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RESEARCH ARTICLE

Love on the developing brain: Maternal sensitivity and infants' neural responses to emotion in the dorsolateral prefrontal cortex

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Abstract

Infancy is a sensitive period of development, during which experiences of parental care are particularly important for shaping the developing brain. In a longitudinal study of $N = 95$ mothers and infants, we examined links between caregiving behavior (maternal sensitivity observed during a mother–infant free-play) and infants' neural response to emotion (happy, angry, and fearful faces) at 5 and 7 months of age. Neural activity was assessed using functional Near-Infrared Spectroscopy (fNIRS) in the dorsolateral prefrontal cortex (dlPFC), a region involved in cognitive control and emotion regulation. Maternal sensitivity was positively correlated with infants' neural responses to *happy* faces in the bilateral dlPFC and was associated with relative increases in such responses from 5 to 7 months. Multilevel analyses revealed caregiving-related individual differences in infants' neural responses to happy compared to fearful faces in the bilateral dlPFC, as well as other brain regions. We suggest that variability in dlPFC responses to emotion in the developing brain may be one correlate of early experiences of caregiving, with implications for social-emotional functioning and self-regulation.

KEYWORDS
developmental neuroscience, emotion, fNIRS, infancy, parenting, sensitivity

1 | INTRODUCTION

Infancy is a sensitive period of development, during which experiences of parental care are particularly important for shaping the developing brain (Fox et al., 2010). Emotionally responsive, "serve-and-return" interactions with caregivers lay the foundation for neural architecture and calibrate the social functions of the human brain, with lasting consequences for children's development (Shonkoff, 2016). Indeed, the development of the infant brain is a key mechanism linking early caregiving experiences to later social competence and emotional health (Callaghan & Tottenham, 2016; Gee & Cohodes, 2021; Tottenham, 2020). Much of the research to date has focused on the deleterious consequences of caregiving *adversity*—experiences of abuse, neglect, and institutionalization (e.g., Wade et al., 2019; Zeanah et al., 2017). Yet to fully understand the neural underpinnings of caregiving and child development, it is also important to understand the neurodevelopmental consequences of *positive* parenting behaviors and normative variation in early caregiving experience.

In the present paper, we examine pathways linking sensitive caregiving to infant neural processing of emotion in a community sample of mothers and infants, followed across the first months of postnatal life. We briefly contextualize our work within the history of the science of maternal care in infancy, review previous research linking caregiving experiences to infant brain development, and describe a novel empirical study examining associations between the quality of maternal care and infants' social brain function in the first months of life.

1.1 | Sociohistorical context

Harlow's (1958) seminal work on the importance of early parental care in rhesus monkeys laid the foundation for Bowlby's (1969/1982) groundbreaking theory of attachment in human infants. Attachment theory emphasizes the role of loving, mutually responsive caregiving experiences in the first years of life in shaping healthy social-emotional development across the life course. But how might something as complex as maternal care be operationalized? Ainsworth's (1967; Ainsworth et al., 1978) observations of mothers and infants in Uganda and the U.S. provided an empirical framework for capturing key dimensions of caregiving behavior, including *sensitivity versus insensitivity to infants' cues* (i.e., responsiveness to signals of need) and *cooperation versus interference with infants' ongoing activity* (i.e., support for autonomous exploration). Ainsworth's (1969) Sensitivity Scales remain the gold standard for studying caregiving behavior in early parent-child relationships, with decades of research demonstrating their predictive power in social-emotional domains such as children's social competence, executive function, and mental health (Deans, 2020).

Yet from a modern developmental neuroscience perspective, a key question remains: what are the *neural correlates* linking parental care to social-emotional development?

1.2 | Evidence linking caregiving to infant social brain development

Early research on this question examined the detrimental effects of social deprivation on children's development (Rutter et al., 1998; Zeanah et al., 2003). A large body of work now demonstrates that caregiving adversity undermines the healthy development of the social brain—particularly brain functions associated with emotion learning and regulation (Belsky & de Haan, 2011; Gee, 2020; Tottenham, 2020). For example, infants with a history of caregiver maltreatment show perceptual biases for angry faces, including increased attention to, faster recognition of, and a larger P300 response (indexing attention and memory) to angry compared to neutral faces (e.g., Pollak et al., 1997, 2001); this work suggests that a heightened neural *threat bias* may develop from early experiences of abuse. Related work has shown that institutionally reared children show mild impairment in face discrimination and reduced peak amplitude in the N170, Nc (Parker & Nelson, 2005), P1, and P400 components (Moulson et al., 2009; see also Mesquita et al., 2015), suggesting that children deprived of responsive social interactions with caregivers may develop *blunted* responses to social stimuli. As Perry and colleagues conclude (2017, p.1), "without sensitive caregiving, infants fail to develop mechanisms needed for later-life emotion and emotion regulation."

Research Highlights

- Infancy is a sensitive period of brain development, during which experiences with caregivers are especially important.
- This study examined links between sensitive maternal care and infants' neural responses to emotion at 5–7 months of age, using functional near-infrared spectroscopy (fNIRS).
- Experiences of sensitive care were associated with infants' neural responses to emotion—particularly happy faces—in the dorsolateral prefrontal cortex.

Critically, however, the development of the social brain in infancy is facilitated not only by the absence of adversity but by the *presence* of positive parenting experiences with responsive caregivers (see Ilyka et al., 2021; Stern & Grossmann, in press). A recent study using functional Near Infrared Spectroscopy (fNIRS) suggests that as early as 5 months of age, experiences of maternal sensitivity are positively associated with infants' functional connectivity in the default mode network (implicated in theory of mind and self-referential thought), even when accounting for family socioeconomic status (Chajes et al., 2022). Maternal care is also related to infant neural responding to positive emotion: an EEG study found that maternal sensitivity was associated with infants' increased Nc amplitude (associated with attentiveness) in response to *happy* faces compared to neutral faces at 7 months (Taylor-Colls & Fearon, 2015). These findings suggest that infants who experience sensitive care may perceive smiling faces to be more rewarding (Clements et al., 2022).

Similarly, research has shown that secure attachment—theorized to result from repeated experiences of sensitive caregiving and co-regulation of emotion (Ainsworth et al., 1978; Bowlby, 1969/1982)—predicts key differences in emotion and cognition associated with social brain development (see Vrtička, 2017). Insecurely attached infants, for instance, show reduced relative left frontal brain activity across baseline and two social interaction conditions (Dawson et al., 2001). In a study by Peltola and colleagues (2020), although maternal sensitivity was unrelated to infant face processing, attachment was associated with significant differences in ERP responses to emotional faces. Specifically, securely attached infants, but not insecurely attached infants, showed age-typical N290 face processing responses differentiating *fearful* vs. non-fearful faces at 7 months. Attachment-related differences in neural development appear to persist beyond childhood; indeed, attachment in infancy predicts differences in brain structure and function as much as 20 years later (Moutsiana et al., 2014, 2015; see Long et al., 2020).

Related findings from hyperscanning studies reveal that infants' brain activity synchronizes with that of adults during social interactions, and that such neural synchrony varies as a function of adult responsiveness, proximity, and emotional valence. In one study of 9- to 15-month-old infants, neural coupling was heightened when infants engaged in social interactions with an adult experimenter, particularly in the prefrontal cortex (PFC) (Piazza et al., 2020). In studies of parents, mothers and their 4-6-month-old infants showed greater neural synchrony in the PFC during proximal face-to-face interactions, particularly those involving affective touch (Nguyen et al., 2021). Moreover, maternal sensitivity was linked with greater neural synchrony, whereas maternal intrusiveness was associated with lower synchrony among mothers and their 5- to 12-month-old infants (Endevelt-Shapira & Feldman, 2023). Finally, mothers and their 10-month-old infants showed stronger neural integration when mothers expressed positive compared to negative affect (Santamaria et al., 2020). These cross-sectional studies suggest that experiences of mutually responsive caregiver–infant interactions may involve coordinated neural processes, particularly in prefrontal regions.

1.3 | The role of the dorsolateral prefrontal cortex

Despite early views that the infant prefrontal cortex was functionally silent, mounting evidence reveals that prefrontal regions are active within the first months of life (Grossmann, 2015), develop rapidly, and are especially sensitive to environmental inputs such as caregiver behavior (see Hodel, 2018). One area in particular, the dorsolateral prefrontal cortex (dlPFC), may be especially important for understanding associations between maternal care and infant neural processing of emotion. Maternal sensitivity has been linked to connectivity between the hippocampus and brain regions implicated in emotion regulation and social-emotional functioning including the dlPFC at 6 months of age (Rifkin-Graboi et al., 2015). Moreover, infants of mothers who show greater behavioral engagement during play at 5 months demonstrate increased neural responses in the left dlPFC to social threat (i.e., *angry* faces), assessed with fNIRS, as well as more effective visual orienting to social threat, assessed with eye-tracking, at 7 months (Thrasher et al., 2021). In this same sample, researchers found that maternal engagement was associated with infants' detection of *fearful* faces at 7 months, as indicated by heightened initial attention (i.e., first fixation duration) and lower neural responses in the left dlPFC; infants' detection of fearful faces, in turn, predicted their prosocial helping behavior in the second year of life. The authors suggest that the dlPFC may be a potential neural mechanism linking early maternal care to later social behavior (Grossmann et al., 2018).

1.4 | The present study

To date, however, few studies have examined longitudinal links of sensitive caregiving to infant prefrontal response to emotion over more than one time point in the first months of life. Thus, the aim of the present longitudinal study was to examine how maternal sensitivity relates to the development of infant emotion processing in the dlPFC, focusing on a sensitive window of neurodevelopment spanning 5–7 months, when emotion processing undergoes critical development (Grossmann, 2012; Jessen & Grossmann, 2020; Peltola et al., 2009). We leveraged a multi-method longitudinal dataset following infants from birth through age 7 months, integrating Ainsworth's (1969) classic observational methods for assessing maternal behavior with cutting-edge infant neuroimaging technology at two time points. Specifically, we used functional near-infrared spectroscopy (fNIRS), an optical neuroimaging technique that uses near-infrared light to measure changes in blood flow indicating brain activity in cortical regions. FNIRS has a number of advantages for developmental research: it is non-invasive and safe for use with infants, has better spatial resolution than EEG and is more cost-effective than fMRI, and can be implemented with awake and engaged infants (see Wilcox & Biondi, 2015).

Building on prior work with this age group (Bayet et al., 2021; Grossmann et al., 2018; Thrasher et al., 2021), we examined infants' neural response to three facial expressions of emotion: *happy*, *fearful*, and *angry*.[1] Research suggests that infants discriminate angry from happy faces by 3 months of age, demonstrate a visual preference for happy faces by 4 months of age, and then begin to show an attentional preference and differentiated neural response to fearful faces between 5 and 7 months of age (for reviews see Grossmann, 2015; Ruba & Repacholi, 2020). Thus, we aimed to capture individual differences in the neurodevelopment of emotion recognition as it first comes online in early ontogeny. Critically, by examining infant neural responses at both 5 and 7 months, we aimed to gain a more fine-grained understanding of developmental continuity and change during this period, as infants first become able to discriminate fear from other expressions of emotion around 7 months of age (Grossmann, 2015).

We hypothesized that maternal sensitivity would be related to greater neural sensitivity to emotional faces localized in the dlPFC—particularly fear—given prior work linking maternal engagement and secure attachment to infants' neural responses to fearful faces (Grossmann et al., 2018; Peltola et al., 2020). In exploratory follow-up analyses, we examined potential developmental shifts in infant neural responses across ages 5 to 7 months as a function of maternal sensitivity to test two competing possibilities: On the one hand, insensitive caregiving may be associated with accelerated maturation of the PFC (e.g., Thijssen et al., 2017), but on the other hand, sensitive caregiving may be linked to adaptive increases in the neural bases of emotion regulation and cognitive control (e.g., Kerr et al., 2019). Given the dearth of research on maternal sensitivity and cortical response to emotion at this early age, we did not have a priori hypotheses about other brain regions. However, building on previous work examining the social brain in infancy (Grossmann, 2015; Ilyka et al., 2021; Stern & Grossmann, in press), in exploratory analyses we also examined infant neural responses in the medial prefrontal cortex (mPFC), temporal cortex (TC), inferior frontal cortex (IFC), and temporo-parietal junction (TPJ); results are reported in Supplementary materials.

The central hypothesis, pre-processing pipeline for all fNIRS data, and regions of interest computed for analyses were pre-registered as part of the larger longitudinal study from which the data were drawn (https://osf.io/cpmxg; Hypothesis A). Transparent changes to the preregistration include (a) focusing hypotheses primarily on the dlPFC, following a careful review of the literature presented here, and (b) improving the data analytic approach in response to reviewer feedback.

2 | METHOD

2.1 | Participants and procedure

Participants were drawn from an ongoing longitudinal study of $N = 121$ mothers and babies recruited from a local hospital in the mid-Atlantic United States when infants were newborns (for details see Kelsey et al., 2021). In line with the Declaration of Helsinki, parents gave informed consent for their infant to participate and all procedures were approved by the university's institutional review board (protocol #20381). Participants received monetary compensation for their participation. Data collection took place from 2018–2019 (prior to the pandemic). At the initial assessment, the majority of mothers ($M_{age} = 31.73$, $SD = 4.59$) were married (77%) and reported that fathers were involved in infants' care (97%).

Of the initial sample, $N = 106$ participated returned to the lab when infants were 5 months old and participated in a mother-infant free play session, from which maternal sensitivity was coded. Demographic characteristics for families who participated in this session are summarized in Table 1. Infants completed two fNIRS recording sessions at 5 months and again at 7 months of age.

Participants were excluded from the present analyses because (a) the fNIRS cap deviated beyond 1.5 cm from the correct placement ($n = 4$), (b) equipment or experimental error occurred for the fNIRS or free-play paradigm ($n = 4$), and (c) infants failed to meet looking criteria for the fNIRS paradigm ($n = 29$). To be included in analyses, infants had to participate in the 5-month mother-infant free-play ($n = 106$) and have usable data for at least one fNIRS recording at 5 months ($n = 87$) or 7 months ($n = 76$). Therefore, infants were excluded if they participated in either the 5- or 7-month visit but were unable to provide sufficient useable fNIRS data at either time point ($n = 11$). Thus, a total of $N = 95$ infants and their mothers were included in the final analytic sample. There were no significant differences in baseline characteristics between infants who were excluded compared to those included in the analytic sample (all $ps > 0.05$).

TABLE 1 Sample characteristics.

	N	(%)
Child sex		
Female	45	44.6
Male	56	55.4
Child race[a]		
Black	19	17.9
White	95	89.6
American Indian/Alaska Native	1	0.9
Asian	3	2.8
South Asian (Pakistani/Indian/Bangladeshi)	4	3.8
Pacific Islander	2	1.9
Other	3	2.8
Child ethnicity: % Hispanic	5	4.7
Maternal education		
Some High School	2	1.9
High School Diploma/GED	16	15.1
Some College/Associate's Degree	23	21.7
Bachelor's Degree	26	24.5
Graduate Degree (e.g., Master's or Ph.D.)	39	36.8
Household Income		
Less than $15,000	7	6.7
$15,001–$30,000	16	15.2
$30,001–$45,000	16	15.2
$45,001–$60,000	9	8.6
$60,001–$75,000	6	5.7
$75,001–$90,000	8	7.6
$90,001–$110,000	13	12.4
$110,001–$125,000	6	5.7
$125,001–$175,000	13	12.4
$175,001–$225,000	6	5.7
$225,001+	5	4.8

[a] *Note*: Child race totals greater than 100%, as participants could select more than one racial identity.

2.2 | Maternal sensitivity

2.2.1 Free-play procedure

Participants were invited to a laboratory playroom, where infants were placed on their backs on a blanket at the center of the room (following Grossmann et al., 2018). The experimenter asked mothers to "play with your child as you normally would"; then the experimenter left the room. Mother–infant dyads were observed for 5 min, following previous work (Bigelow et al., 2010; Grossmann et al., 2018; Stern et al., 2023; Thrasher et al., 2021) and to minimize participant burden after a long laboratory session that could be taxing to parents and young infants. Two wall-mounted cameras recorded the free-play session: one focused on the infant's face and body, and the other focused on the mother. All participants were provided with a standardized set of objects (toys and a book) and were free to select which objects, if any, they wished to explore.

2.2.2 Coding

Video recordings were coded by a team of coders trained to use Ainsworth's (1969) gold-standard Sensitivity Scales using the two most widely-used scales: *sensitivity versus insensitivity* to the infant's signals and *cooperation versus interference* with the infant's ongoing activity (i.e., support for the child's autonomy). Each video is assigned a score on a 9-point scale for maternal sensitivity (1 = *highly insensitive*, 5 = *inconsistently sensitive*, 9 = *highly sensitive*) and for cooperation (1 = *highly interfering*, 5 = *mildly interfering*, 9 = *conspicuously cooperative*). All videos were coded by two independent raters, and discrepancies were resolved via conferencing at weekly meetings to prevent coder drift. Krippendorff's alpha (Hayes & Krippendorff, 2007; Krippendorff, 2011) demonstrated good interrater reliability for sensitivity (*K*-alpha = 0.70) and cooperation (*K*-alpha = 0.75).

2.3 | Infant fNIRS recording session

2.3.1 fNIRS procedure

Infants sat on their caregiver's lap approximately 60 cm from the computer monitor in a small, quiet testing area. Caregivers were asked to refrain from interacting with their infant during the experiment. The experimental paradigm was presented using Presentation software (Neurobehavioral systems, USA) and trials were manually initiated by the experimenter to maximize infants' looking to the screen during experimental trials. fNIRS recording sessions took approximately 12 min to complete, and video recordings of the testing sessions were used to conduct offline behavioral coding.

2.3.2 Stimuli

Color photographs of adult White females with happy, angry, and fearful facial expressions were chosen from a validated stimulus set (FACES database; Ebner et al., 2010). Each experimental block started with an audio-visual attention getter (i.e., a shaking rattle accompanied by changing tones) followed by three trials (one for each emotion). The trials lasted approximately 6 s and contained a pseudo-dynamic repeated presentation of a female face with a neutral expression (500 ms), followed by an emotional expression (e.g., happy face for 700 ms). A 6-s minimum non-social (pseudo-dynamic presentation of vegetables) interstimulus interval followed each trial. Trial order was pseudo-randomized such that no actress and no emotional expression were repeated more than twice in a row.

2.3.3 Data acquisition

Infants' fNIRS data were recorded using a NirX Nirscout continuous-wave system and NIRStar acquisition software. fNIRS quantifies the relative concentration changes of oxygenated hemoglobin (oxyHb) and deoxygenated hemoglobin (deoxyHb), providing an indirect assessment of brain activity at a probing depth of approximately 1.5 cm below the cerebral cortex surface (for a review of this method see Lloyd-Fox et al., 2010). Optodes (16 sources and 16 detectors) were placed within an elastic Easy Cap resulting in 49 channels (2.5 cm distance) covering the frontal, temporal, and parietal regions. Data were recorded at a sampling rate of 3.9 Hz. Near-infrared light was emitted at two wavelengths (760 nm, 850 nm) with a power of 25 mW/wavelength.

At the beginning of the visit, the infant's head circumference was measured, and an appropriately sized cap (within 1.5 cm) was selected. Caps were placed with reference to anatomical landmarks, and video recordings were used to document cap placement. Infants were fitted with overalls which hooked into the cap and wore over-cap netting to help maintain desired cap placement.

2.3.4 Excluding non-usable data

Cap placements and looking behaviors were reviewed by trained research assistants. For cap placements, if the cap deviated more than 1.5 cm from the cap location, the infant's data were excluded. In addition, infants' looking behaviors toward the screen were coded offline from video recordings. Infants needed to look for at least 70% (4.2 s) of the time for a trial to be included. A second trained coder reviewed 60 videos, and there was a high degree of reliability (95.5% agreement) for looking time assessments. Infants needed to have adequate looking for at least three trials per emotional condition to be included (see Participants section above for details). On average, infants contributed data for a total of 36.3 trials, *SD* = 14.3 (*Mean* Happy = 7.05, *SD* = 2.82; *Mean* Angry = 6.09, *SD* = 3.01; *Mean* Fear = 6.74, *SD* = 2.86).

2.3.5 Average hemodynamic response calculation

fNIRS data were preprocessed following a pre-registered pipeline using Homer2 and custom MATLAB scripts (see Powell, 2020 for more information on the processing pipeline). First, raw intensity data were converted to optical density (hmrIntensity2OD). Next, channel quality was inspected and channels were excluded if they had mean intensities outside the system recommended values (enPruneChannels; dRange = [dmin = 10^{-2}, dmax = 10^{9}]). Then, motion correction was performed using a flexible targeted Principal Component Analysis with up to three iterations (hmrMotionCorrectPCArecurse; tMotion = 1.0, tMask = 1.0, Std Thresh = 100, Amp Thresh = 0.1, nSV = 0.97). Data were then band-passed filtered (0.083–0.3 Hz[2]; see Grossmann et al., 2018; Kelsey et al., 2021; Kelsey et al., 2023 for other fNIRS studies with similar ages and filter parameters). OD data were converted to concentration changes using the modified Beer–Lambert law and a developmentally appropriate partial pathlength factor of 5 (Bayet et al., 2021; Cope & Delpy, 1988; Duncan et al., 1996; Pirazzoli et al., 2019). OxyHb and deoxyHb concentration changes were then averaged across a 5–10-s post stimulus time window. The time window was chosen based on the peak response of all channels measured (see Figures S1 and S2). Lastly, data were visually inspected and rejected if artifacts remained in the data.

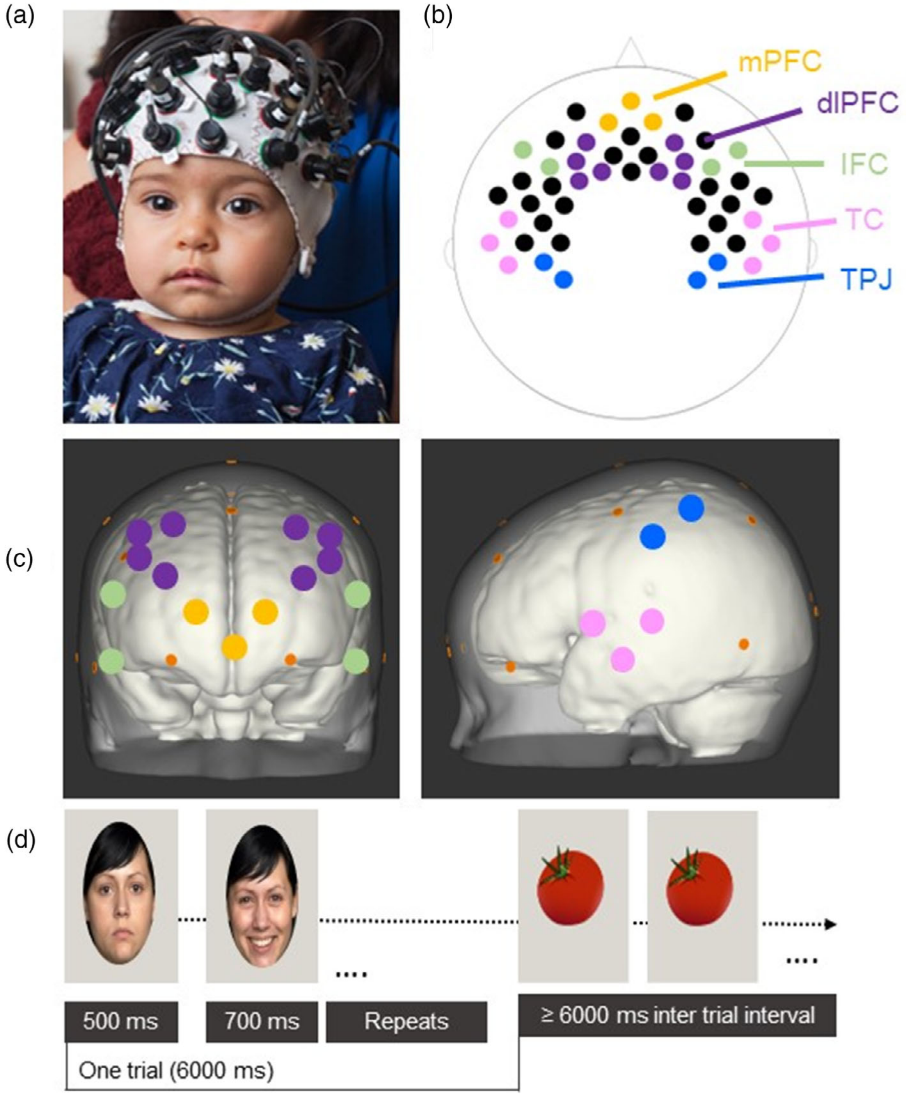

FIGURE 1 fNIRS array displayed on an infant (A), in 2D space (B), and in 3D space (C), and the paradigm schematic (D). *Note*. In panels B and C colorful circles indicate areas of interest: Purple is the dorsolateral prefrontal cortex (dlPFC), the hypothesized focal region of interest. Other colors show exploratory regions of interest: Blue is the temporal parietal junction (TPJ), pink is the temporal cortex (TC), green is the inferior frontal cortex (IFC), and yellow is the medial Prefrontal Cortex (mPFC). The 3D head models (C) show group level projections of channel locations (large colorful circles) on an infant (ages 5–8 months) atlas (top) and small orange dots indicate 10–20 locations.

2.3.6 Anatomical localization

Regions of interest were identified at the group level using photon propagation simulation with realistic, age-appropriate (6- and 7.5-month-old) head models using the devFOLD toolbox (Fu & Richards, 2021). Channels were identified for the dlPFC, as well as the exploratory regions of interest (mPFC, IFC, TC, TPJ), using the LONI atlas and based on their 10–20 reference points (see Figure 1).

2.4 | Analytic plan

In preliminary analyses, we examined distributional properties of the data and conducted Pearson correlations between maternal sensitivity scores and infant neural responses to each emotion condition in the dlPFC at each time point. All study hypotheses are based upon changes in oxygenated hemoglobin (oxyHb). OxyHb tends to have higher variability and is more often reported compared to deoxyHb (for a review see Lloyd-Fox et al., 2010). Therefore, we did not have any specific hypotheses about changes in deoxyHb; however, we report any significant correlations found using this chromophore in Supplementary materials.

The multilevel structure of the data is illustrated in Figure 2. To test our focal hypothesis, we ran multilevel models in SPSS v.28 with emotion condition, maternal sensitivity, and time predicting infant brain response (change in oxyHb) in the dlPFC. Multilevel modeling is a powerful alternative to ANCOVA because it (a) does not rely on assumptions of homogeneity of regression slopes and (b) is more robust

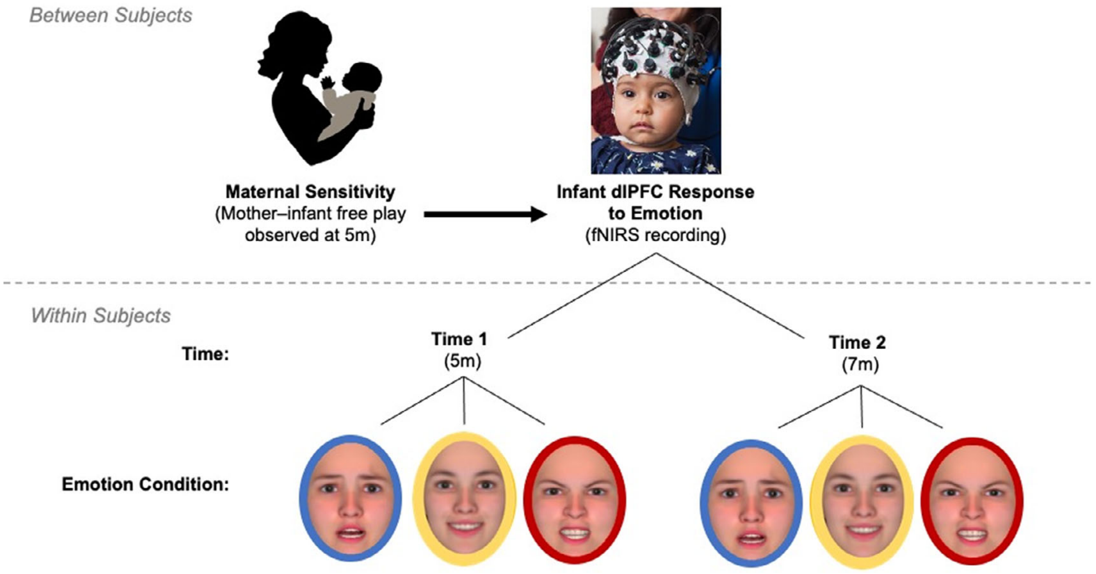

FIGURE 2 Summary of study design and multilevel model examining links of maternal sensitivity to infant neural responses, assessed across three emotion conditions (happy, fearful, and angry) at two time points (5 and 7 m).

to missing data, using maximum likelihood estimation to yield unbiased estimates. Using this approach, the analytic sample comprised $N = 95$ mother–infant dyads. Emotion condition (dummy-coded) and time (0 = 5 m, 1 = 7 m) were modeled as within-subjects fixed factors, with maternal sensitivity entered as a between-subjects continuous covariate, using the *Repeated* command and diagonal covariance structure to account for the nested structure of the data. Predictors were entered in 3 steps: (1) main effects of maternal sensitivity, emotion condition, and time; (2) two-way interactions of sensitivity*emotion and sensitivity*time; (3) 3-way interaction of sensitivity*emotion*time. Post-hoc analyses of the three emotion conditions used Bonferroni correction to account for multiple comparisons, $\alpha = 0.05/3 = 0.0167$. In exploratory follow-up analyses, we also examined main effects and interactions of hemisphere (0 = left, 1 = right), to examine whether effects of sensitivity on infant neural response to emotion were lateralized on the left or right hemisphere. Significant interactions were probed using simple slopes analysis. Note that due to limited statistical power, we could not examine 4-way interactions.

3 | RESULTS

3.1 | Preliminary analyses

Scores for maternal sensitivity (range: 1.50–9.00; $M = 6.26$, $SD = 1.77$) and cooperation (range: 1.00–9.00; $M = 5.88$, $SD = 2.05$) spanned the full 1—9 scale and were normally distributed, with mean scores slightly above the scale midpoint, in the "inconsistently sensitive"/ "mildly interfering" to "sensitive"/"cooperative" range, respectively. Detailed descriptive statistics are provided in Table S1.

Correlations between maternal behavior and infant neural responses to emotion showed small effect sizes (see Table S2). Maternal sensitivity scores were positively associated with infants' oxyHb responses to *happy* faces in the bilateral dlPFC at 5 months ($r = 0.24$, $p = 0.029$) Maternal cooperation/ support for autonomy scores were positively associated with infants' oxyHb responses to *happy* faces in the bilateral dlPFC ($r = 0.27$, $p = 0.028$) at 7 months. No correlations with dlPFC responses to fearful or angry faces were significant. Consistent with previous research, there was a high intercorrelation between the sensitivity and cooperation scales ($r = 0.81$, $p < 0.001$); thus, we averaged the two scales to create a composite score for further analyses, following previous work (e.g., Stern et al., 2020).

3.2 | Hypothesis testing

Results of multilevel models examining associations of maternal sensitivity, emotion condition, and time with infant dlPFC responses are shown in Table 2. There were no significant main effects of maternal sensitivity, emotion condition, or time on infant dlPFC responses. Results were qualified by a significant interaction between sensitivity and emotion condition. Post-hoc analyses showed that maternal sensitivity was related to infants' greater dlPFC response to *happy* compared to fearful faces ($b = 0.09$, 95% CI [0.03, 0.16], $p = 0.006$). As shown in Figure 3, simple slopes analysis revealed that maternal sensitivity was significantly associated with infants' greater dlPFC response in the happy face condition ($b = 0.06$, $p = 0.004$), but not in the fearful ($b = -0.03$, $p = 0.279$) or angry face conditions ($b = 0.02$, $p = 0.372$). Moreover, infants showed lower dlPFC responses to happy faces compared to fearful faces at low levels of maternal sensitivity (16th percentile: sensitivity = 3.75; $b = -0.24$, 95% CI [−0.44, −0.05], $p = 0.016$), but not at average (50th percentile: sensitivity = 6.50; $b = 0.01$, 95% CI [−0.12, 0.14] $p = 0.856$) or high levels of sensitivity

TABLE 2 Multilevel model linking maternal sensitivity observed at 5 months to infant dlPFC responses (oxyHb) to emotional faces at 5 and 7 months ($N = 95$).

Type III fixed effects	*df*	*F*	*p*
Intercept	(1, 767)	1.45	0.229
Emotion	(2, 554)	0.95	0.387
Time	(1, 752)	0.63	0.428
Sensitivity	(1, 762)	3.12	0.078
Emotion * Time	(2, 538)	2.09	0.124
Emotion * Sensitivity	(2, 551)	**3.78**	**0.023**
Sensitivity * Time	(1, 750)	0.59	0.442
Emotion * Sensitivity * Time	(2, 539)	0.02	0.976

Note: To account for the nested structure of the data, all models were run with the *Repeated* command in 3 steps (main effects only, 2-way interactions, 3-way interaction). Sensitivity = observed maternal sensitivity/cooperation composite at 5 m; Time (0 = 5 m, 1 = 7 m); oxyHb = oxygenated hemoglobin; dlPFC = dorsolateral Prefrontal Cortex. Boldface indicates significant parameters, $p < 0.05$.

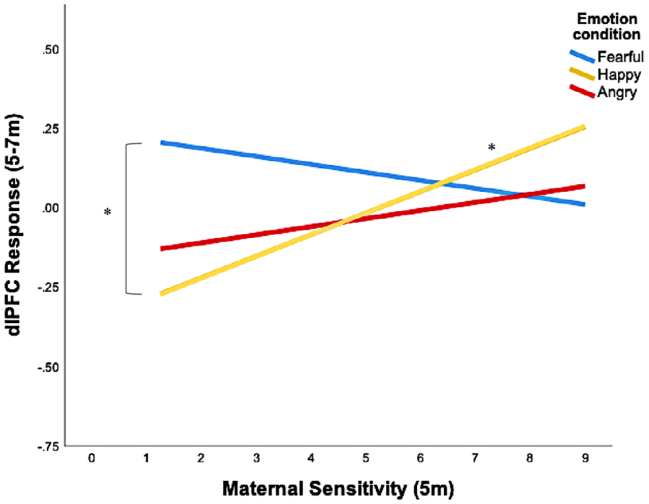

FIGURE 3 Significant interaction between maternal sensitivity and emotion condition predicting change in oxyHb concentrations in the bilateral dlPFC at 5–7 months.

(84th percentile: sensitivity = 7.76: $b = 0.13$, 95% CI [−0.04, 0.30], $p = 0.139$). Effects were not moderated by time, suggesting developmental continuity of associations between sensitivity and infant dlPFC response to emotion at 5 and 7 m.

3.3 | Exploratory analyses

Planned follow-up multilevel models showed that results were not moderated by hemisphere, indicating that links between maternal sensitivity and infant neural responses in the dlPFC occurred bilaterally (see Table S3). To further probe the developmental link between maternal sensitivity and infant dlPFC responses to happy faces over time, a linear regression was run with maternal sensitivity at 5 m predicting residualized change in infant dlPFC response to happy faces from 5 to 7 m. To test the specificity of the link between maternal sensitivity and infant brain development and to rule out potential confounds, maternal education was included as a covariate in the model. Full information maximum likelihood estimation in MPlus was used to handle missing data. Maternal sensitivity was associated with relative increases in infant dlPFC response to happy faces from 5 to 7 m, over and above maternal education (see Table 3).

Exploratory analyses of other brain regions are reported in Supplementary Materials (see Tables S3–S4). In brief, infants showed reduced neural responses to happy versus fearful faces in the left temporal cortex (a region involved in social perception; Richardson et al., 2021) specifically at low levels of maternal sensitivity ($b = -0.25$, $p = 0.016$). Additionally, there was a main effect of maternal sensitivity on infants' neural responses to emotion in the TPJ (involved in theory of mind and emotion recognition; Skerry & Saxe, 2015) ($b = 0.04$, $p = 0.024$); results were not moderated by emotion condition, time, or hemisphere. Sensitivity was not significantly associated with infant neural response to emotion in the mPFC or IFC after adjusting for multiple comparisons.

4 | DISCUSSION

The present study examined longitudinal links between maternal sensitivity and infant neural response to emotion in the dlPFC in the first months of life. Integrating observations of sensitive mother–infant interactions with fNIRS neuroimaging sessions at 5 and 7 months, this study contributes to a growing body of work examining links between parental caregiving and the neural underpinnings of social-emotional development (Ilyka et al., 2021). We found that infants of less-sensitive mothers showed reduced neural responses to happy compared to fearful facial expressions in the bilateral dlPFC, a region involved in cognitive control and self-regulation (Kelsey et al., 2023; Weissman et al., 2008). Results were driven principally by positive associations between maternal sensitivity and infant dlPFC responses to *happy* facial expressions. Preliminary analyses of developmental change suggest that maternal sensitivity at 5 m is associated with relative increases in infant dlPFC responses to happy faces from 5 to 7 m, even after accounting for maternal education. We discuss each finding in turn and outline avenues for future research at the intersection of caregiving experiences and developmental neuroscience.

In partial support of hypotheses, lower maternal sensitivity was related to infants' neural differentiation of fearful versus happy emotions in the dlPFC. Specifically, infants of less-sensitive mothers showed a comparatively greater neural response to fear and lower response to happy faces in this region. This is somewhat consistent with previous work in a German sample demonstrating that mothers' behavioral engagement during free play with their infants was associated with 7-month-olds' lower neural response to fearful faces in the left dlPFC (Grossmann et al., 2018). In the present study, however, neural differentiation of fearful versus happy faces was observed bilaterally, and results appeared to be driven by the positive association between sensitivity and dlPFC responses to *happy* facial expressions (rather

TABLE 3 Regression model linking maternal sensitivity observed at 5 m to infant dlPFC responses (oxyHb) to happy faces at 7 m, controlling for maternal education and corresponding dlPFC responses at 5 m.

Model predicting infant dlPFC response to happy faces (7 m)	β	SE	p	R^2
				.08
Infant dlPFC response to happy faces (5 m)	−0.07	0.15	0.670	
Maternal education	−0.17	0.12	0.161	
Maternal sensitivity (5 m)	**−0.23**	**0.11**	**0.040**	

Note: dlPFC = dorsolateral prefrontal cortex; infant age of assessment is indicated in parentheses.

than lower dlPFC responses to fearful ones). Importantly, however, maternal engagement and sensitivity are distinct constructs; while mother-directed play, verbal instruction, and physical movement of the child's body would indicate high engagement, these behaviors were explicitly coded as "interfering with the child's ongoing activity" on the *cooperation versus interference* dimension of Ainsworth's (1969) sensitivity scales. Thus, behavioral engagement may be more relevant for infants' developing attention to fear, whereas sensitive responsiveness may have unique implications for responding to happy facial expressions. Future work measuring multiple dimensions of caregiving could illuminate the unique and interactive effects of different caregiver behaviors on the developing brain (see, e.g., Bernier et al., 2019).

Developmentally, links between maternal sensitivity and infant dlPFC responses were not moderated by time, suggesting developmental continuity in the magnitude of the association between maternal sensitivity and infant dlPFC response to emotion over this period. Exploratory analyses revealed that maternal sensitivity was associated with relative increases in infant dlPFC responses to happy faces from 5 to 7 months, even after accounting for maternal education as a potential confound. This aligns with theory and research that experiences with responsive caregivers may set the stage for the maturation of self-regulatory brain regions (Callaghan & Tottenham, 2016). For example, one previous study found that secure attachment to caregivers in infancy predicted more efficient regulation of positive emotion in prefrontal regions 20 years later (Moutsiana et al., 2014). Findings also align with behavioral evidence that both mothers' and fathers' sensitive behavior were associated with young children's inhibitory control, while intrusive parental behavior predicted slower increases in children's inhibitory control over time (Geeraerts et al., 2021). The present study builds on this work by suggesting that caregiving-related individual differences in the development of prefrontal regulatory regions may be observable as early as the first months of life. Future longitudinal studies with additional time points may uncover caregiving-related differences in trajectories of dlPFC function over longer developmental periods. The present findings extend research linking maternal sensitivity to functional connectivity between hippocampal regions and the dlPFC (Rifkin-Graboi et al., 2015), as well as fNIRS hyperscanning work showing greater mother–child inter-brain synchrony in the dlPFC during cooperative interactions (Miller et al., 2019; Reindl et al., 2018). In adults, dlPFC activity in threatening contexts can be socially regulated by the presence of a supportive partner (Coan et al., 2006, 2017). Thus, it is possible that early experiences of sensitive care may calibrate the function of the dlPFC to help infants co-regulate their response to threat (see Callaghan & Tottenham, 2016; Thrasher et al., 2021) and direct the brain's resources toward *social reward* (e.g., smiling faces) and positive social engagement with others (e.g., cooperation). This aligns with research demonstrating that sensitive caregiving and secure attachment are robust predictors of children's developing self-regulation, social competence, and prosociality (Deans, 2020; Gross et al., 2017; Stern & Cassidy, 2018). Indeed, dlPFC function has been proposed as one neural mechanism linking early experiences of maternal care to later prosocial behavior (Grossmann et al., 2018).

Among the most striking patterns to emerge from these data is that sensitive caregiving was consistently positively linked to infants' neural responses to *happy* facial expressions— more so than negative emotions such as anger and fear —in the dlPFC as well as other brain regions, such as the TPJ. This is surprising, given previous work highlighting the importance of an early-emerging *fear bias* in the development of socially cooperative interactions with caregivers and others (see Grossmann, 2023); in contrast, the present findings align more with *positivity bias* perspectives highlighting the salience and importance of happy faces in early social information processing (see Herbert et al., 2023; Riddell et al., 2023). One potential explanation is cultural context: Whereas prior studies of infant fear responding were largely conducted in Germany and India, the present findings may be specific to a U.S. context characterized by greater individualism and positive emotional expressiveness. Moreover, according to attachment theory, a central function of caregiving is to provide protection and regulation of threat, so that infants can explore the broader environment (Bowlby, 1969); thus, the presence of a sensitive caregiver may help to regulate distress so that infants can orient neural resources toward social reward, approach, and cooperation. Previous work has demonstrated that mothers' own ability to distinguish happiness from other emotions prospectively predicts more sensitive behavior toward her infant (Stern et al., 2023). Thus, it is possible that the detection of happy faces is transmitted intergenerationally via sensitive caregiving, which often involves caregiver co-regulation of negative emotion and experiences of "mutual delight" or shared positive affect (Ainsworth, 1967). Critically, sensitivity appears to be independent of mothers' *expression* of positive emotion within the same mother-infant interaction— that is, sensitive mothers are not simply more expressive or "smiley," but rather emotionally attuned to the signals of the infant (Stern et al., 2023). Together, results suggest that the recognition of *positive* emotion is an important and underappreciated facet of early caregiver–child interaction, with implications for the development of the social brain.

In sum, sensitive caregiving behavior observed in the first months postpartum is associated with individual differences in emotion processing in the infant dlPFC as early as 5–7 months of age, as indexed by changes in oxyHb (note that results were highly similar using deoxyHb; see Supplementary materials). Findings contribute to a growing literature linking early caregiving experience to the neural bases of cognitive control and regulatory capacities. It is important to note that effect sizes in the present study were small, and thus substantial variance in infants' neural response to emotion is left to be explained by other factors within the child (e.g., genetics), as well as in the mother–child relationship, family system, and broader social ecology (e.g., neighborhood characteristics, systems of marginalization). We outline promising avenues for future research in the following pages.

4.1 | Strengths, limitations, and future directions

Strengths of the study include its prospective longitudinal design, integration of Ainsworth's (1969) classic observational measure of maternal behavior with cutting-edge neuroimaging techniques, assessment of infant brain function across two time points in the first months of life, and pre-registration of the fNIRS processing pipeline and regions of interest. However, the study's findings should be contextualized in light of its limitations, in part to illuminate avenues for future work. First, although fNIRS offers a number of methodological advantages for examining infant neurodevelopment (Wilcox & Biondi, 2015), it cannot capture subcortical activity. Advances in infant fMRI may help to illuminate the role of caregiving experiences in shaping early limbic function (e.g., Graham et al., 2015).

Second, the study's sample was small and majority White, middle-class, and educated; included only biological mothers; and was drawn from a Western context— common limitations in infant neuroimaging research (Ilyka et al., 2021). Future work could leverage the strengths of fNIRS (portability, non-invasiveness) to include more diverse cultures, contexts, and racial-ethnic groups. Importantly, researchers in the fields of cultural psychology and anthropology have suggested that Ainsworth's conceptualization of maternal sensitivity is culturally bound (e.g., Keller et al., 2018), and attachment researchers have called for greater attention to culture and context when assessing parenting behavior (e.g., Stern et al., 2022). Thus, future work should incorporate measures of culture and context-specific parenting behaviors (e.g., norms regarding emotional expression and social interaction with infants) that may be important for the development of the social brain in infancy. Furthermore, given that fathers and grandparents have unique effects on children's development (Sadruddin et al., 2019; Volling & Cabrera, 2019)—including effects of paternal sensitivity on infant brain development (Kok et al., 2015; Sethna et al., 2019)—future work should include other caregivers within the child's social environment.

Finally, the correlational design cannot test causal links between caregiving behavior and infant brain development. It is possible, for example, that genetic factors contribute to both caregivers' sensitive responses to infants' emotional cues and infants' neural sensitivity to others' emotions. Indeed, temperament and genetic factors are important predictors and moderators (i.e., susceptibility factors) of the link between caregiving and child neural and behavioral development (see Belsky & van IJzendoorn, 2017); future work should incorporate measures of genetic variation.

Nevertheless, mounting causal evidence from intervention studies shows that programs to enhance maternal sensitivity and secure attachment in infancy (e.g., Attachment and Biobehavioral Catch-Up; Dozier & Bernard, 2019) have lasting effects on children's cortical development (Bick et al., 2019) and improve children's neural function in brain regions associated with social cognition, which in turn predicts fewer behavior problems in middle childhood (Valadez et al., 2020). Moreover, children with a history of early deprivation who were randomized to a foster care intervention in infancy showed improvements in cortical function (Marshall et al., 2008), neural face processing (Moulson et al., 2009; Moulson et al., 2015), and brain structure specifically in the lateral and medial prefrontal cortex years later (Sheridan et al., 2022; see also Nelson et al., 2007). At the behavioral level, attachment-based parenting interventions have been shown to improve children's inhibitory control (Cassidy et al., 2017), a skill subserved by dlPFC function (e.g., Durston et al., 2002). Future work should continue to examine the causal effects of parenting interventions on early brain development.

5 | CONCLUSIONS

Leveraging data from a multimethod longitudinal dataset, we find evidence that observed maternal sensitivity is meaningfully related to the development of the social brain in the first months of life. Specifically, experiences of sensitive caregiving as early as 5 months were related to infant neural responses to emotional facial expressions—particularly happy faces—in the dlPFC, a region involved in cognitive control and emotion regulation (Ochsner & Gross, 2005). Findings have implications for understanding the neural underpinnings of well-established links between sensitive care and later social competencies, such as self-regulation, empathy, prosociality, and emotion understanding (Deans, 2020). We join others in suggesting that policies and programs that support caregivers to be able to engage in mutually responsive, "serve-and-return" interactions with their infants (e.g., paid family leave, access to affordable mental health services for caregivers) represent an important investment in children's brain development and social-emotional functioning (Center on the Developing Child at Harvard, 2017; Teti et al., 2017).

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data are available upon reasonable request from the corresponding author.

ETHICS STATEMENT

All procedures were carried out in accordance with APA ethical guidelines and approved by the University of Virginia Institutional Review Board for Health Sciences Research (IRB-HSR approval #20381).

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ENDNOTES

[1] We recognize that there is rich debate as to whether facial expressions reflect internal states, which can then be recognized by others. However, here we use the terms *happy*, *angry*, and *fearful faces* to avoid confusion, and to be consistent with previous literature using these terms.

[2] Note that this parameter differs slightly from the pre-registered value of 0.2. The change was made to reflect more recent work supporting the use of larger values.

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