 38. <https://doi.org/10.1037/dev0000230>.
- Johnson, M.H., Dziurawiec, S., Ellis, H., Morton, J., 1991. Newborns' preferential tracking of face-like stimuli and its subsequent decline. *Cognition* 40, 1–19. [https://doi.org/10.1016/0010-0277\(91\)90045-6](https://doi.org/10.1016/0010-0277(91)90045-6).
- Kadosh, K.C., Johnson, M.H., 2007. Developing a cortex specialized for face perception. *Trends Cognit. Sci.* 11, 367–369. <https://doi.org/10.1016/j.tics.2007.06.007>.
- Kelly, D.J., Quinn, P.C., Slater, A.M., Lee, K., Ge, L., Pascalis, O., 2007. The other-race effect develops during infancy: evidence of perceptual narrowing. *Psychol. Sci.* 18, 1084–1089. <https://doi.org/10.1111/j.1467-9280.2007.02029.x>.
- Key, A.P.F., Stone, W., Williams, S.M., 2009. What do infants see in faces? ERP evidence of different roles of eyes and mouth for face perception in 9-month-olds. *Infant Child Dev.* 18, 149–162. <https://doi.org/10.1002/icd.600>.
- Kobayashi, M., Macchi Cassia, V., Kanazawa, S., Yamaguchi, M.K., Kakigi, R., 2018. Perceptual narrowing towards adult faces is a cross-cultural phenomenon in infancy: a behavioral and near-infrared spectroscopy study with Japanese infants. *Dev. Sci.* 21. <https://doi.org/10.1111/desc.12498>.
- Kuefner, D., de Heering, A., Jacques, C., Palmero-Soler, E., Rossion, B., 2010. Early visually evoked electrophysiological responses over the human brain (P1, N170) show stable patterns of face-sensitivity from 4 years to adulthood. *Front. Hum. Neurosci.* 3, 67. <https://doi.org/10.3389/fnhum.2010.0067>.
- Kuhl, P.K., 2010. Brain mechanisms in early language acquisition. *Neuron* 67, 713–727. <https://doi.org/10.1016/j.neuron.2010.08.038>.
- Lewin, C., Herlitz, A., 2002. Sex differences in face recognition—Women's faces make the difference. *Brain Cogn.* 50 (1), 121–128. [https://doi.org/10.1016/S0278-2626\(02\)00016-7](https://doi.org/10.1016/S0278-2626(02)00016-7).
- Liu, S., Quinn, P.C., Wheeler, A., Xiao, N., Ge, L., Lee, K., 2011. Similarity and difference in the processing of same-and other-race faces as revealed by eye tracking in 4-to 9-month-olds. *J. Exp. Child Psychol.* 108, 180–189. <https://doi.org/10.1016/j.jecp.2010.06.008>.
- Lochy, A., de Heering, A., Rossion, B., 2017. The non-linear development of the right hemispheric specialization for human face perception. *Neuropsychologia*. <https://doi.org/10.1016/j.neuropsychologia.2017.06.029>.
- Luck, S.J., 2005. *An Introduction to the Event-Related Potential Technique*. MIT Press, Cambridge, MA.
- Luyster, R.J., Powell, C., Tager-Flusberg, H., Nelson, C.A., 2014. Neural measures of social attention across the first years of life: characterizing typical development and markers of autism risk. *Developmental cognitive neuroscience* 8, 131–143. <https://doi.org/10.1016/j.dcn.2013.09.006>.
- Macchi Cassia, V., Turati, C., Simion, F., 2004. Can a nonspecific bias toward top-heavy patterns explain newborns' face preference? *Psychol. Sci.* 15 (6), 379–383. <https://doi.org/10.1111/j.0956-7976.2004.00688.x>.
- Macchi Cassia, V., Kuefner, D., Westerlund, A., Nelson, C.A., 2006. A behavioural and ERP investigation of 3-month-olds' face preferences. *Neuropsychologia* 44, 2113–2125. <https://doi.org/10.1016/j.neuropsychologia.2005.11.014>.
- Macchi Cassia, V.M., Picozzi, M., Kuefner, D., Bricolo, E., Turati, C., 2009. Holistic processing for faces and cars in preschool-aged children and adults: evidence from the composite effect. *Dev. Sci.* 12, 236–248. <https://doi.org/10.1371/journal.pone.0099942>.
- Macchi Cassia, V., Bulf, H., Quadrelli, E., Proietti, V., 2014. Age-related face processing bias in infancy: evidence of perceptual narrowing for adult faces. *Dev. Psychobiol.* 56, 238–248. <https://doi.org/10.1002/dev.21191>.
- Maurer, D., Werker, J.F., 2014. Perceptual narrowing during infancy: a comparison of language and faces. *Dev. Psychobiol.* 56, 154–178. <https://doi.org/10.1002/dev.21177>.
- McCleery, J.P., Akshoomoff, N., Dobkins, K.R., Carver, L.J., 2009. Atypical face versus object processing and hemispheric asymmetries in 10-month-old infants at risk for autism. *Biol. Psychiatry* 66, 950–957. <https://doi.org/10.1016/j.biopsych.2009.07.031>.
- Melinder, A., Gredebäck, G., Westerlund, A., Nelson, C.A., 2010. Brain activation during upright and inverted encoding of own-and other-age faces: ERP evidence for an own-age bias. *Dev. Sci.* 13, 588–598. <https://doi.org/10.1111/j.1467-7687.2009.00910.x>.
- Pascalis, O., de Haan, M., Nelson, C.A., 2002. Is face processing species-specific during the first year of life? *Science* 296, 1321–1323. <https://doi.org/10.1126/science.1070223>.
- Pascalis, O., Scott, L.S., Kelly, D.J., Shannon, R.W., Nicholson, E., Coleman, M., Nelson, C.A., 2005. Plasticity of face processing in infancy. *Proc. Natl. Acad. Sci. Unit. States Am.* 102, 5297–5300. <https://doi.org/10.1073/pnas.0406627102>.
- Pascalis, O., Dole, M., Loevenbruck, H., 2017. More evidence of the linkage between face processing and language processing. *Br. J. Psychol.* 108, 31–33. <https://doi.org/10.1111/bjop.12228>.
- Petit, L.A., Berens, M.S., Kovelman, I., Dubins, M.H., Jasinska, K., Shalinsky, M., 2012. The “Perceptual Wedge Hypothesis” as the basis for bilingual babies' phonetic processing advantage: new insights from fNIRS brain imaging. *Brain Lang.* 121, 130–143. <https://doi.org/10.1016/j.bandl.2011.05.003>.
- Peyskarjou, S., Hoehl, S., 2013. Three-month-olds' brain responses to upright and inverted faces and cars. *Dev. Neuropsychol.* 38, 272–280. <https://doi.org/10.1167/15.12.794>.
- Peyskarjou, S., Westerlund, A., Macchi Cassia, V., Kuefner, D., Nelson, C.A., 2013. The neural correlates of processing newborn and adult faces in 3-year-old children. *Dev. Sci.* 16, 905–914. <https://doi.org/10.1111/desc.12063>.
- Peyskarjou, S., Pauen, S., Hoehl, S., 2014. How do 9-month-old infants categorize human and ape faces? A rapid repetition ERP study. *Psychophysiology* 51, 866–878. <https://doi.org/10.1111/psyp.12238>.
- Picci, G., Scherf, K.S., 2016. From caregivers to peers: puberty shapes human face perception. *Psychol. Sci.* 27, 1461–1473. <https://doi.org/10.1177/0956797616663142>.
- Picton, T.W., Bentin, S., Berg, P., Donchin, E., Hillyard, S.A., Johnson, R., et al., 2000. Guidelines for using human event-related potentials to study cognition: recording standards and publication criteria. *Psychophysiology* 37, 127–152. <https://doi.org/10.1111/1469-8986.3720127>.
- Proietti, V., Rigoldi, M., Croci, E., Macchi Cassia, V., 2018. Sibling experience modulates perceptual narrowing toward adult faces in the first year of life. *Dev. Psychobiol.* <https://doi.org/10.1002/dev.21616>.
- Rennels, J.L., Davis, R.E., 2008. Facial experience during the first year. *Infant Behav. Dev.* 31, 665–678. <https://doi.org/10.1016/j.infbeh.2008.04.009>.
- Righi, G., Westerlund, A., Congdon, E.L., Troller-Renfree, S., Nelson, C.A., 2014. Infants' experience-dependent processing of male and female faces: insights from eye tracking and event-related potentials. *Developmental Cognitive Neurosci.* 8, 144–152. <https://doi.org/10.1016/j.dcn.2013.09.005>.
- Rivera-Gaxiola, M., Silva-Pereyra, J., Kuhl, P.K., 2005. Brain potentials to native and non-native speech contrasts in 7- and 11-month-old American infants. *Dev. Sci.* 8, 162–172. <https://doi.org/10.1111/j.1467-7687.2005.00403.x>.
- Rossion, B., Caharel, S., 2011. ERP evidence for the speed of face categorization in the human brain: disentangling the contribution of low-level visual cues from face perception. *Vis. Res.* 51, 1297–1311. <https://doi.org/10.1016/j.visres.2011.04.003>.
- Rossion, B., Jacques, C., 2008. Does physical interstimulus variance account for early electrophysiological face sensitive responses in the human brain? Ten lessons on the N170. *Neuroimage* 39, 1959–1979. <https://doi.org/10.1016/j.neuroimage.2007.10.011>.
- Rossion, B., Delvenne, J.F., Debatiste, D., Goffaux, V., Bruyer, R., Crommelinck, M., Guérin, J.M., 1999. Spatio-temporal localization of the face inversion effect: an event-related potentials study. *Biol. Psychol.* 50, 173–189. [https://doi.org/10.1016/S0301-0511\(99\)00013-7](https://doi.org/10.1016/S0301-0511(99)00013-7).
- Rossion, B., Joyce, C.A., Cottrell, G.W., Tarr, M.J., 2003. Early lateralization and orientation tuning for face, word, and object processing in the visual cortex. *Neuroimage* 20, 1609–1624. <https://doi.org/10.1016/j.neuroimage.2003.07.010>.
- Scherf, K.S., Scott, L.S., 2012. Connecting developmental trajectories: biases in face processing from infancy to adulthood. *Dev. Psychobiol.* 54 (6), 643–663. <http://doi.org/10.1002/dev.21013>.
- Scott, L.S., Monesson, A., 2009. The origin of biases in face perception. *Psychol. Sci.* 20, 676–680. <https://doi.org/10.1111/j.1467-9280.2009.02348.x>.
- Scott, L.S., Monesson, A., 2010. Experience-dependent neural specialization during infancy. *Neuropsychologia* 48, 1857–1861. <https://doi.org/10.1016/j.neuropsychologia.2010.02.008>.
- Scott, L.S., Shannon, R.W., Nelson, C.A., 2006. Neural correlates of human and monkey face processing in 9-month-old infants. *Infancy* 10, 171–186. <https://doi.org/10.1207/s15327078in10024>.
- Sebastian-Gallés, N., Bosch, L., 2009. Developmental shift in the discrimination of vowel contrasts in bilingual infants: is the distributional account all there is to it? *Dev. Sci.* 12, 874–887. <https://doi.org/10.1111/j.1467-7687.2009.00829.x>.
- Simpson, E.A., Varga, K., Frick, J.E., Fragasz, D., 2011. Infants experience perceptual

- narrowing for nonprimate faces. *Infancy* 16 (3), 318–328. <https://doi.org/10.1111/j.1532-7078.2010.00052.x>.
- Singh, L., 2018. Bilingual infants demonstrate advantages in learning words in a third language. *Child Dev.* 89 (4), e397–e413. <https://doi.org/10.1111/cdev.12852>.
- Stets, M., Stahl, D., Reid, V.M., 2012. A meta-analysis investigating factors underlying attrition rates in infant ERP studies. *Dev. Neuropsychol.* 37 (3), 226–252.
- Sugden, N.A., Mohamed-Ali, M.I., Moulson, M.C., 2014. I spy with my little eye: typical daily exposure to faces documented from a first-person infant perspective. *Dev. Psychobiol.* 56, 249–261. <https://doi.org/10.1002/dev.21183>.
- Taylor, M.J., 2002. Non-spatial attentional effects on P1. *Clin. Neurophysiol.* 113 (12), 1903–1908. [https://doi.org/10.1016/S1388-2457\(02\)00309-7](https://doi.org/10.1016/S1388-2457(02)00309-7).
- Taylor, M.J., Batty, M., Itier, R.J., 2004. The faces of development: a review of early face processing over childhood. *J. Cogn. Neurosci.* 16, 1426–1442. <https://doi.org/10.1162/0898929042304732>.
- Valenza, E., Simion, F., Cassia, V.M., Umiltà, C., 1996. Face preference at birth. *J. Exp. Psychol. Hum. Percept. Perform.* 22, 892–903. <https://doi.org/10.1037/0096-1523.22.4.892>.
- Vogel, M., Monesson, A., Scott, L.S., 2012. Building biases in infancy: the influence of race on face and voice emotion matching. *Dev. Sci.* 15, 359–372. <https://doi.org/10.1111/j.1467-7687.2012.01138.x>.