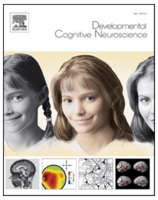
Developmental Cognitive Neuroscience 48 (2021) 100918

Contents lists available at ScienceDirect

Developmental Cognitive Neuroscience

journal homepage: www.elsevier.com/locate/dcn



Maturation of hemispheric specialization for face encoding during infancy and toddlerhood

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ARTICLE INFO

Keywords:
Infant
Magnetoencephalography
Face
Fusiform gyrus
Right hemisphere

ABSTRACT

Little is known about the neural processes associated with attending to social stimuli during infancy and toddlerhood. Using infant magnetoencephalography (MEG), fusiform gyrus (FFG) activity while processing Face and Non-Face stimuli was examined in 46 typically developing infants 3 to 24 months old (28 males). Several findings indicated FFG maturation throughout the first two years of life. First, right FFG responses to Face stimuli decreased as a function of age. Second, hemispheric specialization to the face stimuli developed somewhat slowly, with earlier right than left FFG peak activity most evident after 1 year of age. Right FFG activity to Face stimuli was of clinical interest, with an earlier right FFG response associated with better performance on tests assessing social and cognitive ability. Building on the above, clinical studies examining maturational change in FFG activity (e.g., lateralization and speed) in infants at-risk for childhood disorders associated with social deficits are of interest to identify atypical FFG maturation before a formal diagnosis is possible.

1. Introduction

Orienting to social cues, such as showing a preference for face over non-face stimuli, is an ability that develops during infancy (de Heering and Rossion, 2015). In particular, throughout infancy and toddlerhood the brain develops a network that recognizes faces as salient visual stimuli, with this ability considered essential to acquiring the social communication skills that emerge during preschool years (Dawson et al., 2004; Sperdin et al., 2018).

In adults, an evoked response referred to as N170 in electroencephalography (EEG) (Pizzagalli et al., 2002) and M170 in magnetoencephalography (MEG) (Liu et al., 2000) occurs ~170 ms after stimulus onset, and is larger and earlier to faces versus objects (Bentin et al., 1996; Rebai et al., 2001). The N170/M170 response is largest over occipital and temporal scalp locations, and localizes to left and right fusiform gyrus (FFG) (Deffke et al., 2007; Henson et al., 2009; Halgren et al., 2000). In infants and young children, the evoked responses associated with processing faces are referred to as the N290 and P400 (de Haan et al., 2003; Halit et al., 2003; de Haan and Nelson, 1999). N290 and P400 amplitude differences between faces and meaningless patterns or objects are frequently reported (Halit et al., 2004; Kouider et al., 2013; de Haan and Nelson, 1999; Peykarjou and Hoehl, 2013; Gliga and Dehaene-Lambertz, 2007). As an example comparing ERPs between faces and toys in 4.5- to 7.5-month-old infants, Guys et al. (Guy et al., 2016) showed a larger N290 amplitude to faces than toys, versus a larger P400 amplitude to toys than faces. This study also showed different cortical sources for N290 and P400, with N290 reflecting activity in occipital-temporal regions and P400 reflecting activity in midline frontal, parietal, temporal and occipital regions (i.e., many brain areas). And in a study examining only face stimuli, Xie et al. (Xie et al., 2019) showed differences between angry, fearful, and happy faces in 5-, 7-, and 12-month-old infants. In particular, they observed a larger right occipital N290 response to fearful faces versus other conditions, and a larger P400 and Nc response to angry faces versus the other conditions (and with P400/Nc reflecting activity in posterior cingulate cortex (PCC) and Precuneus areas). Interestingly, this effect of facial

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https://doi.org/10.1016/j.dcn.2021.100918
Received 30 April 2020; Received in revised form 28 December 2020; Accepted 8 January 2021

emotion emerged at 5 months, was firmly established at 7 months, but then was not observed at 12 months. The above studies highlight regional differences in brain activity when viewing faces as well as demonstrate the need to examine brain activity at the resolution of milliseconds.

With respect to regional differences, during infancy a hemisphere specialization for faces seems to be important for developing 'face expertise' (Le Grand et al., 2003), with studies showing that socially advantaged humans are more right lateralized for face processing than socially disadvantaged humans (Boliek and Obrzut, 1995; Geffner and Hochberg, 1971; McGlone, 1978). A right-hemisphere preference for faces may emerge during infancy (de Heering and Rossion, 2015), and thus it is possible that the degree of hemispheric lateralization for faces early in life might serve as a measure of when the brain starts to specialize in identifying social stimuli, and thus a potential index of how the brain prepares for the higher-level cognitive and social processes needed later in life.

Although brain responses associated with face processing are observed during infancy, little is known about the maturation of hemispheric specialization for faces during the first two years of life. Neural responses associated with face processing involve a wide network of brain regions (Fusar-Poli et al., 2009; Haxby et al., 2000), with the FFG a central node in the face processing network, as demonstrated by fMRI and MEG studies (Grill-Spector et al., 2004; Halgren et al., 2000; Haxby et al., 1999; Kanwisher et al., 1997; Pourtois et al., 2010; Watanabe et al., 1999). There is thus a need for infant studies that evaluate FFG face processing at the source (brain) level rather than sensor measures in order to optimally understand how FFG matures during infancy. To this end, the present study used an infant whole-head MEG system (Artemis 123; (Roberts et al., 2014)), optimized to accommodate infants and young children up to the median 3-year-old head circumference, to assess the maturation of left and right FFG activity to face stimuli in typically developing (TD) infants.

The infant MEG system is optimal for studying brain activity in infants and young children given the reduced distance between sources of brain activity and the MEG sensors (Okada et al., 2006; Roberts et al., 2014; Okada et al., 2016; Johnson et al., 2010), therefore providing greater sensitivity and spatial resolution (Okada et al., 2006). Two other whole-head infant MEG systems have been developed. The Artemis 123™ (Tristan Technologies Inc., San Diego, California, US), used in the present study, was designed for use with children from birth to 3 years of age (Roberts et al., 2014). The second and most recently developed infant MEG system BabyMEG (Tristan Technologies Inc., San Diego, California, US), is located at Boston Children's Hospital (Okada et al., 2016). Given that customized whole-head infant MEG systems have only been recently developed, very few studies have studied the maturation of infant neural activity (lower-level sensory processes as well as higher-level social and cognitive processes). In particular, to date, MEG studies have only examined face processing in children 3 years and older (see review in (Chen et al., 2019)). To our knowledge, no study has used MEG with distributed source modeling to examine the maturation of FFG responses to faces from infancy to toddlerhood.

Study goals were: (a) identify FFG responses (latency and amplitude) to face stimuli in infants 3 to 24 months; (b) evaluate FFG responses and hemispheric specialization to face and non-face stimuli as a function of age; and (c) examine associations between FFG activity and social and cognitive ability. It was hypothesized that FFG response latency to face stimuli would decrease and FFG strength increase as a function of age, with stronger FFG responses occurring in the right than left hemisphere, and with faster processing of face stimuli associated with better social and cognitive ability. Findings would provide FFG 'growth curves' associated with face processing.

2. Materials and methods

2.1. Participants

Fifty-nine TD infants were enrolled. Evaluable MEG data were obtained from 46 TD infants 3 to 24 months (28 males, mean age 358 ± 196 days). Thirteen MEG datasets were excluded due to excessive artifact, the infant unable to tolerate the scan, or the infant falling asleep (8 male, mean age 197 days). Inclusion criteria were: (1) no seizure disorder in the infant or immediate family member; (2) no premature birth (later than 37 weeks gestation); (3) no non-removable metal in the body; (4) no known hearing or visual impairment; and (5) no concerns regarding language or developmental delay. Participants were included or excluded based on parental report and review of medical records. The study was approved by the Children's Hospital of Philadelphia IRB and all families gave written consent.

2.2. Stimuli

Stimuli consisted of 80 color images of Face stimuli (NimStim) and 80 matched visual noise images that served as Non-Face stimuli (Fig. 1A). Face stimuli were color photos of faces exhibiting a happy expression (37 female adults, 43 male adults), selected from the NimStim Face Stimulus Set (Tottenham et al., 2009). Using the approach described in Halit et al. (Halit et al., 2004), the Non-Face stimuli were created to match the frequency content (spatial frequency), color distribution, and outer contour of the Face stimuli. Given that studies have shown that face-selective response in infants and toddlers might be due to differences in spatial frequency (Cassia et al., 2004; de Heering et al., 2008; Simion et al., 2007; Macchi Cassia et al., 2011), such Non-Face control stimuli are ideal for use across infants and adults. It is, however, of note that the control stimuli used in infant face research is a topic of discussion. For example, although houses or toys are sometimes used as control Non-Face stimuli, these stimuli are generally not matched to the face stimuli with respect to low-level psychophysical properties such as spatial frequency. As described in Halit et al. (Halit et al., 2004), this is a concern in infant studies where such factors are known to influence preference and processing of visual stimuli (Banks and Salapatek, 1981) as well as possibly engaging other brain regions or circuits involved in action planning (e.g., 12-month-old infants who view images of toys they might plan to grab versus 3-month-old infants who view images of houses although they might not have yet seen the outside of a house) (Kaufman et al., 2003). In addition, and with respect to the present study, it is of note that images of non-face objects such as houses or toys have a vastly different importance to children 3 months old versus 2 years old (and even across different 2-year-old children). Given the purpose of the present study, using toy or house objects as a contrast condition was not ideal given the goal of evaluating the maturation of cortical responses to faces from 3 to 24 months of age. As such, in the present study, Non-Face stimuli were produced by randomizing the phase spectrum of each face picture (overlaid on a head shape). Non-Face stimuli thus retained the amplitude and color spectra as well as the contour of the face stimulus, but were not identifiable as a face (see Fig. 1A).

All stimuli were presented against a black background with a horizontal visual angle of 12.6 degrees, a vertical angle of 18.9 degrees, and a viewing distance of 45 cm. Stimulus duration was 1500 ms and the inter-stimulus interval varied randomly between 800 and 1200 ms (Fig. 1A). Face and Non-Face stimuli were randomly presented and no stimulus was repeated. Thus, each participant was shown 80 unique Face and 80 unique Non-Face stimuli.

2.3. Social and cognitive measures

Socialization skills were measured using the Vineland Adaptive Behavior Scales-Third Edition (VABS-III; (Sparrow et al., 2016).

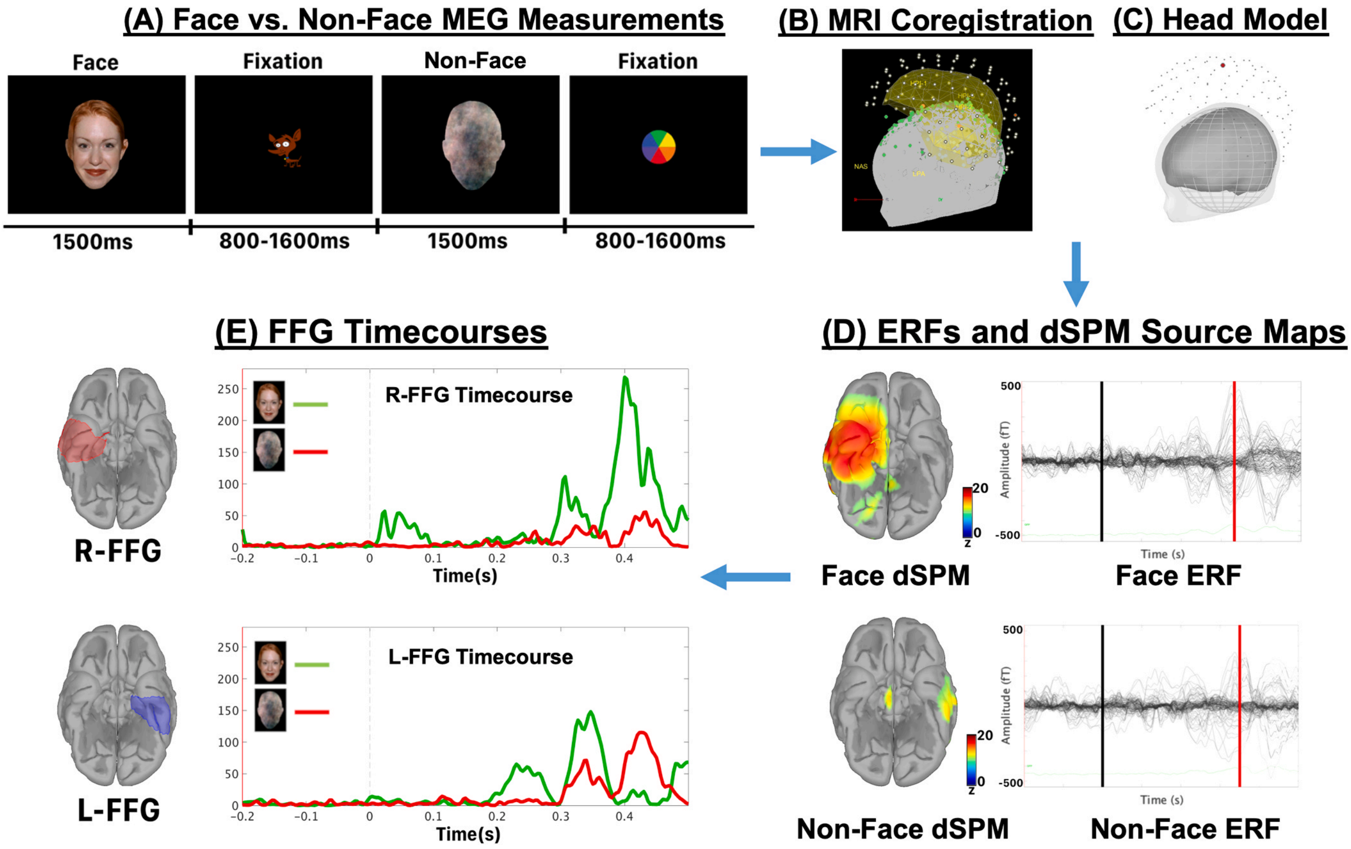

Fig. 1. Illustration of MEG task and analysis pipeline. (A) Face versus Non-Face paradigm; (B) The relative locations of the MEG sensors and digitized head surface points after MEG and MRI coregistration; (C) Overlapping spheres head model; (D) Averaged event-related fields (ERFs) and dSPM solutions for Face and Non-Face conditions from a 6-month-old infant; (E) Averaged source time course, averaging activity across all FFG vertices, and assessing left and right FFG activity for the Face (green line) and Non-Face (red line) conditions from a 6-month-old infant (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

VABS-III is a parent-report questionnaire of everyday skills in the domains of Communication, Daily Living Skills, Socialization, and Motor Skills. Social ability was operationalized as the total raw score of the Socialization Domain from the VABS-III, which includes the ‘Interpersonal Relationships’, and ‘Play and Leisure Time’ subdomains.

Cognitive ability was measured using either the Bayley Scales of Infant and Toddler Development-Third Edition (BSID; (Bayley, 2006) or the Mullen Scales of Early Learning (MSEL; (Mullen, 1995)). The BSID provides a clinical assessment of motor (fine and gross), language (receptive and expressive), and cognitive development in infants and toddlers from birth to 42 months. The MSEL provides a clinical assessment of verbal and non-verbal abilities, and is appropriate for children from birth to 68 months. The MSEL includes Visual Reception, Fine Motor, Receptive Language, and Expressive Language domains. Cognitive ability was operationalized as the age equivalent (in months) for the MSEL Visual Reception domain or the BSID Cognitive subscale. Age equivalents are derived (from the assessment tool’s standardization sample) as the median raw scale score for a particular age level.

2.4. MEG data acquisition

Infant whole-head MEG data were recorded in a magnetically shielded room (Vacuumschmelze GmbH & Co. KG, Hanau, Germany) using Artemis 123™ (Tristan Technologies Inc., San Diego, CA, USA) with a sampling rate of 5000 Hz and a 0.1 Hz high-pass filter. The Artemis 123 was designed for use with children from birth to 3 years of age (Roberts et al., 2014; Edgar et al., 2015). This system has 123 sensors (first-order axial gradiometers) and a helmet circumference of 50 cm, which corresponds to the median head circumference of a 3 year old in the US. The Artemis 123 employs a coil-in-vacuum sensor configuration to minimize the distance between the helmet surface and sensors (6 to 9 mm). During the MEG recording, the child’s head position was continuously monitored using 4 head position indicator (HPI) coils attached to a fabric cap the child wore during the scan.

Several strategies helped keep the child calm and engaged during the MEG exam. First, a research assistant with experience scanning infants and young children stood next to the child and helped the parent keep the child calm and alert during the exam. Second, if needed, short breaks were provided, with snacks (e.g., bottle) or age-appropriate toys provided to calm the child. Third, if the parent allowed, children younger than 9 months were swaddled to reduce motion. Forth, as infants prefer novel stimuli, if the child appeared to be losing interest in the face task we briefly paused the task to instead show an age-appropriate movie or provided toys to hold in their hands.

2.5. Magnetic source analyses

MEG data were analyzed using Brainstorm (Tadel et al., 2011) (http://neuroimage.usc.edu/brainstorm). MEG data were down-sampled to 300 Hz and then band-pass filtered 3 to 55 Hz (low transition: 1.5 to 3.0 Hz, high transition: 55 to 63.25 Hz, stopband attenuation at 60 Hz) and with a 60 Hz notch filter. Heartbeat artifact was removed via independent component analyses (ICA). Other artifacts (e.g., movement, environmental noise) were visually identified and manually removed. During the scan, the time when the child was not attending to the stimuli was noted (e.g., crying, falling asleep) and these periods manually removed. In addition to removing data containing excessive artifacts due to motion or magnetic noise, trials with amplitude exceeding 500 fT were excluded. The average length of the MEG recording was 714 second, including breaks (SD = 106 seconds; range = 559 to 1172 seconds). The average amount data removed due to artifact (e.g., movement, magnetic noise) was 65 seconds (SD = 54 seconds; range 5 to 269 second).

Face and Non-Face event-related fields (ERFs) were created by averaging epochs 200 ms pre-stimulus to 500 ms post-stimulus. On average 71.8 ± 12.9 Face trials and 72.8 ± 12.4 Non-Face trials were averaged to obtain Face and Non-Face ERFs. There was no significant difference in number of accepted trials between conditions. For each child, MEG data were coregistered to a 1-year-old infant MRI template with Tzourio-Mazoyer surface atlas (http://neuroimage.usc.edu/forum

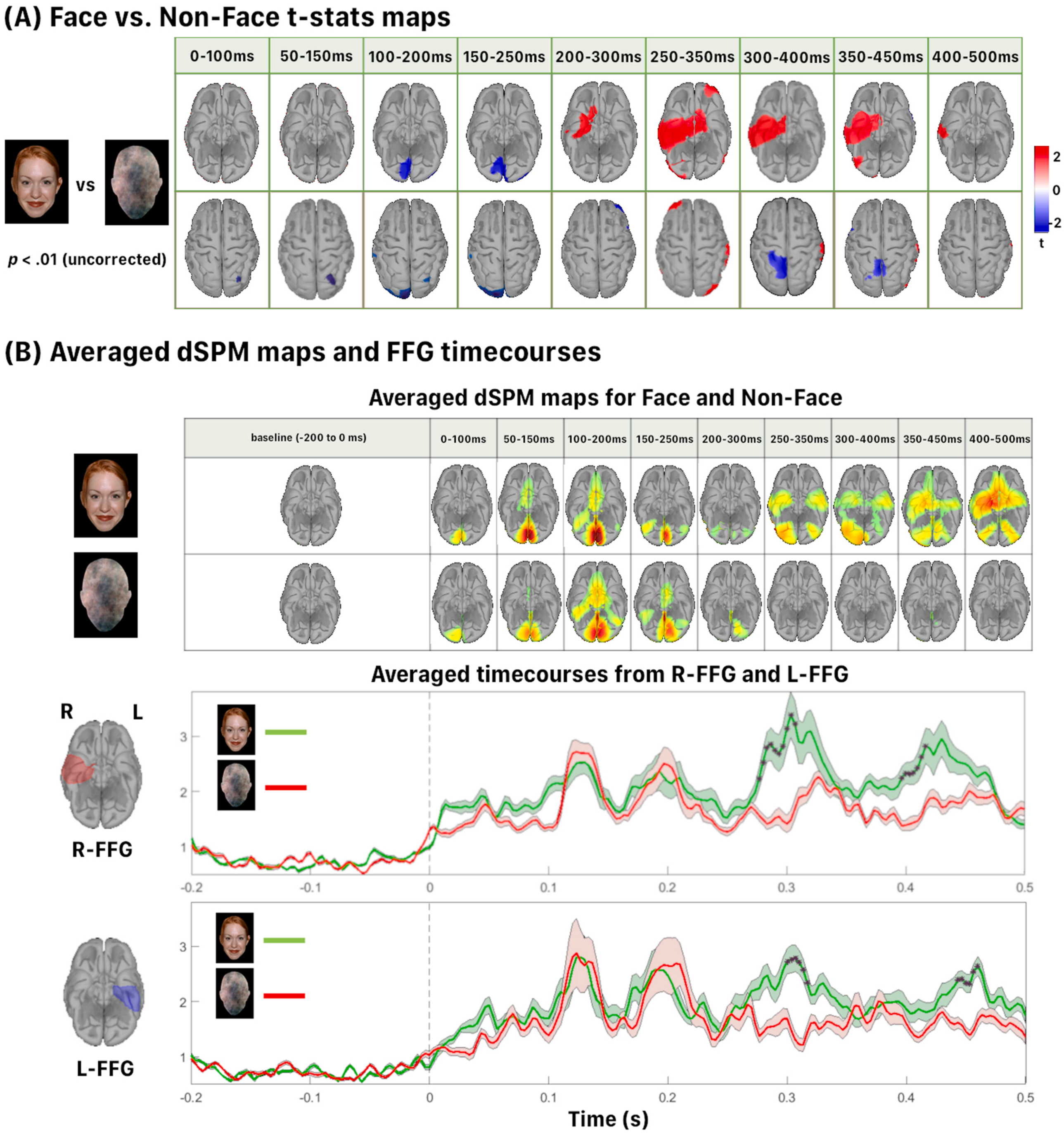

Fig. 2. Infant whole-brain responses to Face and Non-Face stimuli. (A) Face versus Non-Face t-statistic (vertices by vertices t-tests) contrast maps of dSPM solutions for each time window. The top and the bottom rows show the ventral and dorsal views of the condition difference, respectively. Red blobs indicate stronger activity in the Face than Non-Face condition, and blue blobs weaker activity in the Face than Non-Face condition ($p < 0.01$, uncorrected). There was no Face and Non-Face condition difference during the baseline period (0 to 200 ms pre-stimulus). (B) Averaged dSPM maps and FFG timecourses across children. The top panel shows dSPM maps for Face and Non-Face for each time window. The bottom panel shows averaged timecourses with the shading showing +/− 2 standard errors of the mean for the right FFG (R-FFG) and left FFG (L-FFG) ROIs identified in averaged dSPM maps during the 300–400 ms post-stimulus window. Asterisks (*) mark significant FFG amplitude Face versus Non-Face condition differences, obtained via a paired-sample *t*-test at each time point for each ROI, and with a cluster threshold of $p < 0.05$ for 20 ms+ family-wise correction applied (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

s/showthread.php?2123-Atlas-for-1-year-old-babies) using an affine transformation to accommodate global scale differences between the subject anatomy and atlas. Before MEG acquisition, each child's head shape, the three fiducial landmarks (nasion, right, and left preauriculars), as well as the location of the 4 HPI coils were digitized using the Probe Position Identification (PPI) System (Polhemus). The points representing the shape of the child's head (at least 250 points) were used to co-register the MEG and MRI template surface (warped to fit the MRI surface; Fig. 1B). Given that all children were scanned in a supine position, and thus with the back of their head on the helmet surface, the minimum distance between occipital regions and the parietal and occipital MEG sensors provided optimal coverage of visual cortex and fusiform gyrus areas.

Distributed source modeling provided estimates of neural activity throughout the brain. An advantage of using MEG to study early brain development is that MEG is much less sensitive than EEG to distortion of the volume current caused by open fontanels and sutures and to inaccurate estimates of skull conductivity (see review in (Chen et al., 2019) and (Lew et al., 2013)). In particular, Lew et al. (Lew et al., 2013) showed that the spatial distribution of the magnetic fields outside the head are less affected by the open sutures and fontanels and by variations in skull conductivity than the electrical fields measured by EEG.

To calculate the MEG forward solution, an overlapping spheres head model was created for each child (Fig. 1C). Dynamical Statistical Parametric Mapping (dSPM; (Dale et al., 2000)) with unconstrained orientation estimated activity associated with Face and Non-Face stimuli (Fig. 1D). For computing each child's dSPM solution, an MEG noise covariance matrix for each child was obtained from an empty room recording immediately prior to the child's scan. dSPM solutions were computed with normalization as part of the inverse routine based on the noise covariance, resulting in a z-score map.

2.6. *Group analyses and statistics*

2.6.1. *Face versus Non-Face (Hemispheres x Conditions x Time Windows)*

Grand average dSPM source maps for the Face and Non-Face condition were computed at each time window (Fig. 2B). To reduce the number of analyses, the dSPM Face and Non-Face maps were averaged across time for each child at nine time windows (0–100 ms, 50–150 ms, 100–200 ms, …, 350–450 ms, 400–500 ms) as well as a baseline period (−200–0 ms). The nine time windows were then averaged across children to obtain grand averaged Face and Non-Face maps (Fig. 2B). From the grand average Face dSPM z-score map, left and right FFG regions of interest (ROIs) were identified via thresholding the grand average Face image at each time window to a z-value of 2. As shown in Fig. 2B, large responses were observed in the left and right FFG (L-FFG and R-FFG, respectively) only in the face condition at the 250–350 ms and 300–400 ms time windows. The L-FFG and R-FFG ROIs were obtained from the 300–400 ms time window (almost identical ROI from the 250–350 ms time window). With the L-FFG and R-FFG ROIs identified and applied to each child, evoked source time courses were obtained for the Face and Non-Face condition by averaging the source strength from every vertex within the L-FFG and R-FFG ROI at each sampled point (Fig. 2B).

To again constrain the number of analyses, once the L-FFG and R-FFG source time courses were obtained for each child, a single measure of FFG activity was obtained for each child at each of the 5 time windows by summing source strength across the time window. This provided for each child a single FFG source strength value at each time window and hemisphere. To statistically evaluate when FFG activity peaked when viewing faces, a linear mixed-effects regression model assessed FFG source strength with Hemisphere (L-FFG and R-FFG), Condition (Face and Non-Face), Time Window, and their full factorial interactions entered as fixed effects, and with Subjects entered as a random effect.

A different strategy to identify left and right FFG areas was also examined. In particular, Face versus Non-Face group statistics on the dSPM source maps were computed using within-subjects paired t-tests, using the parametric statistical toolkit in Brainstorm. As shown in Fig. 2A, t-tests showed significant Face and Non-Face differences only in the R-FFG. Given a goal of examining L-FFG and R-FFG activity, and given a desire to identify the L-FFG and R-FFG ROIs, the FFG ROI showing the greatest activity (not necessarily analogous regions in the left and right FFG) were determined from the thresholded Face averaged dSPM map. The whole-brain dSPM source map analyses also supported the focus on FFG given that Fig. 2A showed significantly stronger FFG activity in the Face than Non-Face condition.

2.6.2. *Left and right FFG latencies versus age and hemisphere effects*

To identify when FFG activity was strongest, in each child, peak latency in the Face condition was obtained from the L-FFG and R-FFG ROI by selecting the first peak with a z-score >2 that occurred after occipital cortex primary visual activity (0–200 ms post-stimulus). As no peak was observed in most of the children at later time windows for the Non-Face condition, no latency value was obtained from the Non-Face condition.

To evaluate how L-FFG and R-FFG activity changes as a function of age, a mixed-effect regression model was run with FFG latency entered as the dependent variable, and with Hemisphere, Age and their interaction entered as fixed effects, and Subject entered as a random effect. To further assess FFG hemispheric lateralization, a lateralization index (LI) was computed: (L-FFG latency – R-FFG latency)/(L-FFG latency + R-FFG latency), and a Pearson correlation between LI and age assessed if FFG responses to face stimuli become more right lateralized in older versus younger children.

2.6.3. *L-FFG and R-FFG associations with social and cognitive measures*

To evaluate if social and cognitive measures were associated with L-FFG and R-FFG activity, mixed-effect regression models were run with FFG latency entered as the dependent variable, and with Hemisphere, social (VABS) or cognitive measures (Mullen/Bayley age equivalent measures) and their interaction entered as fixed effects, and Subject entered as a random effect.

3. Results

3.1. *Brain regions specific to infant face processing*

Fig. 2A shows the difference in brain activity between the Face and Non-Face conditions 0–500 ms after stimulus onset (i.e., t-statistics for the Face versus Non-Face contrast). Stronger right FFG activity was observed in the Face versus Non-Face condition 250–350 ms and 350–450 ms post-stimulus. In addition, stronger left inferior/middle frontal activity at 250–350 ms was observed in the Face than Non-Face condition. Stronger primary visual activity at 100–250 ms post-stimulus and stronger superior parietal activity at 300–450 ms post-stimulus were observed in the Non-Face than Face condition.

Fig. 2B (top panel) grand averaged dSPM maps (see analysis details in Methods) for the Face and Non-Face conditions showed primary visual activity in the Face and Non-Face conditions from 0 to 200 ms. FFG activity, however, was observed only in the Face condition, strongest from 300 to 500 ms. Fig. 2B (bottom panel) shows the grand average left and right FFG time course. The right and left source time courses show FFG activity peaking at ~300 ms as well as 400–500 ms post-stimulus for the Face condition. Consistent with the dSPM t-statistic maps shown in Fig. 2A, Face stimuli elicited stronger FFG activity than Non-Face stimuli around 300 ms and 400 ms.

Analyses examining FFG source strength showed a main effect of Condition (Face versus Non-Face; $F = 15.40$; $p < 0.0001$; Face: 29.91 ± 26.56 versus Non-Face: 26.45 ± 19.99), a main effect of Time Window ($F = 5.64$; $p < 0.001$), and a Hemisphere X Condition interaction ($F = 5.95$; $p = 0.01$), with simple-effect analysis of the interaction term showed a difference in Face versus Non-Face FFG source strength in the right (Face: 31.55 ± 28.32 vs. Non-Face: 25.94 ± 19.12; $p = 0.01$) but not left FFG (Face: 28.27 ± 24.64 vs. Non-Face: 26.96 ± 20.84; $p = 0.54$).

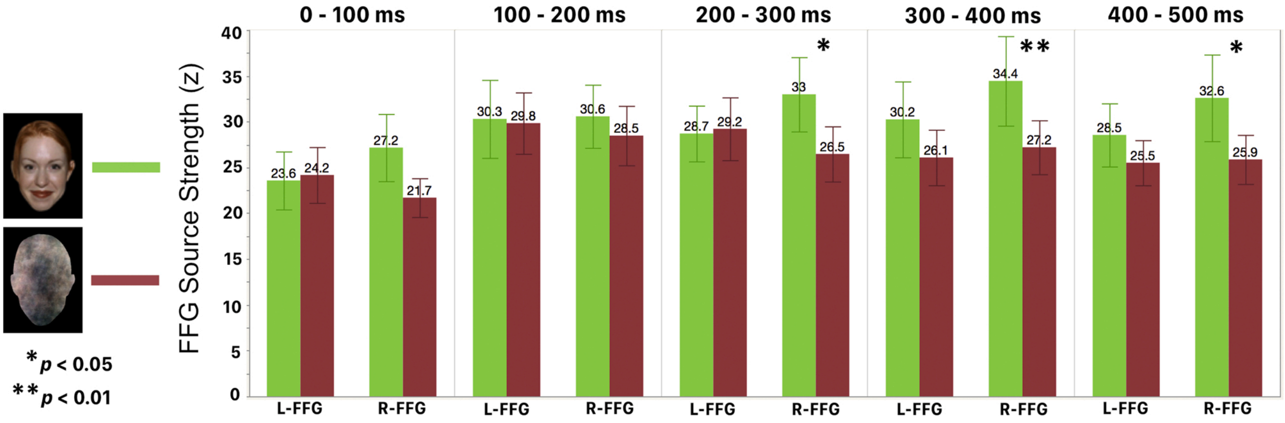

Fig. 3. Mean L-FFG and R-FFG activity for Face and Non-Face conditions across time, with time windows of significant Conditions X Hemispheres interactions marked (*$p < 0.05$, **$p < 0.01$).

Although an interaction with Time was not significant, Fig. 3 shows how L-FFG and R-FFG Face and Non-Face source strength changed across time, with post-hoc exploratory analyses showing stronger FFG activity in the Face than Non-Face condition only in the right FFG during later time windows (200–500 ms post-stimulus), and with the largest difference observed 300–400 ms post-stimulus.

3.2. *Hemispheric maturation of FFG responses involved in face processing*

Analyses examining FFG latency showed an effect of Age (F = 5.15; p = 0.03) as well as a Hemisphere X Age interaction (F = 8.75; p = 0.005). Simple-effect analysis of the interaction showed age-related associations in the R-FFG but not L-FFG (see Fig. 4A).

As shown in Fig. 4B, a Pearson correlation showed an association between the Face lateralization index (LI) and age (R^2 = 0.15, p = 0.001), suggesting that FFG responses to face stimuli become more right lateralized as children age. Fig. 4B shows that the hemisphere latency difference (LI > 0) is most apparent in children older than 1 years old.

3.3. *Associations between Face FFG responses, social development, and cognitive ability*

Analyses showed no association between FFG latency and Social scores (raw scores of the Socialization Domain from the VABS, see details in Methods). A significant Hemisphere X Social scores interaction (F = 15.40; $p < 0.001$) showed that Social scores accounted for significant variance in R-FFG latency (Fig. 5A). The same model for Cognitive scores (computed by averaging the age-equivalence scores (in months) from the Visual Reception subscale from the MSEL, and the Cognitive subscale from the BSID; see details in Method) showed an effect of Cognitive scores (F = 5.26; p = 0.03) and a Hemisphere X Cognitive score interaction (Fig. 5B; F = 8.69; p = 0.006). Regarding associations between the FFG LI and social as well as cognitive development, Pearson correlations showed that a more right-lateralized FFG response was associated with higher Social (R^2 = 0.32, p = 0.002) and Cognitive scores (R^2 = 0.19, p = 0.02).

4. Discussion

4.1. *Maturation of face FFG responses during infancy*

The present study examined maturation of left and right FFG activity during the first 2 years of life. Four main findings were obtained. First, FFG face responses were observed in infants as young as 3 months, indicating that FFG areas are differentially sensitive to Face versus Non-Face stimuli early in life. Second, FFG timecourses (Fig. 2B) showed that FFG responses to Face stimuli peaked at ~300 ms and again at ~450 ms post-stimulus, with these findings consistent with the latency findings

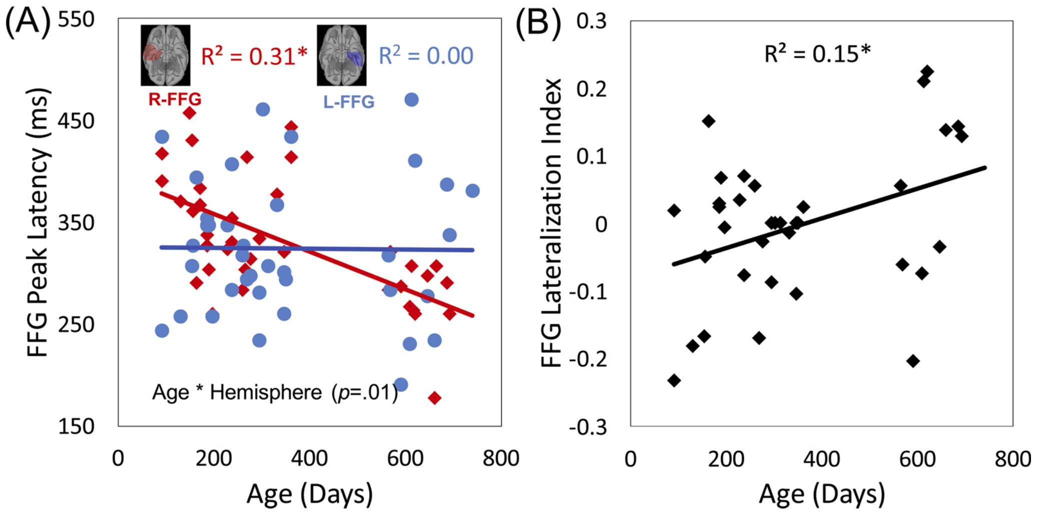

Fig. 4. (A) Scatterplot of Age and left (blue dots) and right FFG (red dots) peak latency. R-FFG peak latency = 394.73 ms − 67.31 ms * Age (Years); L-FFG peak latency = 320.49 ms + 7.28 ms * Age (Years); (B) Scatterplot of Age and FFG LI (black dots) = −0.08 + 0.08 * Age (Years). Linear equation for above correlations are reported in Years to reduce decimal places (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

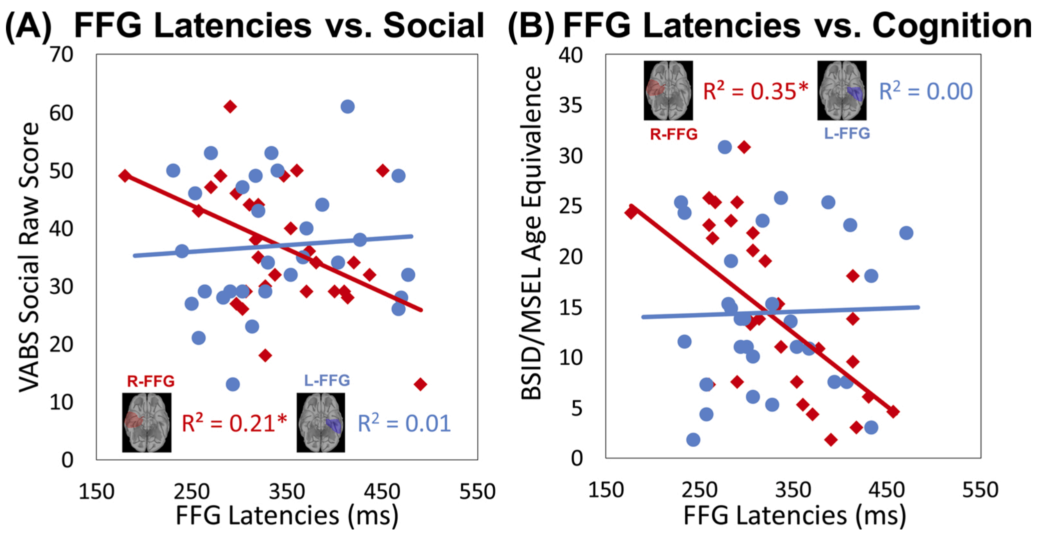

Fig. 5. Scatterplots of (A) Left FFG (blue dots) and right FFG (red dots) peak latencies versus Social Composite score, with significant Social Composite score * Hemisphere interaction ($p < .001$), and (B) Left FFG and right FFG peak latencies versus Cognitive Composite score, with a significant Cognitive Composite score * Hemisphere interaction ($p < .001$) (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

reported in infant EEG studies (Halit et al., 2003, 2004; de Haan and Nelson, 1999; de Haan et al., 2003; Xie et al., 2019; Guy et al., 2016; Leppanen et al., 2007). Third, a stronger Face versus Non-Face FFG response was observed only in the right hemisphere (~ 250–450 ms post-stimulus (Fig. 2)), and FFG latency lateralization (Fig. 4B) suggested that hemispheric specialization for faces starts to emerge around 1 year of age. Finally, an earlier right FFG response to Face stimuli was associated with better performance on tests assessing social and cognitive skills (Fig. 5). The following text discusses present findings within the context of previous studies.

4.2. *Hemispheric maturation of brain responses during face processing*

Although both the left and right FFG responded to face stimuli (as shown in Fig. 2), a Face versus Non-Face difference in FFG source strength was observed only in the right FFG, and only R-FFG latency changed as a function of age (Fig. 4). This suggests an early right-hemisphere lateralization for faces, a finding consistent with studies showing that a right-hemisphere specialization for face processing emerges during infancy (de Heering and Rossion, 2015; Le Grand et al., 2003). R-FFG latencies decreased from 3 months to 2 years age, with a rate-of-change of ~67 ms per year (see Fig. 4A for the linear equation).

Findings suggested that stronger FFG activity in the right than left hemisphere emerges during the first two years of life, with stronger right than left FFG activity most apparent after the first year of life. A right-hemisphere dominance for face perception is hypothesized to be specific to humans (e.g., see reviews from (de Heering and Rossion, 2015; Tsao et al., 2008), perhaps due to the left-hemisphere lateralization for word processing that emerges during reading acquisition (Dundas et al., 2013). In addition, models of hemispheric specialization indicate that whereas the right hemisphere tends to process information in a holistic manner, the left hemisphere tends to process information in a more fine-grained, analytic manner (Banich, 2009). For example, although both hemispheres process face stimuli, the right hemisphere appears to focus on the overall configuration of the face (e.g., shape of the face) and the left hemisphere the detailed features of the face (e.g., eyes, mouth) (Banich, 2009). An advantage of hemisphere specialization is that different aspects of information can be simultaneously and independently processed (= a more efficient use of ‘brain space’).

Studies examining face processing in adults typically report stronger and sometimes earlier activity in right than left occipito-temporal cortex (see review in (Rossion, 2014)). Findings in the EEG infant literature are inconsistent, with differences in EEG findings likely due to differences in stimuli, paradigms, and analysis strategy (sensor or source analyses). For example, Xie et al. (Xie et al., 2019) reported larger N290 components in response to some emotional faces (e.g., fearful faces) compared to others (e.g., happy and angry) in the right fusiform face area at 5 months. N290 differences were more pronounced at 7 months, and then disappeared by 12 months. de Heering et al. (de Heering and Rossion, 2015) reported that 4 to 6 month old infants showed a higher signal-to-noise ratio (SNR) at 1.2 Hz over right occipital areas when infants viewed faces appearing among images of objects at a rapid rate, suggesting that right-lateralized face processing is present during infancy (de Heering and Rossion, 2015).

4.3. *Correlations between FFG response and social and communication abilities*

An earlier right FFG response when viewing faces was associated with better social skills and cognition. To our knowledge, this is the first study to demonstrate that FFG response speed (FFG latency) to face stimuli is associated with social and cognitive ability in infants 0 to 2 years old. Given that previous literature has noted that activity in fusiform face area plays an important role in social perception deficits in older children and adults with autism spectrum disorder (ASD) (Schultz, 2005), the FFG latency and lateralization index obtained in infants may provide an ASD neuroimaging biomarker.

4.4. *Future directions and limitations*

The FFG latency and lateralization index may be of use in studies examining face processing in disorders associated with social processing deficits. Studies exploring the maturation of FFG activity in children with developmental disorders are of particular interest (for a discussion of the effects of maturation on identifying group differences see (Edgar, 2019), with FFG measures during infancy potential candidate endophenotypes for infants at risk for ASD. Present findings indicated a typical trajectory of left and right FFG development, and with hemispheric specialization associated with social and cognitive ability. Longitudinal studies that allow more exact assessment within-subject of rate-of-change in FFG activity are needed.

Present findings showed that the right FFG response to faces decreased at a rate of ~67 ms per year during the first two years of life (see Fig. 4), with the regression equation suggesting that an adult-like

M170 face FFG response should be observed by 4 years of age. This is in line with MEG and EEG studies demonstrating that adult-like M170 or N170 responses during face processing are present by 4 years of age (Taylor et al., 2001; Batty and Taylor, 2006; Itier and Taylor, 2004a, b; Kuefner et al., 2010; He et al., 2014). However, an age-related change may be linear only during the first two years of life, as observed in the present study, with studies exploring FFG face processing in typically developing preschoolers needed to evaluate FFG maturation beyond 2 years of age.

Further assessment of FFG hemisphere differences is needed. Lochy et al. (Lochy et al., 2019) showed that the face-selective response differed in scalp topography in 5-year-old children versus 4- to 6-month-old infants. However, contrary to the face-selective hemisphere results in infants (de Heering and Rossion, 2015) and adults (Rossion et al., 2015) obtained using the same methodology, Lochy et al. found no right-hemispheric lateralization for face-selective responses in their 5-year-old cohort (Lochy et al., 2019). They concluded that there may be a non-linear development of the neural processes underlying face perception, and that hemispheric specialization may change across time (e.g., as a result of reading acquisition during preschool years).

A limitation of examining associations between brain function and cognitive development (behaviors) in very young populations is that age is almost always a 'confound', with age placing limits on our ability to detect brain function and behavior associations that are distinct from shared maturation process (and thus perhaps not casually associated). Whereas larger samples would provide better estimates of the shared brain-behavior variance after accounting for age, larger samples would not necessarily allow examination of brain function and behavior associations without the 'confound' of age. Large samples within a small age range (e.g., 2- to 6-months-old) are of interest, likely providing better brain function and behavior estimates by reducing the influence of maturation. Given that brain function and behavior associations may change as a function of age (e.g., see (Edgar, 2019; Edgar et al., 2020) studies are needed for different ages.

A limitation of the present study was the lack of a third stimulus condition that could be used to help determine if the right-hemisphere FFG lateralization observed in the present study is also observed to other non-Face stimuli. Given that it is difficult for infants and toddlers to stay still for a long time, and that the paradigms used for infants need to have a longer interstimulus interval (ISI) than the ISIs used in adult studies, including a third control condition is difficult (e.g., such paradigms would be too long for infants and likely not provide enough trials to obtain a sufficient signal-to-noise ratio in any condition). Developing an 'optimal' paradigm for studying the development of face-specific neural networks in infants and young children will be difficult. Future studies will need to take into account of the following factors: length of task, number of trials per condition, hardware, analyses pipelines, stimuli that are relevant across a range of ages (for longitudinal studies), control conditions that allow independent assessment of face, attention, and high- and low-level visual processes in infants.

Although not within the scope of the present study, comparing social brain development between male and female infants is of interest. A limitation of the present study is that the sample (28 males and 18 females) was not sufficiently powered to assess what are likely weak gender effects in such a wide range of ages (0 to 2 years old). Another interesting topic to examine is the use of time-frequency analyses to understand the spectral profile of the FFG face response during infancy (e.g., examining total power as well as phase locking).

Last but not least, it is of note that assessment of neural activity to specific 'face features' is of interest. Behavioral studies have investigated not only how infants respond to faces in general, but also how infants respond to particular facial features associated with sex and race (Quinn et al., 2002, 2010, 2019). For example, using different experimental designs with different type of faces (male versus female, familiar versus novel) and including factors such as the primary caregiver's sex, Quinn et al. (Quinn et al., 2002) reportedreported that infants 3 to 4 months showed a preference for female versus male faces. EEG work has also be done in this area; for example, Cassia et al. (Cassia et al., 2006) and de Haan and Nelson (de Haan and Nelson, 1997) investigated the neural processes associated with an infant's preferential response to certain types of faces (e.g., upright face, mother's face). de Haan and Nelson (de Haan and Nelson, 1997) showed that electrophysiological measures (i.e., ERPs) are more sensitive to the recognition of the mother's face than behavioral measures (i.e., time looking at face). EEG and MEG studies that examine how the infant's brain responds to different social categories of faces are needed.

In summary, findings indicated that FFG activity to face stimuli changes during the first two years of life, with earlier right FFG activity predicting better performance on tests assessing social and cognitive ability. Longitudinal studies are needed to better understand FFG maturation. Research evaluating FFG activity in infants at risk for neurodevelopmental disorders such as ASD are of interest.

Data statement

The data will be made available upon reasonable request at the conclusion of the study.

Declaration of Competing Interest

The authors declare no competing interests exist.

Acknowledgements

This research was supported by grants from the National Institute of Mental Health (NIMH) (K01-MH108822 to Dr. Yuhan Chen, K01-MH108762 to Dr. Luke Bloy, R01 DC008871 to Dr. Timothy Roberts), the Eagles Autism Foundation Pilot Grant to Dr. Yuhan Chen, the National Institute of Health (NIH) (R01MH107506 to Dr. J. Christopher Edgar, R01MH092535 to Dr. Hao Huang), and the National Institute of Child Health and Human Development (NICHD) (R01HD093776 to Dr. J. Christopher Edgar, U54HD086984 to Drs. Edgar, Huang, and Roberts). The authors would like to thank the subjects who enrolled in this study and John Dell, Rachel Golembski, Peter Lam, Na'Kiesha Robinson, Erin Huppman, Matt Ku, and Marissa Dipiero who helped with data collection.

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