Preferential responses to faces in superior temporal and medial prefrontal cortex in three-year-old children

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ABSTRACT

Perceiving faces and understanding emotions are key components of human social cognition. Prior research with adults and infants suggests that these social cognitive functions are supported by superior temporal cortex (STC) and medial prefrontal cortex (MPFC). We used functional near-infrared spectroscopy (fNIRS) to characterize functional responses in these cortical regions to faces in early childhood. Three-year-old children (n = 88, M(SD) = 3.15(.16) years) passively viewed faces that varied in emotional content and valence (happy, angry, fearful, neutral) and, for fearful and angry faces, intensity (100%, 40%), while undergoing fNIRS. Bilateral STC and MPFC showed greater oxygenated hemoglobin concentration values to all faces relative to objects. MPFC additionally responded preferentially to happy faces relative to neutral faces. We did not detect preferential responses to angry or fearful faces, or overall differences in response magnitude by emotional valence (100% happy vs. fearful and angry) or intensity (100% vs. 40% fearful and angry). In exploratory analyses, preferential responses to faces in MPFC were not robustly correlated with performance on tasks of early social cognition. These results link and extend adult and infant research on functional responses to faces in STC and MPFC and contribute to the characterization of the neural correlates of early social cognition.

1. Introduction

Perceiving faces and understanding emotions are two cornerstones of human social cognition. As such, these capacities are supported by several brain regions in human adults (for a review, see Spunt and Adolphs, 2019), including superior temporal and medial prefrontal cortex (STC, MPFC). Decades of research with human infants have characterized the developmental origins of these capacities and their neural substrates (e.g., Bayet and Nelson, 2019; Leppänen and Nelson, 2009). Here, we extend this work with a large sample of 3-year-old children (n = 88) – an age group that has received little study in developmental cognitive neuroscience research – using functional near-infrared spectroscopy (fNIRS). We used fNIRS to measure spatially

localized hemodynamic responses as children passively viewed faces and objects to (1) characterize preferential responses to faces in STC and MPFC in early childhood and (2) test hypotheses about the early functions of these brain regions that originate from prior research on face and emotion processing. Specifically, we tested whether responses to faces in these cortical regions vary across emotional expressions, valence, and intensity, and whether early responses to faces in MPFC correlate with early social behaviors.

In adults, subregions along bilateral STC are preferentially recruited during a range of social perception and cognition tasks, including the perception of faces, voices, biological motion, and social interactions (Deen et al., 2015; Isik et al., 2017; Pitcher et al., 2011; Puce et al., 1996). Face-sensitive regions in the STC appear to represent

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"supramodal" information about emotions, i.e. emotion information that generalizes across different kinds of input (e.g., facial expressions, vocal tone; Deen et al., 2015; Peelen et al., 2010; Skerry and Saxe, 2014). MPFC similarly represents supramodal emotional content, as well as other mental state information (Jenkins and Mitchell, 2011; Skerry and Saxe, 2015, 2014), and appears to be particularly important for reasoning about others' emotions. For example, a larger MPFC response during emotion attribution tasks predicts higher subsequent performance on emotion judgment tasks (Zaki et al., 2009). While a majority of research on the function of these regions with adults has been conducted with functional magnetic resonance imaging (fMRI), it is possible to interrogate the responses in these regions using fNIRS, which uses near-infrared light to measure oxy- and de-oxyhemoglobin concentrations in cortical brain areas as a proxy for neural activity.

To date, infant research characterizing the neural correlates of early face perception has primarily used electroencephalography (EEG; de Haan and Nelson, 1999; Haan et al., 2002; Halit et al., 2004). Complementary data from tools with higher spatial resolution, like fNIRS and fMRI, enables localizing the source of early responses to faces to spatially discrete brain regions. Consistent with prior EEG evidence, fNIRS and fMRI research finds early preferential responses to faces, relative to non-social stimuli, in STC and MPFC in infants as young as 3 months of age (Blasi et al., 2007; Csibra et al., 2004; Deen et al., 2017; Grossmann et al., 2008; Kosakowski et al., 2021; Lloyd-Fox et al., 2009; Nakato et al., 2009; Otsuka et al., 2007).

Early attention to faces, and early sensitivity to different facial emotions, may support early social responding, especially prior to the onset of language. Early sensitivity to fearful or angry faces may facilitate detection and response to threats in the environment (Nelson and Dolgin, 1985), while early sensitivity to positively valenced, engaging faces may support the formation of social relationships with (potential) caregivers (De Haan and Nelson, 1998; Farroni et al., 2007). Intense emotions may be particularly informative (and therefore salient), which is consistent with young children's improved performance with more intense emotions in emotion recognition tasks (Bayet et al., 2018; Garcia and Tully, 2020; though see Aviezer et al., 2012).

Despite behavioral evidence that even preverbal infants discriminate among some emotional facial expressions (e.g., happy vs. fear; Bayet and Nelson, 2019; Leppänen and Nelson, 2009) and have expectations about the causal relationship between events and emotions (e.g., an agent who completes a goal will feel happy; Skerry and Spelke, 2014), evidence for differential neural responses to different emotional expressions remains inconclusive. Among infant EEG research, some studies report larger N290 ERP amplitudes – a face-sensitive ERP component (e.g., Halit et al., 2004; Nelson and McCleery, 2008) – to fearful faces relative to other emotions by 7 months of age (Hoehl and Striano, 2008; Xie et al., 2019). Other studies report larger N290 components specifically to angry faces (Kobiella et al., 2008) or to happy faces (Jessen and Grossmann, 2015), and yet others find no differences across emotional faces (Vanderwert et al., 2015).

FNIRS has been proposed as a particularly suitable method for studying emotion processing in infancy (Mauri et al., 2020) but provides similarly conflicting evidence regarding whether hemodynamic responses in STC and MPFC differ across emotions. One fNIRS study found larger responses to fearful faces in temporal (but not frontal) regions in 5-month-old infants (Di Lorenzo et al., 2019), another found differences in the timecourse of responses to happy and angry faces in 6- to 7-month-old infants (Nakato et al., 2011), and a third found no differences in responses by emotion category in 5- to 7-month-old infants (Bayet et al., 2020). Studies of emotion processing that use voice, rather than face, stimuli also present mixed results (Grossmann et al., 2010; Safyer et al., 2020; Zhang et al., 2017). However, one consistent finding from fNIRS and fMRI research relevant to emotion processing is that MPFC responds preferentially to positively valenced, socially relevant stimuli during infancy (Grossmann, 2013; Powell et al., 2018b; Raz and Saxe, 2020). Hemodynamic responses in MPFC are larger when infants

view faces with direct versus averted gaze (Grossmann et al., 2013, 2008; Urakawa et al., 2015), hear or see their own versus a stranger's mother (Imafuku et al., 2014; Minagawa-Kawai et al., 2008; Naoi et al., 2012), and listen to infant-directed versus adult-directed or monotone speech (Naoi et al., 2012; Saito et al., 2007).

Here, we investigate the role of STC and MPFC in perceiving faces and inferring emotions with 3-year-old children. Studying young children, rather than infants, provides information about relatively early functional organization in STC and MPFC while enabling the use of a longer experiment with more conditions than is typically attempted with infants. We used fNIRS to measure cortical responses with typically developing 3-year-old children (n = 88) while they passively viewed dynamic faces expressing different emotions that varied in valence and intensity (100% happy, 100% fearful, 100% angry, 40% fearful, 40% angry, neutral), as well as a non-social dynamic objects condition, in order to test specific hypotheses about the early social functions of STC and MPFC.

This experimental design enabled us to address three goals. First, we aimed to extend prior evidence of preferential responses to faces, relative to non-social stimuli (e.g., objects), in MPFC and STC with infants to a large sample of 3-year-old children.

Second, we tested whether responses in these regions differed by emotion, valence, and intensity. We used a functional channel of interest (fCOI; Powell et al., 2018a) approach to sensitively detect responses that differentiated between (i) faces and objects, (ii) happy vs. neutral faces, (iii) fearful vs. neutral faces, (iv) angry vs. neutral faces, (v) positive (100% happy) vs. negative (100% angry and fearful) emotional faces, and (vi) high (100% angry and 100% fearful) vs. low (40% angry and 40% fearful) intensity emotional faces.

Third, we conducted exploratory analyses to test the hypothesis that early preferential responses to faces in MPFC support early social behaviors (Powell et al., 2018b). We measured correlations between preferential face responses in MPFC and performance on three behavioral tasks of early social cognition: (1) a prosocial behavior task (Warneken and Tomasello, 2006), which plausibly captures children's early efforts to form social connections; (2) a standard theory of mind reasoning task (Wellman and Liu, 2004), which measures children's reasoning about mental states – which has been found to correlate with MPFC development (Bowman et al., 2019; Sabbagh et al., 2009); and (3) a facial "Emotion Sort" task, which was developed to complement our fNIRS experiment and measures children's early recognition of emotional content in faces (Bayet et al., 2018).

2. Methods

2.1. Participants

Eighty-eight 3-year-old children contributed usable fNIRS data (2.98–3.76 years old; M(SD) = 3.15(.16); 35 girls). Participants were recruited from a registry of local births developed by the Laboratories of Cognitive Neuroscience in Boston, Massachusetts as part of a larger project on the development of emotion processing in infancy and early childhood (Bayet et al., 2020, 2018; Ravicz et al., 2015; Xie et al., 2021). Children who completed the fNIRS experiment were a subset of the sample recruited for this larger project – the aims of which included investigating genetic contributions to emotion processing (hence the large sample size); this aim is not addressed here. All participants were born full-term ($\geq$ 37 weeks' gestation) with no known prenatal or perinatal complications and were typically developing. Data included in these analyses were collected between March 2015 and February 2018. Study procedures were approved by the Institutional Review Board at Boston Children's Hospital. Parents provided written consent at the beginning of the study visit. Participants were given a small stipend and a small toy prize.

An additional 71 children participated in the fNIRS study but were excluded from fNIRS data analyses due to insufficient usable data (i.e.,

<3 usable channels in the MPFC search space, no usable channels in the right STC search space, and/or <15 usable trials total, regardless of stimulus condition; see fNIRS Data Analysis section for details; n = 54), refusal to wear the fNIRS cap (n = 6), experimenter or equipment error (n = 10), or ineligibility due to subsequent diagnosis of an autism spectrum disorder (n = 1). This rate of attrition is relatively high; see Supplementary Materials for further discussion and Supplementary Table 1 for additional demographic information about all participants.

2.2. FNIRS experiment

Participants viewed female faces with 100% happy, 40% angry, 100% angry, 40% fearful, 100% fearful, and neutral expressions while undergoing fNIRS. All face stimuli were selected from the MacBrain ("NimStim") stimulus set (Tottenham et al., 2009). Prior research finds that even young infants are sensitive to race and gender information in faces (Vogel et al., 2012). Therefore, the race of the actors shown to each participant was matched to the self-reported race of the participant's mother (White version 1 (n = 40): actors 1, 2, 3, 5, 6; White version 2 (n = 41): actors 6, 7, 8, 9, 10; Black (n = 2): actors 11, 12, 13, 14; Eastern Asian (n = 5): actors 15, 16, 17, 18, 19). Of the mixed/multi-race participants with usable fNIRS data (n = 12), n = 6 viewed White version 1, n = 1 viewed White version 2, n = 2 viewed Black faces, and n = 3 viewed Eastern Asian faces. In post-hoc analyses, we verified that HbO condition differences within each experimental contrast (i.e., our main neural measures of interest) did not differ across the two sets of White actors (all bs < 0.45, ts <1.05, ps>.3).

Stimuli were presented in a block design. Each face block displayed three 2 s dynamic morphs of angry (40% and 100%), fearful (40% and 100%), happy, and neutral face stimuli created with MorphX (http://www.norrkross.com/software/morphx/morphx.php), presented on a grey background and separated by a .2–.4 s inter-stimulus interval (6.4–6.8 s total). Faces within a block expressed the same emotion in terms of category and intensity but varied in actor identity. There were 10 blocks per face condition (60 face blocks total). The experiment did not include a 40% happy face condition due to time-constraints inherent to pediatric neuroimaging research (in pediatric populations, data loss increases as experimental time increases) and because we hypothesized that the manipulation of emotion intensity would be strongest for the negative emotion conditions.

Prior work suggests that dynamic stimuli evoke stronger responses than still images, especially in STC (Pitcher et al., 2011). Our stimuli were dynamic in that angry and fearful faces morphed in intensity from 0 to 40% or 0–100% (mouth open), happy faces morphed from 0 to 100% in intensity (mouth open), and neutral (0% intensity) faces morphed from open to closed mouths. All stimuli morphed over the course of the 2 s stimulus, except the stimuli shown at 40% intensity, which reached maximal intensity at 1 s and then returned back to neutral in the next second. See Fig. 1.

Each face block was followed by an 8 s movie of moving objects (Fig. 1; 60 blocks total). The longer duration of the moving objects

movies provided separation between the averaging windows used to measure responses to face and object conditions (see Supplementary Fig. 1 for visualization of response timecourses and averaging windows). Dynamic objects movies showed one or two objects (3D shapes) moving in straight lines on a blue background. Before each face block, a black fixation cross was shown on a grey background; an experimenter monitored the participant's eye gaze and initiated the block when the participant fixated on the stimulus screen. The experiment lasted 16−20 min, depending on the length of time spent between blocks.

Stimuli were presented via E-Prime 2.0 (Psychological Software Products, Harrisburg, PA) and displayed on a 17″ Tobii T120 eye tracker monitor (Tobii Technology, Stockholm, Sweden) in a dark, quiet room. Participants were seated approximately 60 cm from the monitor and instructed to sit still and stay quiet during the experiment. An experimenter sat quietly near the participant, monitored engagement, and directed the participant's attention to the screen when necessary. To encourage participation and engagement, images from "Finding Nemo" (Stanton, 2003) were interspersed after each block. Simultaneous video data were acquired with a Sony Handycam with Nightshot in order to monitor participant attention.

2.3. FNIRS data acquisition

FNIRS data were acquired on a Hitachi ETG-4000 continuous-wave system using wavelengths of 695 and 830 nm, with a sampling rate of 10 Hz. Eighteen source optodes, emitting light at both wavelengths, were separated from detectors by a distance of approximately 3 cm, resulting in 22 channels distributed over the frontal region of the scalp and 12 channels distributed over each temporal region of the scalp. The optodes were stabilized by a black fabric cap that fit snugly over the child's head and fastened with a chinstrap. The fNIRS cap was positioned just above the participant's brow line, with the middle frontal optode centered and the bottom middle lateral optodes corresponding to T3 and T4 electrode positions of the 10–20 EEG system (see Fig. 2). Consistency of hat placement across participants was ensured via post-hoc examination of hat placement photographs.

2.4. FNIRS data analysis

FNIRS data were preprocessed using the HomER2 NIRS processing package (Huppert et al., 2009) and custom scripts in Matlab 2018b (MathWorks, Inc., Natick, MA). Raw intensity data were visualized and cropped to exclude timepoints prior to and after the experiment and then converted to optical density (OD) units (HomER script: hmrIntensity2OD). We followed procedures for pruning channels and identifying and correcting for artifact described in Powell, 2020. Channels were excluded from further analyses if they had an average raw signal intensity lower than 1 or higher than 4 (HomER script: enPruneChannels; dRange=[1 4], SNRthresh = 0, SDrange = [0 45]).

We quantified the amount of motion within each channel as the number of timepoints during which the optical density data showed
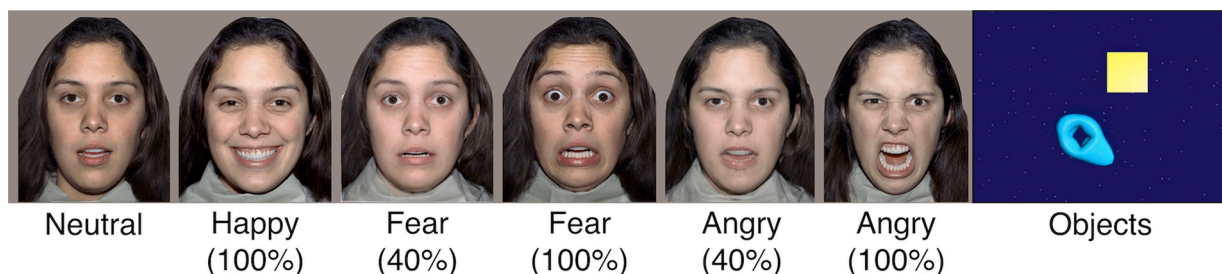

Fig. 1. FNIRS Experiment Stimuli. Face stimuli were 2 s movie clips that morphed from the neutral expression to an emotional expression (happy, 40% fear, 100% fear, 40% angry, 100% angry) or that morphed from a neutral expression with an open to closed mouth. Each face block included three different female actors expressing the same emotion. Objects stimuli were 8 s movies of one or two 3D shapes that moved in straight lines on a blue background.
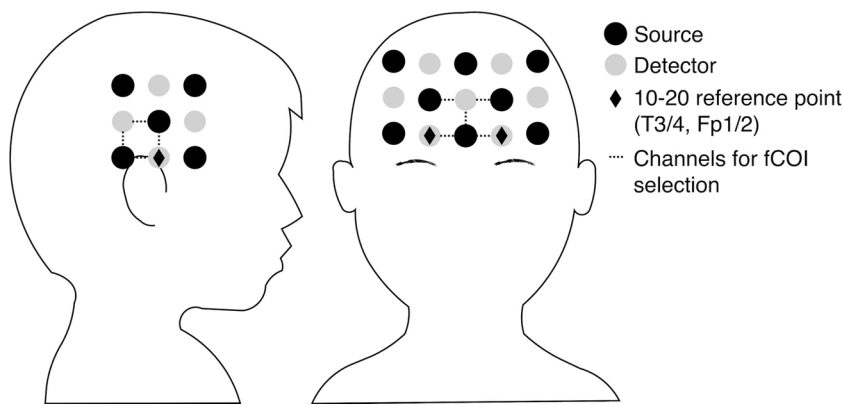
high-frequency amplitude changes of >.10 OD within 1 s (10 measurements) (HomER script: hmrMotionArtifactByChannel_indLambda; tMotion = 1, tMask = 1, STDEVthresh = 100, AMPthresh = .1), and excluded channels that had more than 90% of the data timecourse flagged as motion artifact timepoints. Channels were additionally excluded from further analyses if they contained a large signal spike (i.e., greater than 2 OD units) during an experimental trial (HomER script: hmrMotionArtifactByChannel_indLambda; tMotion = 1, tMask = 0, STDEVthresh = 1000, AMPthresh = 2). We then applied flexible iterative targeted PCA (tPCA) to remaining channels that had more than 10% of the data timecourse flagged as motion artifact timepoints (Yücel et al., 2014). Each iteration of tPCA removed 97% of the shared variance across channels from motion-contaminated portions of the timecourse (HomER script: hmrMotionCorrectPCArecurse; tMotion = 1, tMask = 1, STDEVthresh = 100, AMPthresh = 1, nSV = .97). After each iteration of tPCA, the number of motion artifact timepoints was re-calculated and tPCA was repeated as long as 10% of the timecourse was flagged as motion artifact, for a maximum of two iterations. In this way, the number of tPCA iterations applied to each participant's data depended on the amount of motion artifact in the data. We calculated the proportion of timepoints still identified as motion artifact and used this value as a proxy for participant data quality. These remaining motion artifact timepoints were interpolated over and the full timecourses were submitted to a bandpass filter (Butterworth filter, HomER script: hmrBandpassFilt; HPF = .02, LPF = .8), which removed physiological and systemic noise. Optical density timecourses were converted into oxygenated, deoxygenated, and total hemoglobin units using the modified Beer-Lambert Law (HomER script: hmrOD2Conc; PPF = 5; Duncan et al., 1995). Motion artifact timepoints were subsequently NaNed (i.e., excluded as "Not a Number").

Average oxy- and deoxygenated concentration values per face and object trials were calculated from a 6- or 4-second window, respectively, starting 2 s post-stimulus onset in order to account for the hemodynamic lag. These averaging windows were selected to maximize data inclusion while avoiding contamination between adjacent face and object blocks, and between object blocks and experimental breaks (see Supplementary Fig. 1 for visualization of response timecourses and averaging windows).

One challenge in fNIRS research is determining from where in the brain a given functional response originates. The functional channel of interest (fCOI; Powell, Deen et al., 2018) approach takes into account variability in the layout of functional responses and in brain anatomy across participants and also accommodates small differences in head shape and hat placement. The fCOI approach is particularly suited to the goals of this study because it explicitly and iteratively optimizes channel selection (in independent data) for detecting condition differences in functional responses (Powell, Deen et al., 2018). We used the fCOI approach to sensitively identify channels that showed preferential responses to (1) faces (regardless of emotional valence or intensity) relative to objects, (2) happy faces relative to neutral faces, (3) fearful

(100%) faces relative to neutral faces, (4) angry (100%) faces relative to neutral faces, (5) positive (happy) faces relative to negative (fearful, angry) faces (all 100% intensity), and (6) high (100% fearful, angry) relative to low (40% fearful, angry) intensity faces in bilateral superior temporal cortex (STC) and middle- to dorsomedial prefrontal cortex (MPFC). First, we selected a set of channels ("search space") that reliably covered a region of the scalp plausibly overlaying these three cortical regions across participants, based on their position on the scalp relative to 10–20 EEG landmarks, as guided by prior evidence concerning the cortical projection of the 10–20 EEG system (Kabdebon et al., 2014; see Fig. 2). Within each participant we conducted iterative leave-one-trial-pair-out analyses, which involved identifying the channel (fCOI) within each search space that produced the largest t-value to the preferred > dispreferred condition contrast (calculated in all-minus-one condition trial pairs) and extracting the response to the left-out trial pair from that fCOI. This iterative approach produced response magnitude estimates that were independent from fCOI channel selection. In these fCOIs, we calculated the average response magnitude to the preferred and non-preferred condition for each contrast. We additionally calculated the frequency of the modal fCOI per child (i.e., the proportion of leave-one-trial-pair-out iterations that selected the modal fCOI) and across children.

FCOIs were excluded from analyses if more than 1/3 of the channels in its search space were excluded or if more than 20% of timepoints were identified as motion artifact after implementing motion correction (this threshold was selected based on being 2x the tPCA threshold). Participants were excluded if they had fewer than 6 trials per face condition or 10 trials per object condition (i.e., less than 36 or 40 s of data, respectively); because contrasts differed in the number of contributing conditions (e.g., all faces > objects, vs. only happy faces > objects), contrasts also differed in the number of participants who contributed usable data. Time spent looking during each trial was coded offline from videos of the testing session using Supercoder (Version 1.5; Hollich, 2005). Included trials were those during which the participant looked at the stimuli for at least 60% of the trial.

2.5. FNIRS data quality

We used the proportion of timepoints identified as artifact (post-processing) as a proxy for data quality and included this measure in all statistical tests that concerned individual differences. Data quality in MPFC was uncorrelated with age (r_s = .08), did not differ between boys and girls (Cohen's d = -.19 [negligible]), and did not vary meaningfully with performance on behavioral measures of social cognition (see below; Prosocial helping: η^2 = .03; Prosocial helping latency: r_τ = -.11; Theory of Mind: r_τ = .08; Emotion sort: r_τ = .12).

2.6. Behavioral measures

Prior to the fNIRS session, children completed a behavioral task measuring prosocial behavior – specifically, whether they helped an experimenter who struggled to retrieve a dropped clothespin and how long they waited prior to helping (Warneken and Tomasello, 2006). After the fNIRS session, children completed a standard behavioral measure of theory of mind reasoning (Wellman and Liu, 2004). This task included eight questions across four test scenarios: (1) one test question that required children to reason about diverse desires, (2) one test question about diverse beliefs, and one engagement, control, and test question each about (3) knowledge access and (4) false beliefs of the characters. This task did not include items about the characters' emotions. Summary scores were calculated as the proportion of questions answered correctly, where both control and test questions in the knowledge access and false belief scenarios had to be answered correctly for the child to receive credit (engagement questions were not included in the summary score). This is the standard protocol used to summarize performance on this task. Children additionally completed an "Emotion Sort" behavioral task during which they viewed and sorted 22 happy, angry, fearful, and neutral face cards into cardboard houses associated with emotion categories ("happy," "fearful," "mad" [angry], or "calm" [neutral]). Children were instructed to look at each face card presented, "think about how they're feeling and put them in the house that matches" (Bayet et al., 2018). Summary scores were calculated as the proportion of face cards sorted correctly. See Supplementary Materials for further details on these behavioral tasks.

2.7. Statistical analyses

All statistical tests were conducted in R (Version 3.3.3; R Core Team, 2017), and data were visualized using the ggplot2 package (Wickham et al., 2016). We used Shapiro-Wilk Normality tests to determine whether variables were normally distributed, using a threshold of $p < .05$. We conducted paired one-tailed t-tests (for normally distributed variables) or Wilcoxon signed rank tests (for non-normally distributed variables) to test for differences in concentration values between (1) faces and objects, (2) positive (100% happy) and neutral faces, (3) fearful (100%) and neutral faces, (4) angry (100%) and neutral faces, (5) positive (happy) and negative (fearful, angry) faces (all 100% intensity), and (6) high (100% fearful, angry) and low (40% fearful, angry) intensity faces. We conducted post-hoc sensitivity analyses to determine whether we had sufficient power to detect significant brain-behavior correlations (see Supplementary Materials). We then used linear regressions to test for significant correlations between the magnitude of the MPFC response to the faces > objects contrast and age and performance on three behavioral measures of early social cognition (prosocial behavior, theory of mind reasoning, and facial emotion recognition), controlling for age. All individual difference analyses controlled for individual differences in data quality.

2.8. Data and code availability

Summary data and analysis code for reproducing statistical analyses and figures are available on the Open Science Framework (https://osf.io/7452j/).

3. Results

3.1. Preferential responses to faces

First, we tested whether MPFC and bilateral STC responded preferentially to dynamic faces (across all emotion categories and intensities) relative to dynamic objects. All three cortical regions showed larger HbO concentration values during face trials relative to object trials; bilateral STC additionally showed a significant condition difference in HHb

concentration values (see Table 1 for statistical results and Fig. 3 for visualization). These results were significant after correcting for multiple comparisons (Bonferroni correction: 3 regions/tests, $\alpha = .017$). Like many prior studies, we observed smaller effects in HHb concentration values, relative to HbO concentration values (Cristia et al., 2013). Prior work suggests that HbO concentration values highly correlate with the fMRI BOLD response (Strangman et al., 2002).

3.2. Preferential responses to happy, fearful, or angry, relative to neutral, faces

We tested for functional responses that responded preferentially to 100% happy, fearful, or angry faces, relative to neutral faces (three separate tests). The HbO response in MPFC was larger during happy face trials relative to neutral face trials; this result did not survive a Bonferroni correction for three regions/tests ($\alpha = .017$). MPFC did not respond preferentially to fearful or angry faces relative to neutral faces. Responses in bilateral STC did not vary by emotional content for any of the three contrasts (see Table 1 for statistical results and Fig. 3 for visualization), although note that the smaller sample sizes in STC reduced power to detect effects (ns = 16–20 across contrasts).

3.3. Differential responses by emotional valence and intensity

We tested for differential functional responses by emotional valence and intensity. We did not find evidence for preferential responses to 100% happy faces relative to negative faces (100% fearful and 100% angry; Table 1). Similarly, we did not find evidence for preferential responses to high intensity faces relative to low intensity faces (100% vs. 40% fearful and angry faces; Table 1 and Fig. 3).

3.4. Follow up analysis in children with preferential responses to happy faces in MPFC

Given that analyses of different contrasts were conducted on different subsets of children (due to the trial requirement per condition within each contrast, see sample sizes per contrast in Table 1), in post-hoc analyses we confirmed that MPFC HbO responses did not differ by valence (i.e., positive > negative, one-tailed paired Wilcoxon test: W = 430, CI = [-0.16,Inf], p = .12) or by intensity (i.e., 100% > 40%; one-tailed paired t-test: t(36) = .08, CI=[-0.52,Inf], p = .47) in the subset of children who showed preferential MPFC responses for happy relative to neutral faces (n = 37).

3.5. Individual differences in MPFC response

We conducted exploratory analyses to examine whether functional responses in MPFC to the Faces > Objects contrast correlated with individual differences in social cognitive behaviors (see Supplementary Materials for a full description of the behavioral tasks and sensitivity analyses).

3.6. Behavioral performance

Of the 69 children with available data from the prosocial helping task, 61% (n = 42) exhibited spontaneous prosocial helping behavior, 30% (n = 21) helped once prompted, and 9% (n = 6) did not help. Latency to help (for spontaneous and prompted helpers only) ranged from 1 to 36 s; M(SD) = 13.5(10.6) seconds. Helping behavior and latency did not vary significantly by age (behavior: bs<.60, ts<1.4, CIs=[-.88 to -.27, .92–1.4], ps > .17; latency: b=-.22, t=-1.9, CI=[-.46, .02], p = .07) or gender (behavior: Pearson's Chi-Squared test: X(2) = .20, p < .91; latency: b=-.06, t=-.24, CI=[-.58, .45], p = .81).

Performance on the theory of mind task (n = 76) ranged from 0 to 1, M(SD) = .43(.25). Performance correlated marginally (non-significantly) with age (b = .21, t = 1.9, CI=[-.01, .44], p = .07) and did not

Table 1

Statistical Results. We used a fCOI approach to detect differential response magnitudes in oxygenated (HbO) and deoxygenated (HHb) concentration values in MPFC and bilateral STC across six contrasts. T-tests were used with normally distributed data; Wilcoxon signed rank tests were used with non-normally distributed data. This table reports the number of participants included in each test (n), the test statistic (t or W), the 95% confidence interval, and the p-value. Statistical results where $p < .05$ are shown in bold; note that the MPFC Happy > Neutral result is not significant upon correction for multiple comparisons ($\alpha = .017$). The number of participants included in each statistical test varied due to the trial requirement per condition (and because different contrasts involved comparing different conditions), and the channel requirements per fCOI.

| Contrast	MPFC - HbO	RSTC - HbO	LSTC - HbO	MPFC - HHb	RSTC - HHb	LSTC - HHb
All Faces > Objects	**n = 80, W = 2143, CI = [.09, .67], p = .01**	**n = 44, t (43) = 6.3, CI = [1.3, 2.5], p = 1.2 × 10⁻⁷**	**n = 45, t (44) = 6.1, CI = [1.5, 3.1], p = 2.2 × 10⁻⁷**	n = 80, W = 1628, CI = [-.13, .13], p = .97	**n = 44, t(43) = -6.0, CI = [-1.3, -.64], p = 3.8 × 10⁻⁷**	**n = 45, t(44) = -6.3, CI = [-1.4, -.73], p = 1.3 × 10⁻⁷**
100% Happy > Neutral	**n = 37, W = 490, CI = [.05, 1.5], p = .04**	n = 20, t(19) = .97, CI = [-.81, 2.2], p = .35	n = 16, t(15) = .76, CI = [-.90, 1.9], p = .46	n = 37, t(36) = -.41, CI = [-.28, .19], p = .69	n = 20, W = 103, CI = [-.34, .34], p = .96	n = 16, t(15) = .30, CI = [-.45, .60], p = .77
100% Fear > Neutral	n = 37, t (36) = .48, CI = [-.57, .92], p = .64	n = 20, W = 137, CI = [-.53, 1.8], p = .25	n = 17, t(16) = .03, CI = [-1.6, 1.6], p = .98	n = 37, t(36) = -1.42, CI = [-.41, .07], p = .17	n = 20, t(19) = .42, CI = [-.34, .51], p = .68	n = 17, t(16) = -1.2, CI = [-.74, .20], p = .24
100% Angry > Neutral	n = 37, W = 368, CI = [-.66, .86], p = .81	n = 21, W = 147, CI = [-.81, 2.0], p = .29	n = 17, t(16) = -1.1, CI = [-1.6, .55], p = .31	n = 37, W = 387, CI = [-.20, .35], p = .60	n = 21, t(20) = -1.1, CI = [-.62, .20], p = .29	n = 17, t(16) = -1.0, CI = [-.48, .17], p = .32
Positive > Negative (100% Happy > 100% Angry & Fear)	n = 47, W = 633, CI = [-.37, .77], p = .47	n = 25, t(24) = .97, CI = [-.61, 1.7], p = .34	n = 24, t(23) = -.10, CI = [-1.1, 1.0], p = .92	n = 47, W = 695, CI = [-.06, .34], p = .17	n = 25, t(24) = -.32, CI = [-.39, .29], p = .75	n = 24, t(23) = .11, CI = [-.43, .48], p = .91
High > Low Intensity (100% Angry & Fear > 40% Angry & Fear)	n = 80, W = 1653, CI = [-.39, .48], p = .88	n = 46, W = 574, CI = [-.56, .83], p = .72	n = 45, W = 517, CI = [-.67, .64], p = 1	n = 80, W = 1582, CI = [-.17, .15], p = .86	n = 46, W = 455, CI = [-.39, .13], p = .36	n = 45, W = 548, CI = [-.23, .29], p = .74
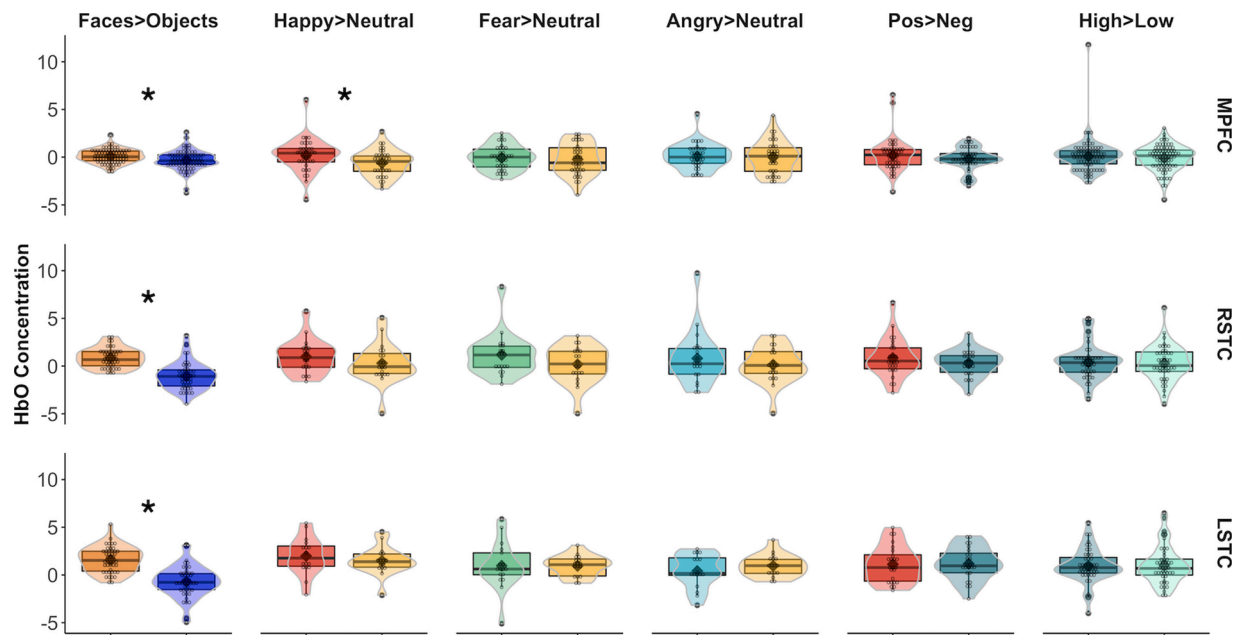
Fig. 3. Oxygenated Hemoglobin (HbO) Concentration Values per Condition Contrast and Region. Boxplots show HbO values (y-axis) per condition in each contrast (x-axis) in medial prefrontal cortex (MPFC) and bilateral superior temporal cortex (STC). In all boxplots, the center line reflects the median, the box reflects the inter-quartile range (IQR), and the whiskers show the first and third quartile -/+ 1.5*IQR. Violin plots visualize the distribution of values; individual participant data points are shown as dots and group means are shown as black diamonds. Asterisks indicate where statistical tests for condition differences resulted in p-values < .05; note that the MPFC Happy > Neutral result is not significant upon correction for multiple comparisons ($\alpha = .017$).

differ by gender (b=-.15, t=-.64, CI=[-.61, .31], p = .52).

Overall performance on the emotion sort task (n = 74) ranged from .27 to .86, M(SD) = .61(.15) and did not vary by age (b = .03, t = .25, CI=[-.21, .26], p = .80) or gender (b=-.25, t=-1.1, CI=[-.72, .21], p = .28). For a full description of task performance in a large sample of 3-year-old children (n = 208) including the participants described here and participants who were not recruited for the fNIRS study, see Bayet et al., 2018.

3.7. Brain-behavior correlation analyses

The magnitude of the MPFC face response (HbO Faces > Objects) increased with age (b = .25, t = 2.3, CI=[.04, .47], p = .02, controlling for data quality) and did not differ by gender (b=-.04, t=-.20, CI=[-.50, .41], p = .85, controlling for data quality).

The magnitude of the MPFC face response was significantly larger among children who helped spontaneously during the prosocial helping task, compared to those who did not help (effect of helping behavior:

spontaneous helpers (n = 42), relative to non-helpers: b = .87, t = 2.0, CI=[.01, 1.7], p = .047, prompted helpers (n = 21), relative to non-helpers: b = .61, t = 1.3, CI=[-.30, 1.5], p = .19, controlling for data quality); this effect was not significant when additionally controlling for age (b = .78, t = 1.8, CI=[-.09, 1.7], p = .08) and is based on a very small number of non-helpers (n = 6, out of n = 69 children who completed this task and contributed MPFC fNIRS data). Due to the small number of non-helpers, we conducted additional analyses of children's latency to help. Latency to help was uncorrelated with MPFC response (b=-.01, t=-.09, CI=[-.26, .24], p = .93, controlling for data quality). Performance on the theory of mind task was uncorrelated with the magnitude of the MPFC face response (n = 83; b = .29, t = 1.7, CI=[-.05, .61], p = .09, controlling for data quality). Finally, the magnitude of the MPFC face response was not significantly correlated with overall performance on the emotion sort task (n = 80; b = .23, t = 1.9, CI=[-.009, .47], p = .059, controlling for data quality). This correlation remained non-significant when additionally controlling for age (b = .22, t = 1.9, CI=[-.01, .45], p = .06; effect of age: b = .26, t = 2.3, CI=[.04, .49], p = .02). Note that effects would need to survive a Bonferroni correction for multiple comparisons (three behavioral measures/tests, α = .017) to reach significance and would need to be near this corrected threshold to be considered marginal.

4. Discussion

Accurately perceiving and understanding emotions are important aspects of healthy social-emotional development (Carter et al., 2010). We used functional near-infrared spectroscopy (fNIRS) to characterize early organization of functional MPFC and STC responses to faces that varied in emotional content, valence, and intensity. Bridging prior work in infants and adults, we observed functional responses in bilateral STC and MPFC that responded preferentially to faces relative to objects in 3-year-old children. MPFC additionally showed preferential responses to happy faces relative to neutral faces. While this latter result did not survive correction for multiple comparisons across regions, it is consistent with prior evidence that MPFC is recruited to process positively valenced social stimuli in infants (for review, see Powell et al., 2018b). We did not detect preferential MPFC or STC responses to angry or fearful faces or generalized differences in response magnitude in these regions by emotional valence or intensity.

Our results add to a growing body of neuroimaging evidence for relatively early preferential STC and MPFC responses to faces (Deen et al., 2017; Kosakowski et al., 2021). These findings are perhaps surprising in light of the protracted structural and functional developmental trajectory of these regions (Carter and Pelphrey, 2006; Giedd et al., 1999; Gogtay et al., 2004; Kilford et al., 2016; Mills et al., 2013; Somerville et al., 2013). However, these two views of development can be consistent: together, they provide evidence for continuity in the neural system that supports social cognitive functions across development. Within this continuous neural system, there are signatures of early organization as well as developmental change (Bowman et al., 2019; Richardson et al., 2018). Additional research is necessary to better understand the neural mechanisms of developmental change in MPFC function and how different aspects of brain development support developmental improvements in reasoning about emotions throughout childhood (Harris et al., 2005; Nelson et al., 2006; Pons et al., 2004; Widen, 2016). Are individual differences in early MPFC function stable, such that individual differences in early functional responses predict individual differences later in life?

Our results also are consistent with evidence that MPFC responds preferentially to positively valenced social stimuli early in life (Grossmann, 2013; Powell et al., 2018b; Raz and Saxe, 2020). However, the observed preferential response in MPFC to happy faces relative to neutral faces presents a puzzle: If MPFC preferentially processes positively valenced emotional stimuli, why did we not observe a similar preferential response for 100% happy faces relative to the 100%

negative emotion expressions (fear and angry)? It is unlikely that this pattern of results is a consequence of insufficient power: The positive > negative emotion contrast included more trials and participants than the happy > neutral contrast. Additionally, in post-hoc analyses we confirmed that the subset of children included in analyses of the happy > neutral contrast did not show differential MPFC responses by valence or intensity.

One speculative explanation is that early MPFC responses are evoked by both positively valenced and socially relevant stimuli and that the happy > neutral contrast best leverages both of these stimulus features. By this account, we did not observe differential responses between happy and negative high intensity faces because of the social relevance of high intensity negative faces (thus minimizing the MPFC response difference between happy and negative faces, relative to the difference between happy and neutral faces). This account implies that positively valenced, socially rewarding stimuli drive MPFC responses more than negatively valenced, socially relevant stimuli, and is supported by our finding that MPFC responded preferentially to happy faces but not fearful or angry faces relative to neutral faces. Future research is necessary to test this prediction directly, especially given that "social reward" and "social relevance" often track together. In infant research, preferred stimuli (e.g., own mother's face or voice, hearing one's own name, infant-directed speech) are often both more socially rewarding and more socially relevant to infants than non-preferred stimuli (e.g., face or voice of strangers, hearing others' names, adult-directed speech). Studies that orthogonally manipulate social reward and social relevance are necessary to determine the extent to which these two aspects of social stimuli drive early MPFC responses.

We did not find evidence that functional responses in MPFC and STC vary by emotional category. That is, we did not observe differences in the magnitude of response to fearful or angry, relative to neutral, faces. While null results should be interpreted with caution, these results are consistent with prior fMRI evidence in adults. In adults, the response magnitude to emotional stimuli in these regions does not vary by emotion category or valence (Fusar-Poli et al., 2009; Lindquist et al., 2012). Instead, the magnitude of response in adult middle MPFC appears to be modulated by self-relevance (Tamir and Mitchell, 2010; see Denny et al., 2012 for a meta-analysis). By contrast, the magnitude of response in ventromedial PFC is modulated by valence/reward value (Bartra et al., 2013; Clithero and Rangel, 2014; Kim et al., 2011; Skerry and Saxe, 2014). Patients with VMPFC lesions have selective impairments in emotion understanding (Shamay-Tsoory and Aharon-Peretz, 2007) and responding (Baez et al., 2016). While our protocol did not enable us to measure from VMPFC, it may be possible to optimize optode arrangement and cap placement for VMPFC measurement in future fNIRS studies (Kabdebon et al., 2014). Such studies will be important for determining whether MPFC supports multiple distinct social functions (reward processing in VMPFC, reasoning about mental states, including emotions, in M/DMPFC) in infancy and early childhood, and how these functions operate together when individuals reason about emotions.

While fMRI research in adults suggests that the magnitude of response in MPFC and STC is similar across emotion categories, there is also evidence that this information is represented in these regions. Fine-grained analyses of response patterns across voxels within these regions find distinct patterns for distinct emotions in M/DMPFC and STC (Dobs et al., 2018; Kliemann et al., 2018; Koster-Hale et al., 2017; Peelen et al., 2010; Skerry and Saxe, 2015, 2014). Such fine-grained analyses are not possible with fNIRS data, given the low spatial resolution. FNIRS enables analyzing response patterns across regions, at the level of centimeters, but not within brain regions, at the level of millimeters (Emberson et al., 2017). While challenging, fMRI research using child-friendly experiments may be necessary to investigate fine-grained organization of emotion representations in young children (Murray et al., 2020).

Finally, we did not find strong evidence that MPFC responses support early social behaviors, although some statistical results were in the predicted direction. While encouraging and consistent with recent

evidence in infants (Krol and Grossmann, 2020) and prior evidence with older children (Bowman et al., 2019; Sabbagh et al., 2009), additional research is necessary to characterize the relationship between functional responses in MPFC and early social behaviors. Identifying reliable, early neural markers of social cognitive development may enable earlier identification of and support for individuals at risk for clinical disorders characterized by social cognitive features (e.g., autism spectrum disorder, social anxiety).

Additional limitations of the current study include the non-representative sample composition (i.e., primarily White children raised in high socioeconomic status families (Falk et al., 2013; Nielsen et al., 2017)); relatively high attrition rates (see Supplementary Materials); the constraint inherent to fNIRS of only measuring from cortical structures (omitting subcortical regions relevant for emotion processing, such as the amygdala (Adolphs et al., 1994)); and the use of a passive-viewing experiment that presented emotional faces in the absence of other sources of input about emotions (e.g., body language, vocal tone, linguistic content) and in the absence of context, which is informative for inferring emotions (Anzellotti et al., 2019; Barrett et al., 2019).

5. Conclusion

Perceiving and understanding emotions is an important aspect of our social lives. Here, we provide a link between research characterizing functional responses in MPFC and STC in adults and research characterizing early functional responses and social behaviors in infants. These results also further clarify early MPFC functions: Responses in MPFC differed between happy and neutral faces but not between other emotion categories. Finally, our results motivate several avenues of future research to understand the role of MPFC in supporting early social behaviors.

Data statement

Summary data and analysis code for reproducing statistical analyses and figures are available on the Open Science Framework (https://osf.io/7452j/).

Declaration of Competing Interest

The authors report no declarations of interest.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.dcn.2021.100984.

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