Developmental Cognitive Neuroscience 73 (2025) 101565

Contents lists available at ScienceDirect

Developmental Cognitive Neuroscience

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

Behaviorally inhibited preschoolers experience stronger connectivity among social-related neural regions while interacting with a stranger

Caitlin Aloisio [a,*], Lindsay Taraban [b], Kathleen Mowatt [c], Hendrik Santosa [d], Theodore J. Huppert [e], Jennifer S. Silk [f], Koraly Pérez-Edgar [g], Judith K. Morgan [b,f]

[a] *University of Pittsburgh Medical Center, Pittsburgh, PA, USA*
[b] *Department of Psychiatry, University of Pittsburgh, Pittsburgh, PA, USA*
[c] *Dietrich School of Arts and Sciences, University of Pittsburgh, Pittsburgh, PA, USA*
[d] *Department of Radiology, University of Pittsburgh, Pittsburgh, PA, USA*
[e] *Department of Electrical and Computer Engineering, University of Pittsburgh, Pittsburgh, PA, USA*
[f] *Department of Psychology, University of Pittsburgh, Pittsburgh, PA, USA*
[g] *Department of Psychology, Penn State University, State College, PA, USA*

ARTICLE INFO

Keywords:
Behavioral inhibition
Preschool
Anxiety
FNIRS
Stranger Approach

ABSTRACT

Social behavioral inhibition (BI), or wariness in response to unfamiliar social stimuli, is a temperament trait that, when present in preschool-age children, predicts neural alterations and anxiety disorders by adolescence. The current study assessed neural functioning associated with BI during the preschool years. Our sample was enriched for BI based on mother report and included 59 preschool-age children (54 % female, $M_{age} = 3.7$ years). Children interacted with an unfamiliar experimenter via the Stranger Approach paradigm from the preschool version of Lab-TAB, and neural data were collected simultaneously to measure neural response to an unfamiliar social encounter. Children who exhibited more social BI-related behaviors experienced stronger functional connectivity between multiple social-related neural regions, including the temporoparietal junction, superior temporal gyrus, and medial and lateral prefrontal cortex while interacting with a stranger. Additionally, children who experienced stronger connectivity between the right and left temporoparietal junction had greater mother-reported anxiety symptoms one year later. Our results suggest that observable social BI during early childhood is associated with distinct neural patterns, which may elucidate biomarkers that underlie risk for later anxiety.

1. Introduction

Behavioral inhibition (BI) – defined as fearfulness, shyness, or wary behavior in unfamiliar situations that are viewed as threats (Fox et al., 2005; Kagan et al., 1984) – is estimated to be present in 15–20 % of preschool-aged children (Kagan et al., 1989). BI is reliably observable during the preschool years (Reznick et al., 1986) and is a robust predictor of anxiety disorders in later childhood and adolescence (Beesdo et al., 2009; Chronis-Tuscano et al., 2009; Paulus et al., 2015). Notably, preschool-age children who display high levels of BI are three to seven times more likely to develop clinically significant anxiety before adulthood in comparison with uninhibited children (Clauss and Blackford, 2012). Despite this increased risk, not all preschoolers with high BI develop meaningful symptoms of anxiety later in life (Degnan and Fox, 2007; Kagan et al., 1984; Pfeifer et al., 2002). Understanding sources of heterogeneity in the trajectories of preschoolers with high BI could illuminate biomarkers that place BI children at risk of developing later anxiety.

BI is typically measured via parent-report or observations of child behavior in response to unfamiliar stimuli while in a controlled laboratory setting (Buss, 2011; Kim et al., 2011, Pfeifer et al., 2002; , Reznick et al., 1986). Laboratory-based observations of behaviors associated with BI are categorizable as being "social" or "non-social", depending on the nature of the task. Social BI consists of inhibited behavior directed toward unfamiliar people in social situations, whereas non-social BI includes fear directed toward novel non-social objects, such as an unfamiliar toy (Dyson et al., 2011; Tan et al., 2024). While sensitivity to social and non-social stimuli are often subsumed under a single BI umbrella (Dyson et al., 2011; Kochanska, 1991; Rubin et al., 1997; Tan et al., 2024), these temperament subtypes are dissociable from one

* Correspondence to: 121 Meyran Ave. Ste. 241, Pittsburgh, PA 15213, USA.
E-mail address: caitlinaloisio@gmail.com (C. Aloisio).

https://doi.org/10.1016/j.dcn.2025.101565
Received 21 October 2024; Received in revised form 14 February 2025; Accepted 27 April 2025
Available online 7 May 2025
1878-9293/

another during early childhood and predict different psychosocial outcomes later in life. Of note, social BI present during early childhood predicts a wider range of anxiety symptoms and more internalizing problems by adolescence in comparison to non-social BI (Dyson et al., 2011; Tan et al., 2024).

The literature suggests that high levels of behaviorally observed social BI may be related to functional differences at the neural level (Fox et al., 2021). Although not widely examined during the preschool years, some studies have assessed activation patterns associated with social BI traits in early childhood as measured via electroencephalogram (EEG). Right frontal asymmetry, defined as greater right hemispheric activity, is associated with withdrawal behaviors in young children (Fox, 1994; Liu et al., 2021), consistent with those exhibited by BI children. Indeed, one study (Diaz and Bell, 2012) found that ten-month-old infants who experienced greater right frontal EEG asymmetry simultaneously showed higher levels of fear behaviors as they encountered an unfamiliar person via the widely used Stranger Approach paradigm from infant version of Lab-TAB (Goldsmith and Rothbart, 1999), suggesting that neural differences related to later patterns of social BI are present within the first year of life.

Specific frontal neural regions that support social functioning include the lateral prefrontal cortex (LPFC), which is involved in affect regulation, cognitive control, and threat response (Badre and Wagner, 2007; Li et al., 2022; Monk et al., 2008; Sylvester et al., 2018) and the anterior medial prefrontal cortex (AMPFC), which is a part of the inferior frontal gyrus, and is involved in emotion expression and social cognition (Japee et al., 2015; Jarcho and Guyer, 2018). Beyond the frontal lobe, additional brain regions that are involved in social functioning include the temporoparietal junction (TPJ), which supports theory of mind, social interactions, and communication (Jarcho and Guyer, 2018; Hakuno et al., 2020; Van Hoeck et al., 2014; Sylvester et al., 2018), and the superior temporal gyrus (STG), which is involved in emotion perception (Robins et al., 2009; Sylvester et al., 2018). Although the function of these neural regions individually has previously been established, less is known about how they work with one another in the context of BI to support positive social interactions. Some studies have shown that adolescents who were once socially inhibited children experience altered functional connectivity in social-related neural regions while encountering aversive socio-emotional stimuli (i.e., angry faces, fearful faces; Clauss et al., 2014; Hardee et al., 2013), although these findings are mixed in directionality regarding connectivity strength. A recent study by Bulgarelli et al. (2023) found that preschool-age children experience stronger functional connectivity among multiple social-related neural regions, most significantly between the medial PFC and the TPJ, while engaging in a non-preferred social interaction in comparison to a preferred social interaction. Stronger medial PFC-TPJ functional connectivity has also been associated with negative social-related emotions (i.e., embarrassment, guilt; Burnett and Blakemore, 2009). It seems likely that socially inhibited preschoolers may also display stronger functional connectivity between the medial PFC and the TPJ in response to unfamiliar social situations, given that novel social encounters produce heightened discomfort and negative social-related emotions in socially BI children (Fox et al., 2005; Kagan et al., 1984), much like how a non-preferred social interaction would produce these feelings within the general population.

Despite evidence supporting the presence of altered functional connectivity in adolescence as it relates to observable social BI during early childhood, little is known about how observable social BI may *concurrently* be related to functional connectivity among social neural regions during the preschool years. Presumably, preschool-age children with high levels of observable social BI, when interacting with an unfamiliar person, would concurrently experience stronger functional connectivity between the AMPFC and the TPJ, given that stronger connectivity among these regions is associated with non-preferred or negative social contexts (Bulgarelli et al., 2023; Burnett and Blakemore, 2009). If stronger AMPFC-TPJ connectivity does occur concurrently with higher observable social BI during the preschool years, then this may help to explain heterogeneity in outcomes among preschoolers with observable social BI. Specifically, stronger AMPFC-TPJ functional connectivity may help differentiate preschoolers who go on to develop significant anxiety from those who decrease in BI over childhood (Abend et al., 2020).

Although other subcortical regions (e.g., amygdala, cingulate, striatum) are also implicated in socioemotional functioning (Blackford et al., 2010; Delgado et al., 2000; Fox et al., 2021; Ridderinkhof et al., 2004), not all regions can be visualized during naturalistic social interactions. In contrast, the AMPFC, TPJ, STG and LPFC are accessible via functional near-infrared spectroscopy (fNIRS) and therefore associated neural functioning can be readily observed during live social interactions (Bulgarelli et al., 2023; Hakuno et al., 2020). Evaluation of functional connectivity with fNIRS could clarify how these neural regions work in tandem with one another to support social interactions as early as the preschool years. One reason for the lack of prior research on associations between observable social BI and neural function in early childhood has been methodological constraints, as most neuroimaging techniques are not conducive to natural settings and are sensitive to motion artifacts. Given that BI children often show signs of distress in novel situations, the compliance rate for physically restrictive imaging methods that may be unfamiliar to a child, such as functional magnetic resonance imaging (fMRI), would likely be low.

fNIRS is an ideal imaging technique to use when working with young BI children because it is minimally restrictive and less sensitive to movement than other types of neuroimaging, such as fMRI and EEG (Lloyd-Fox et al., 2010; Wilcox and Biondi, 2015). This allows children to freely engage in live social interactions without feeling physically confined. fNIRS also produces more precise localization of neural activity than EEG (Lloyd-Fox et al., 2010; Wilcox and Biondi, 2015), allowing us to specifically examine social neural regions as opposed to cortical and subcortical hemispheres. fNIRS has been successfully used in previous studies measuring neural activity within samples of preschool-age children (Bulgarelli et al., 2023; Kerr-German et al., 2022; Morgan et al., 2023).

To examine potential relations between functional neural connectivity and observable social BI during the preschool years, we collected fNIRS and behavioral data from a group of preschool-aged children while they engaged in a standardized task designed to elicit social BI-related behaviors. We controlled for non-social BI in the present analyses given that social and non-social BI often coexist with one another (Dyson et al., 2011; Kochanska, 1991; Rubin et al., 1997; Tan et al., 2024), and because all tasks within the present study were performed in a lab environment, which may be unfamiliar to children. Our primary aims were (1) to test whether observable behavioral indices of social BI in preschool-age children were concurrently related to altered functional connectivity among social neural regions, and (2) to examine whether behavioral and neural indices associated with high levels of social BI would predict mother-reported child anxiety symptoms one year later after controlling for baseline levels of child anxiety. Based on a small body of prior literature, we hypothesized that higher levels of observed social BI would be related to stronger functional connectivity between the AMPFC and the TPJ. We also expected stronger connectivity across other social related neural regions (i.e., LPFC, AMPFC, TPJ, and STG) in the context of higher observable social BI, although we did not make additional predictions about specific regions given the novelty of this research question. Additionally, we predicted that children who experience stronger AMPFC-TPJ connectivity during a task designed to measure social BI would show greater levels of mother-reported anxiety symptoms at one-year follow-up, considering that many children who are socially inhibited during the preschool years go on to develop more severe anxiety symptoms later in childhood.

2. Methods

2.1. Participants

Data for the present study were drawn from the Shyness and Inhibition and New Experiences (SHINE) Study, which included 59 biological mother-child dyads residing within the greater Pittsburgh area. Children were between three and five years old, with an average age of 3.7 years (*SD* =.73 years). Roughly half (54 %; $n = 32$) of the children were female. Children in the sample were primarily White (75 %; $n = 44$), with the remaining children identified as Black/African American (13 %; $n = 8$), or Multi-racial/Other (12 %; $n = 7$). In terms of ethnicity, 9 % ($n = 5$) of children identified as Hispanic or Latinx. Exclusion criteria for children included developmental delay or disability, but children with current or past clinical diagnoses at baseline as evaluated via the Kiddie Schedule for Affective Disorders and Schizophrenia – Early Childhood Version (K-SADS-EC; Gaffrey and Luby, 2012; Whalen et al., 2020) remained eligible (2 % of sample, $n = 1$, current social anxiety disorder and specific phobia). These children remained eligible for the present study to more accurately represent the diversity of children that present with childhood BI, and consistent with prior research in this area (Fox et al., 2005; Paulus et al., 2015). Recruitment was designed to ensure adequate variability in BI within the sample. To accomplish this, we oversampled for BI via mother report on the Behavioral Inhibition Questionnaire (BIQ) – a widely used measure to assess for BI in preschool-age children (Bishop et al., 2003). Specifically, 40 of the original 65 participants were required to have a score of 119 or higher on the BIQ, which has previously been associated with stable high BI in children over time (Broeren and Muris, 2010,Fu et al., 2017).

2.2. Procedure

At baseline, mother-child dyads completed two lab visits, with each visit lasting approximately two hours. At the first visit, mothers completed the K-SADS-EC which was used to evaluate their child's psychiatric and developmental history and completed questionnaires regarding their child's symptoms of BI and anxiety. At the second visit—scheduled an average of 10.3 weeks (*SD* = 8.4 weeks) after the first visit—children engaged in a series of tasks designed to measure their BI. We chose two widely used paradigms from the preschool version of Lab-TAB, the Stranger Approach paradigm and the Risk Room paradigm (Goldsmith et al., 1995), to measure social BI and non-social BI, respectively. Child fNIRS data were collected during Stranger Approach, and all tasks performed during this lab visit were videotaped for later coding of observable BI traits. Approximately one year ($M = 52.2$ weeks, $SD = 4.48$ weeks) after the first baseline lab visit, mothers completed a follow-up measure of their child's anxiety symptoms. All study procedures were approved by the University of Pittsburgh Human Research Protections Office and parents and children provided informed consent and assent, respectively.

2.3. Measures

2.3.1. Observed social BI

During the Stranger Approach paradigm, which was used to measure social BI, mothers remained in the room with their child but were asked to refrain from speaking or interacting with them. An unfamiliar experimenter entered the room and asked the child questions about what toys they like to play with as well as questions about an experimenter that they had previously encountered. The unfamiliar experimenter informed the child that they were looking for several pieces of paper that they had misplaced. The unfamiliar experimenter then proceeded to ask the child where the familiar experimenter had gone. After about one minute of interaction, the unfamiliar experimenter left the room, and the familiar experimenter returned. The familiar experimenter asked the child about the stranger that they had just encountered. After about one minute of the child interacting with the familiar experimenter, the unfamiliar experimenter re-entered the room and told the child that they had found their papers before exiting the room for a final time.

Using variables defined in the Lab-TAB coding manual, we selected variables most relevant for social BI, consistent with previous work in this area (Dyson et al., 2011; Planalp et al., 2017). We created an observed social BI composite which included z-scores of the following variables: presence of nervous fidgeting (binary score), child's peak verbal hesitancy to respond to the stranger (*0*: absent to *2:* no verbal interaction with stranger), child's peak gaze aversion from the stranger (*0*: absent to *3:* no eye contact with stranger), the peak intensity of the child's decreased activity level when interacting with the stranger (*0*: absent to *3:* extremely present), the child's fear response toward the stranger (*0*: absent to *3:* extremely present), and the child's latency to first fear response (in seconds; reverse scored). A coder who remained naïve to the BI status of participants received extensive training from a primary coder and achieved reliability (80% agreement) prior to coding independently. Following data collection, 20.3 % of videos ($n = 12$) were double coded by the primary coder and inter-rater reliability was moderate to high (ICCs =.729–.975). The composite measure had good reliability within our study ($\alpha = 0.81$) and was marginally associated with children's BIQ scores ($r = .251$, $p = .056$).

2.3.2. Neural response when interacting with a stranger

fNIRS data were collected during the Stranger Approach task as a measure of functional neural connectivity in response to encountering a stranger. Because we coded for social BI across the entire Stranger Approach task, fNIRS data were collected for the entire duration of the task, including when the familiar experimenter returned to the room to talk to the child about the stranger who was previously in the room. The task lasted an average of 120.54 seconds ($SD = 20.36$), which is above the minimum recommended duration of 1.5 minutes for functional connectivity accuracy in fNIRS (Wang et al., 2017). The average duration of time of the task in which the stranger was in the room was 53.78 seconds ($SD = 11.91$) and the average percentage of the task in which the stranger was in the room was 43.34 % (*SD* =.43). The interaction was video recorded for later behavioral coding, and we included percentage of the task in which the stranger was in the room as a covariate of no interest in analyses.

Neural data were collected using a TechEn CW6 NIRS system (TechEn, Milford, MA) at a sampling rate of 20 Hz. The data were measured simultaneously at two wavelengths (690 nm and 830 nm). Light intensity was automatically adjusted by the system to provide optimal gain. Child fNIRS data were measured from a total of 12 channels, from 6 sources and 9 detectors, where the distance between each source and detector was approximately 3 cm. Sensors were mounted on a NIRx EasyCap which was sized based on the child's head circumference. Within the present study, our fNIRS probe extended over the inferior frontal gyrus, including the AMPFC (Brodmann Area 10) to the parietal regions. For each participant, the appropriately sized fNIRS cap was positioned according to the international 10–20 coordinate system with the center of the lower edge of the probe (detector 5; see Fig. 1) aligned with FpZ to ensure that the same anatomical regions were being assessed for all participants (Jasper, 1958; Okamoto et al., 2004). Using the AnalyzIR toolbox (Santosa et al., 2018), localization of anatomical regions of interest was based on the fNIRS probe registration to the AAL2 brain atlas (Tzourio-Mazoyer et al., 2002) adjusted for the participant's head circumference (Zhai et al., 2020).

2.3.3. Non-social BI

Children's non-social BI—which was used as a covariate in all analyses to isolate the effects of social BI from general fearfulness—was coded from videotapes of children participating in the Lab-TAB Risk Room paradigm (Goldsmith et al., 1995). A composite non-social BI

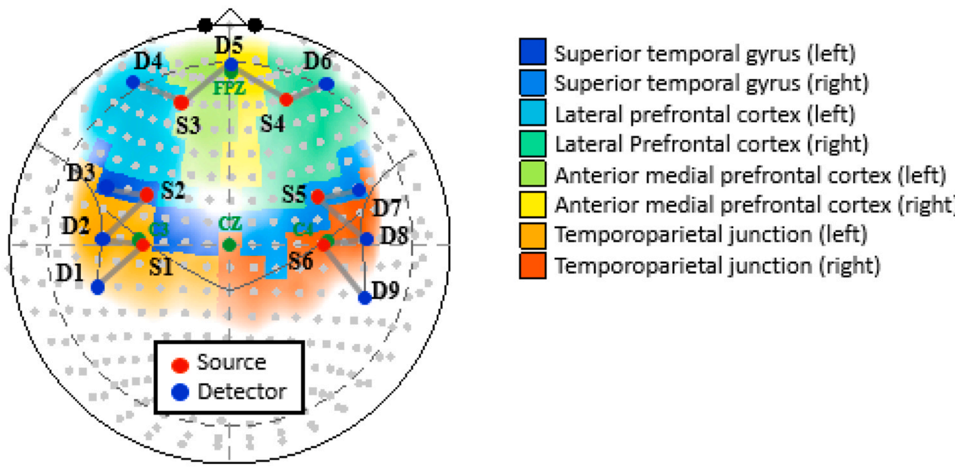

Fig. 1. NIRS probe. Note. Regions of Interest (ROIs) are identified from probe registration to the AAL2 atlas.

variable was created by using relevant variables from the Lab-TAB manual, consistent with past research (Buss, 2011; Kiel and Buss, 2011; Kochanska and Knaack, 2003; Pfeifer et al., 2002; Dyson et al., 2011). This composite was a sum of seven z-scored values: tentativeness of play for each of the five novel objects; average rating of fearful affect shown toward each of the five objects; average level of compliance with experimental request to play with each of the five objects (reverse scored), average latency to touch each of the five objects, latency to vocalize across the task, average rating of approaches to parent, and total amount of time playing with each object (reverse scored). Coder training and reliability checks followed the same process as the above description for observed social BI. Inter-rater reliability was moderate to high (ICCs =.759–.947; $n = 13$ videos), and the internal reliability of the composite measure was good ($\alpha = 0.74$). This measure of non-social BI was significantly correlated with BIQ scores ($r = .278$, $p = .033$).

2.3.4. *Child anxiety symptoms*

At baseline and again at the one-year follow-up, mothers reported on their child's symptoms of anxiety using the 34-item Preschool Anxiety Scale (PAS; Spence and Rapee, 1999). Items are rated on a 5-point Likert Scale (0 =Not True at All to 4 =Very Often True). The PAS is a widely used measure of anxiety symptoms in preschoolers and has demonstrated high reliability and validity in past research (Broeren and Muris, 2008; Hudson et al., 2011; Spence et al., 2001; Zhou et al., 2024). At follow-up, 51 (86 %) of the 59 mothers with baseline data re-completed the PAS. Internal consistencies for the PAS scores at baseline and follow-up were very good ($\alpha_{\text{baseline}} = .923$; $\alpha_{\text{follow-up}} = .899$).

2.4. *Preprocessing and analytic plan*

fNIRS data collected during Stranger Approach were preprocessed in MATLAB™ (Math-works, Natick, MA, 2021a) as part of an open-source AnalyzIR toolbox (Santosa et al., 2018). Raw fNIRS signals were first resampled to 4 Hz and converted to changes in optical density. Then, the measured intensity data of the two wavelengths were converted to relative oxy- and deoxy-hemoglobin concentration changes using the modified Beer-Lambert law (Cope et al., 1988). First-level resting state connectivity analyses employed an autoregressive, robust Pearson's correlation model (see associated literature [Santosa et al., 2017]). This analysis model accounted for both serially correlated noise (due to systemic physiology) and heavy-tailed noise caused by motion artifacts, using a robust statistical (outlier rejection) algorithm based on bisquare weighting (Santosa et al., 2017). No participants were excluded from analyses. Prior work has demonstrated the robustness of this technique by showing improved sensitivity-specificity characteristics (reduced false discovery rates) and has shown that it yields more reliable estimates in the presence of serially correlated errors and statistical outliers due to motion artifacts (Santosa et al., 2018).

For our second level (group) model to address our first aim (i.e., testing associations between behavioral and neural indices of BI), we ran a mixed effects linear model in the AnalyzIR toolbox in MATLAB using the Fisher z-transformed correlations from the first level model as the dependent variable. This mixed effects linear model included an intercept and two slopes as fixed effects. The intercept was the average resting state connectivity and the two slope terms were observed social BI and observed non-social BI. Because observed and neural measures of social BI (as measured by the Stranger Approach paradigm) were both assessed in a laboratory setting, which was likely unfamiliar to children in the present study, we controlled for non-social BI in all analyses to reduce the effect that an unfamiliar physical environment may have on children's behavioral and neural responses to encountering a stranger. We also included percentage of task in which the stranger was present in the room as a fixed effect of no interest to control for between-subject variability in time spent with the stranger. We examined whether findings survived corrections for multiple comparisons using a false discovery rate (q) < .05 (Benjamini and Hochberg, 1995) and report the corrected p (q) for each finding.

Our second aim was to test behavioral and neural indices of social BI as a predictor of child anxiety one year later. Because the AnalyzIR toolbox is only coded to run mixed effect models in which the fNIRS data is the dependent variable, we conducted Aim 2 using SPSS. First, we extracted estimates of the correlation coefficients (i.e., z-estimates) between neural channels of interest as a measure of functional connectivity during the Stranger Approach task using the AnalyzIR toolbox. Next, using SPSS, we conducted bivariate correlations between these extracted estimates and child anxiety at follow-up in SPSS to examine associations between functional connectivity and child anxiety symptom severity a year later. To reduce Type 1 error, we limited bivariate associations to include only those channels that were also significantly associated (at $p < .05$) with observed social BI in the mixed effects linear model for Aim 1. For those bivariate associations that were significant, we further probed the association between observed social BI, functional connectivity when interacting with a stranger, and child anxiety symptoms one year later after controlling for baseline anxiety symptoms and non-social BI using a multiple regression model in SPSS.

3. Results

3.1. *Descriptive statistics and bivariate correlations*

Descriptive statistics and bivariate correlations among primary study variables are presented in Table 1. Consistent with our goal of recruiting

Table 1
Descriptive statistics and bivariate correlations.

	Variable	Timepoint	*Mean (SD)*	Range	1	2	3	4	5
1	Child age	Baseline	3.75 (.76)	3–5	-				
2	Non-social BI	Baseline	−.21 (4.21)	−7.48–10.10	−.116	-			
3	Observed social BI	Baseline	.16 (4.27)	−6.00–12.09	−.057	.122	-		
4	Parent-Reported BIQ	Baseline	112.25 (46.02)	34–194	−.072	.278*	.251	-	
5	Total anxiety at baseline	Baseline	18.52(15.25)	0–69	.039	.271*	.01	.668**	-
6	Total anxiety at follow-up	Follow-Up	15.12(11.98)	0–50	−.123	.153	.088	.570**	.565**

* $p < 0.05$.
** $p < 0.01$.

a sample enriched for BI, 61% of children in this sample ($n = 36$) had a BIQ score above 119 ($M = 111.47$; $SD = 46.58$), which has been empirically linked with stable observations of BI in children over time (Broeren and Muris, 2010; Fu et al., 2017). At baseline, 14% ($n = 8$ of 59 children with baseline data) of children in this study had an elevated PAS score and 12% of children ($n = 6$ of 51 children with 12-month data) had an elevated PAS score at the 12-month follow-up point (i.e., T-score > 60; Spence et al., 2001). Observed social BI was not significantly correlated with non-social BI, child anxiety at baseline, or child anxiety at follow-up.

3.2. *Observed social BI and functional connectivity*

Our first aim tested whether functional connectivity between social neural regions, specifically between the AMPFC and the TPJ, when interacting with a stranger was stronger as a function of observed social BI. Contrary to our hypothesis, functional connectivity between the TPJ and AMPFC was not significantly related to observed social BI. However, we did find positive associations between BI and other social neural regions. Specifically, when controlling for non-social BI, higher levels of observed social BI were associated with stronger connectivity between the right TPJ and the left TPJ, and between the right TPJ and the right STG. Further, higher levels of observed social BI were associated with stronger connectivity between the right STG and the left AMPFC (Fig. 2). Of note, only the association between observed social BI and greater connectivity among right STG and right TPJ passed corrections for multiple comparisons. Full results from oxyhemoglobin models are presented in Table 2, and deoxyhemoglobin findings are presented in Supplemental Table 1.

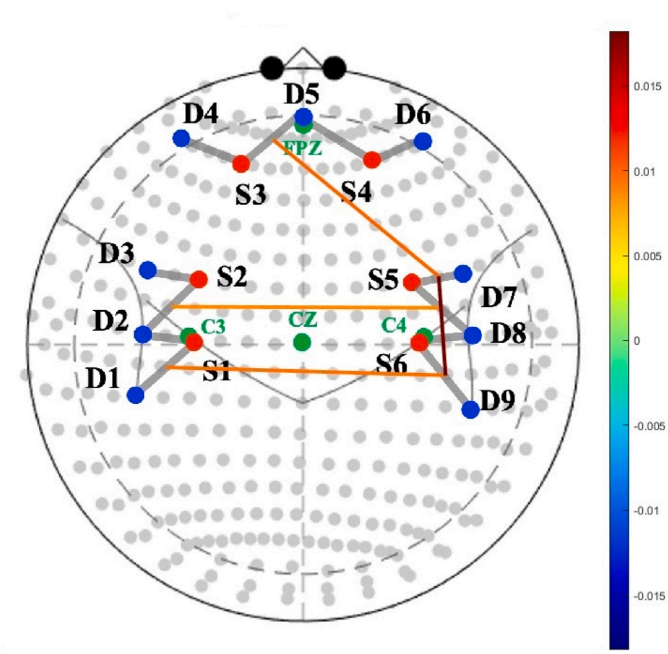

Fig. 2. Higher observable social BI is associated with stronger neural connectivity within multiple social regions while encountering a stranger. Note. Color-coding of bar reflects direction of association, with red lines=positive associations and blue lines=negative associations.

3.3. *Stranger Approach measures and child anxiety*

Our second aim tested whether functional connectivity between social brain regions while interacting with a stranger predicted child anxiety at follow-up. Because observed social BI was not associated with AMPFC-TPJ connectivity in Aim 1, we did not include it in our regression model testing predictors of anxiety at follow-up, thus, that hypothesis was not supported. However, one of the four connectivity channels (i.e., left and right TPJ connectivity [S2D2-S5D8]) that were significantly associated with observed social BI was correlated with child anxiety at follow-up ($r = .287$, $p = .028$). We subsequently ran one regression model evaluating left and right TPJ connectivity on child anxiety at follow-up while controlling for baseline levels of child anxiety, observed social BI, and non-social BI. This regression model included the one significant channel ($F(df) = 10.23(49)$, $p < .001$; $R^2 = .36$). Even after controlling for baseline levels of child anxiety and non-social BI, stronger connectivity between the child's left and right TPJ significantly predicted higher levels of child anxiety at follow-up ($\beta = .32$, $p = .014$; see Fig. 3). Observed social BI was not associated with child anxiety at follow-up in this model ($\beta = -0.10$, ns).

4. Discussion

This study is among the first to demonstrate that higher levels of observed social BI during the preschool period are associated with stronger functional connectivity between social-related neural regions implicated in perspective-taking and social cognition when encountering a stranger. Our findings extend a wealth of behavioral research and suggest that BI, which is observable early in childhood and is one of the strongest and earliest predictors of anxiety longitudinally (Clauss and Blackford, 2012), is associated with neural alterations in social brain regions as early as the preschool years. Notably, as evidence of ecological validity, our study investigated neural indices of social BI using a non-restrictive neuroimaging modality (fNIRS) that captured neural activity during a naturalistic in vivo interaction with a stranger.

Contrasting with our initial hypothesis, we did not find AMPFC-TPJ functional connectivity to be associated with observable social BI while children interacted with a stranger. Although stronger connectivity among these regions has previously been implicated in negative social-related emotions (Burnett and Blakemore, 2009) as well as non-preferred social encounters during the preschool years (Bulgarelli et al., 2023), this was the first study to measure neural connectivity in tandem with observable BI traits during the preschool years. Some studies have indicated that functional connectivity among these regions may be related to social preferences and self-processing during early childhood (i.e., in-group versus out-group; Bulgarelli et al., 2019, 2023). Therefore, it is possible that AMPFC-TPJ functional connectivity strength may be less related to BI-driven social discomfort during the preschool years, and more closely tied with social partner trait

Table 2
Associations between observed social BI and neural connectivity while interacting with a stranger.

Source origin	Detector origin	Region	Source destination	Detector destination	Region	*Z*	*t*	*p*	*q*
5	7	Right STG	6	9	Right TPJ	0.02	4.03	<0.0001	0.0003
3	5	Left AMPFC	5	7	Right STG	0.01	2.24	0.03	0.11
1	1	Left TPJ	6	9	Right TPJ	0.01	2.38	0.02	0.08
2	2	Left TPJ	5	8	Right TPJ	0.01	2.04	0.04	0.17

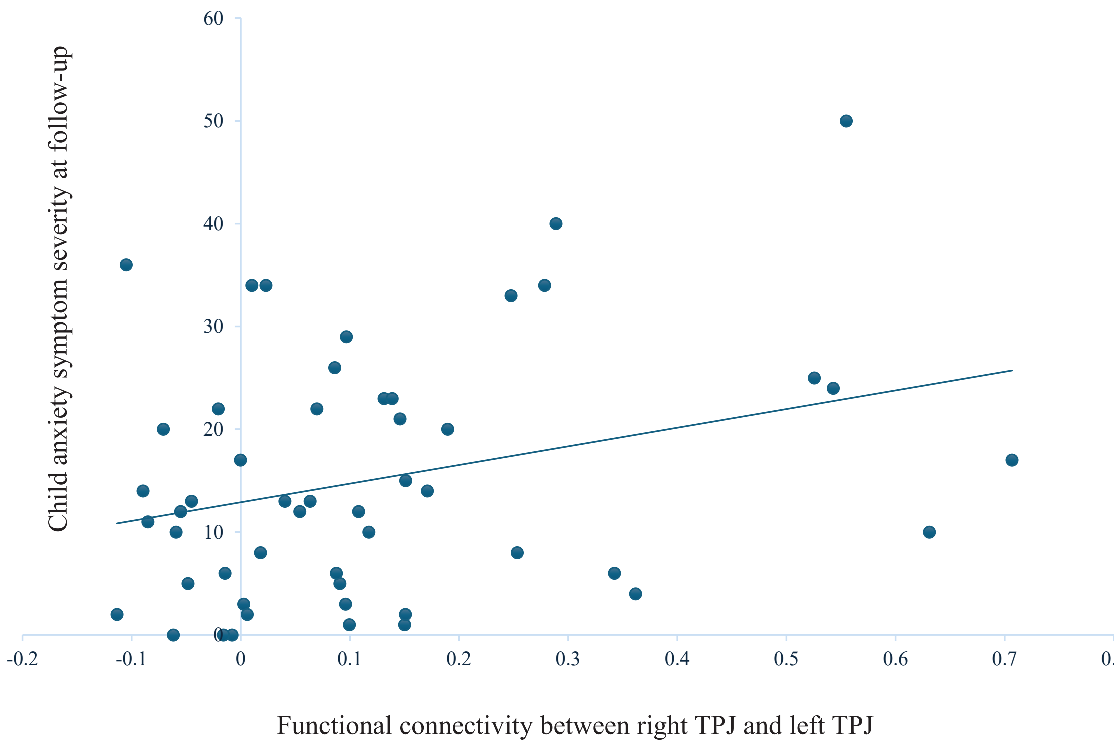

Fig. 3. Stronger functional connectivity between right and left TPJ while interacting with a stranger is associated with higher anxiety symptoms 12 months later. Note. Anxiety symptoms were assessed using the Preschool Anxiety Scale (PAS) at 12-month-follow up. Potential range of scores= 0–136.

preferences (i.e., race, gender, age, etc.). In the present study, our "stranger" was consistently an adult female, which may have impeded our preschool-aged participants' ability to categorize them as in-group regardless of BI status.

Nonetheless, we found that higher levels of observed social BI were related to stronger functional connectivity between the right STG and right TPJ while controlling for non-social BI and adjusting for multiple comparisons (i.e., *q*-corrected). The right STG is implicated in emotion perception and detection (Robins, 2009), while the right TPJ supports contingent responsiveness (Hakuno et al., 2020). Thus, BI children may need to engage in higher levels of emotion perception and social processing to engage responsively with a stranger compared to children without significant symptoms of BI in social contexts.

In addition, we found that higher levels of observed social BI were related to stronger functional connectivity between the left TPJ and the rightTPJ, as well as between the right STG and the left AMPFC. It is important to note that our findings for left TPJ-right TPJ and right STG-left AMPFC connectivity did not survive *q*-corrections for multiple comparisons and should be interpreted cautiously in the absence of replication. However, as this is the first study to use fNIRS to examine neural connectivity in preschoolers with BI, we think it worthwhile to briefly contextualize these findings. As noted above, the left AMPFC is involved in emotion expression (Japee et al., 2015). When coupled with the right STG, which is involved in emotion perception and detection (Robins et al., 2009), this finding suggests that children with higher BI require greater coupling in these emotion regulatory and perception regions to both modulate their own emotions while working to understand the feelings of others. In terms of leftTPJ-right TPJ connectivity, the left TPJ is implicated in theory of mind, which is the ability to understand the thoughts and intentions of others (Van Hoeck et al., 2014), while the right TPJ supports contingent responsiveness during social encounters (Hakuno et al., 2020). Thus, stronger functional connectivity among these regions while encountering a stranger may implicate that BI children utilize these regions more effortfully to understand the intentions of a stranger while simultaneously responding to their social cues.

Overall, findings from our first aim suggest that socially inhibited preschool children may require stronger coupling of social-related neural regions—particularly those related to perceiving the emotions of others and responding to social cues — to effectively engage with a stranger. In other words, compared to less inhibited children for whom social interactions are more intuitive or automatic, BI preschoolers may need to work harder to perceive a stranger's emotional responses, understand what they may be thinking, and respond appropriately. Further, our findings were significant after controlling for non-social BI, suggesting that these neural patterns of stronger functional connectivity are specific to higher social BI traits, rather than being indicative of fearfulness in general.

Regarding our second aim examining observable social BI and functional connectivity as a predictor of anxiety symptoms one year later, stronger coupling between the left TPJ and the right TPJ when encountering a stranger emerged as a distinguishing predictor of child anxiety symptoms one year later, even after controlling for baseline anxiety symptoms, observed social BI, and non-social BI. This finding suggests that greater neural expenditure in regions implicated in understanding the thoughts and feelings of a stranger may convey risk for the development of anxiety symptoms as early as the preschool years. Although a small number of children in our study already met criteria for an anxiety disorder, we controlled for baseline anxiety symptoms, suggesting that stronger connectivity between the left and right TPJ may predict a worsening of anxiety symptoms over time. Indeed, our findings suggest that this neural connectivity pattern may predict child anxiety problems beyond observable child BI traits, which is already understood to be one of the earliest and strongest predictors of later anxiety (Clauss and Blackford, 2012).

Notably, right STG-right TPJ connectivity was the only finding that passed corrections for multiple comparisons in our first aim but was not associated with follow-up child anxiety. Although little work to-date has explored functional connectivity among these regions regarding BI, one interpretation of this finding is that this neural pattern may be associated with *lower* risk of developing more severe anxiety symptoms over time. As demonstrated in prior literature, 50 % of preschool-age BI children do not develop clinically significant anxiety later in childhood (Degnan and Fox, 2007). Given the importance of the STG and the TPJ in emotion perception and responsive social communication, respectively (Hakuno et al., 2020; Robins et al., 2009; Sylvester et al., 2018), it is possible that BI children who utilize these regions more when encountering a stranger *improve* at responding contingently and appropriately to unfamiliar people over time by assessing their emotions and comprehending what they say rather than continuing to fear their presence solely due to the novelty of the encounter. However, future work should explore this neural pattern and its longitudinal associations in more depth given the novelty of this finding.

Surprisingly, observed social BI was not related to child anxiety at baseline or at follow-up, although non-social BI was related to baseline anxiety. This finding contrasts with prior literature which suggests that observable social BI during the preschool years is longitudinally related to higher anxiety (Dyson et al., 2011; Tan et al., 2024). We measured observed social BI using an established coding system (Dyson et al., 2011; Planalp et al., 2017) with good inter-rater reliability (ICCs =.73–.98) and internal consistency ($\alpha = 0.81$), and observed social BI was marginally correlated with BIQ scores ($r = .25$, $p = .056$). Thus, we do not believe that the lack of association between observed social BI and child anxiety in this study is an artifact of our observed social BI measure. Instead, it may be that neural markers of BI serve as a unique predictor of later anxiety, even in the absence of behaviorally observable anxiety symptoms in preschool-age children. This is consistent with prior research demonstrating stronger predictive power of neural over behavioral measures in predicting internalizing symptoms in young children. For example, a recent study by Quiñones-Camacho et al. (2022) compared neural and behavioral measures of parent-child interaction (i.e., dyadic synchrony) during the preschool years and found that while behavioral synchrony predicted initial externalizing symptoms, only neural synchrony significantly predicted changes in child internalizing symptoms over time. Although future research is necessary, it is possible that interpersonal correlates (i.e., response during social interactions) of internalizing symptoms are more difficult to detect behaviorally early in development despite being measurable at the neural level.

Our investigation had a few limitations. Although the use of fNIRS has clear advantages for evaluating preschool neural functioning (i.e., examination of brain activity during in vivo social interactions), we were unable to examine function in subcortical regions (e.g., amygdala) that may have also been altered forBI preschoolers in the context of social interactions. We only examined child anxiety symptom severity one year later, which limited our ability to examine longer-term associations between preschool neural connectivity and anxiety symptom severity in adolescence and beyond. Of note, prior work has demonstrated that anxiety disorders emerge earlier in development for children with BI traits (Hirshfeld-Becker et al., 2007). Because we measured social BI and functional connectivity during a naturalistic social interaction concurrently, we lacked the temporal requirements for a mediation model. Future work should measure how social BI traits in early childhood are related to changes in functional connectivity during social situations, and how this connectivity is related to anxiety problems later in development. Although we controlled for observed non-social BI, a measure of general fearfulness, we did not measure neural connectivity in response to novel non-social objects, as children needed to be able to move more freely during the Risk Room paradigm (e.g., physically explore novel surroundings). This examination could have provided even greater specificity of our findings.

Regardless, our longitudinal, multi-method study has multiple strengths, including (1) the use of cutting-edge technology (i.e., fNIRS) that allows for examination of child neural activity during in vivo naturalistic interactions with a stranger paired with (2) gold-standard, widely used preschool laboratory tasks that were coded by trained and reliable observers, and (3) longitudinal assessment of childhood anxiety symptoms across a one-year period in a sample enriched for BI.

Future studies should further the present findings by exploring neural correlates associated with non-social BI in response to unfamiliar non-social stimuli in preschool-age children. The literature suggests that social and non-social BI are distinct at the behavioral level during this timeframe (Dyson et al., 2011; Tan et al., 2024), and therefore it seems logical that observable non-social BI would likewise be associated with distinct neural patterns. Interestingly, we did find that non-social BI was associated with significantly weaker connectivity between social-related neural regions during the Stranger Approach paradigm (Supplemental Figure 1; see Supplemental Table 2 for full results of oxyhemoglobin models; see Supplemental Table 3 for full results of deoxyhemoglobin models). Although this finding was not related to our main study aims, it may help to clarify that social and non-social BI are distinct from one another during the preschool years, even at the neural level.

Additionally, future studies should aim to address the longitudinal progression of functional neural connectivity as it relates to observable BI traits during the preschool years. Although observable BI during childhood is associated with altered neural connectivity involving social neural regions during adolescence (Clauss et al., 2014; Hardee et al., 2013), we do not know how the strength of this connectivity changes across development. Likewise, future work should seek to investigate how BI-related neural function during the preschool years is predictive of anxiety severity during adolescence and adulthood. Nevertheless, the present study is among the first to explore functional connectivity associated with BI during the preschool years, and therefore the opportunity to explore related longitudinal associations has not previously been widely available. With the use of technology that allows for neural measurements in tandem with live social interaction (i.e., fNIRS), it may be possible to identify children most at risk of developing more severe anxiety problems from a neurobiological standpoint, even before associated symptoms become observable.

CRediT authorship contribution statement

Caitlin Aloisio: Writing – review & editing, Writing – original draft, Visualization, Methodology, Data curation, Conceptualization. **Lindsay Taraban:** Writing – review & editing, Writing – original draft, Methodology, Conceptualization. **Kathleen Mowatt:** Writing – review & editing, Methodology, Data curation. **Hendrik Santosa:** Writing – review & editing, Software, Resources, Formal analysis, Data curation. **Theodore J. Huppert:** Writing – review & editing, Software, Resources, Formal analysis, Data curation. **Jennifer S. Silk:** Writing – review & editing, Conceptualization. **Koraly Pérez-Edgar:** Writing – review & editing, Conceptualization. **Judith K. Morgan:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Methodology, Investigation, Funding acquisition, Formal analysis, Data

curation, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

This work was funded by the Brain and Behavior Research Foundation (BBRF) as a NARSAD Young Investigator Award (PI: Judith K. Morgan). We are appreciative of the mothers and children who took part in this study and give thanks to all those who aided in data collection.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.dcn.2025.101565.

References

Abend, R., Swetlitz, C., White, L.K., Shechner, T., Bar-Haim, Y., Filippi, C., Kircanski, K., Haller, S.P., Benson, B.E., Chen, G., Leibenluft, E., Fox, N.A., Pine, D.S., 2020. Levels of early-childhood behavioral inhibition predict distinct neurodevelopmental pathways to pediatric anxiety. Psychol. Med. 50 (1), 96–106. https://doi.org/10.1017/S0033291718003999.

Badre, D., Wagner, A.D., 2007. Left ventrolateral prefrontal cortex and the cognitive control of memory. Neuropsychologia 45 (13), 2883–2901. https://doi.org/10.1016/j.neuropsychologia.2007.06.015.

Beesdo, K., Knappe, S., Pine, D.S., 2009. Anxiety and anxiety disorders in children and adolescents: developmental issues and implications for DSM-V. Psychiatr. Clin. N. Am. 32 (3), 483–524. https://doi.org/10.1016/j.psc.2009.06.002.

Benjamini, Y., Hochberg, Y., 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. J. R. Stat. Soc.: Ser. B (Methodol.) 57 (1), 289–300.

Bishop, G., Spence, S.H., Mcdonald, C., 2003. Can parents and teachers provide a reliable and valid report of behavioral inhibition? Child Dev. 74 (6), 1899–1917. https://doi.org/10.1046/j.1467-8624.2003.00645.x.

Blackford, J.U., Buckholtz, J.W., Avery, S.N., Zald, D.H., 2010. A unique role for the human amygdala in novelty detection. NeuroImage 50 (3), 1188–1193. https://doi.org/10.1016/j.neuroimage.2009.12.083.

Broeren, S., Muris, P., 2008. Psychometric evaluation of two new parent-rating scales for measuring anxiety symptoms in young Dutch children. J. Anxiety Disord. 22 (6), 949–958. https://doi.org/10.1016/j.janxdis.2007.09.008.

Broeren, S., Muris, P., 2010. A psychometric evaluation of the behavioral inhibition questionnaire in a non-clinical sample of Dutch children and adolescents. Child Psychiatry Hum. Dev. 41, 214–229. https://doi.org/10.1007/s10578-009-0162-9.

Bulgarelli, C., Blasi, A., de Klerk, C.C.J.M., Richards, J.E., Hamilton, A., Southgate, V., 2019. Fronto-temporoparietal connectivity and self-awareness in 18-month-olds: a resting state fNIRS study. Dev. Cogn. Neurosci. 38, 100676. https://doi.org/10.1016/j.dcn.2019.100676.

Bulgarelli, C., Pinti, P., Aburumman, N., Jones, E.J.H., 2023. Combining wearable fNIRS and immersive virtual reality to study preschoolers' social development: a proof-of-principle study on preschoolers' social preference. Oxf. Open Neurosci. 2, kvad012. https://doi.org/10.1093/oons/kvad012.

Burnett, S., Blakemore, S.J., 2009. Functional connectivity during a social emotion task in adolescents and in adults. Eur. J. Neurosci. 29, 1294–1301. https://doi.org/10.1111/j.1460-9568.2009.06674.x.

Buss, K.A., 2011. Which fearful toddlers should we worry about? Context, fear regulation, and anxiety risk. Dev. Psychol. 47 (3), 804–819. https://doi.org/10.1037/a0023227.

Chronis-Tuscano, A., Degnan, K.A., Pine, D.S., Perez-Edgar, K., Henderson, H.A., Diaz, Y., Raggi, V.L., Fox, N.A., 2009. Stable early maternal report of behavioral inhibition predicts lifetime social anxiety disorder in adolescence. J. Am. Acad. Child Adolesc. Psychiatry 48 (9), 928–935. https://doi.org/10.1097/CHI.0b013e3181ae09df.

Clauss, J.A., Avery, S.N., VanDerKlok, R.M., Rogers, B.P., Cowan, R.L., Benningfield, M. M., Blackford, J.U., 2014. Neurocircuitry underlying risk and resilience to social anxiety disorder. Depress. Anxiety 31 (10), 822–833. https://doi.org/10.1002/da.22265.

Clauss, J.A., Blackford, J.U., 2012. Behavioral inhibition and risk for developing social anxiety disorder: a meta-analytic study. J. Am. Acad. Child Adolesc. Psychiatry 51 (10), 1066–1075.e1. https://doi.org/10.1016/j.jaac.2012.08.002.

Cope, M., Delpy, D.T., Reynolds, E.O.R., Wray, S., Wyatt, J., Van der Zee, P., 1988. Methods of quantitating cerebral near infrared spectroscopy data. Oxyg. Transp. Tissue X 183–189.

Degnan, K.A., Fox, N.A., 2007. Behavioral inhibition and anxiety disorders: multiple levels of a resilience process. Dev. Psychopathol. 19 (3), 729–746. https://doi.org/10.1017/S0954579407000363.

Delgado, M.R., Nystrom, L.E., Fissell, C., Noll, C., Fiez, J.A., 2000. Tracking the Hemodynamic Responses to Reward and Punishment in the Striatum. J. Neurophysiol. 84 (6), 3072–3077. https://doi.org/10.1152/jn.2000.84.6.3072.

Diaz, A., Bell, M.A., 2012. Frontal EEG asymmetry and fear reactivity in different contexts at 10 months. Dev. Psychobiol. 54 (5), 536–545. https://doi.org/10.1002/dev.20612.

Dyson, M.W., Klein, D.N., Olino, T.M., Dougherty, L.R., Durbin, C.E., 2011. Social and non-social behavioral inhibition in preschool-age children: differential associations with parent-reports of temperament and anxiety. Child Psychiatry Hum. Dev. 42, 390–405. https://doi.org/10.1007/s10578-011-0225-6.

Fox, N.A., 1994. Dynamic cerebral processes underlying emotion regulation. Monogr. Soc. Res. Child Dev. 59 (2–3), 240. https://doi.org/10.2307/1166143.

Fox, N.A., Buzzell, G.A., Morales, S., Valadez, E., Wilson, M., Henderson, H., 2021. Understanding the emergence of social anxiety in children with behavioral inhibition. Biol. Psychiatry 1 (7), 681–689. https://doi.org/10.1016/j.biopsych.2020.10.004.

Fox, N.A., Henderson, H.A., Marshall, P.J., Nichols, K.E., Ghera, M.M., 2005. Behavioral inhibition: linking biology and behavior within a developmental framework. Annu. Rev. Psychol. 56 (1), 235–262. https://doi.org/10.1146/annurev.psych.55.090902.141532.

Fu, X., Taber-Thomas, B.C., Pérez-Edgar, K., 2017. Frontolimbic functioning during threat-related attention: relations to early behavioral inhibition and anxiety in children. Biol. Psychol. 122, 98–109. https://doi.org/10.1016/j.biopsycho.2015.08.010.

Gaffrey, M.S., Luby, J.L., 2012, Kiddie Schedule for Affective Disorders and Schizophrenia—Early Childhood Version (K-SADS-EC). Washington University School of Medicine..

Goldsmith, H.H., Reilly, J., Lemery, K.S., Longley, S., Prescott, A., 1995. Unpublished Manuscript. Lab. Temperam. Assess. Battery.: Presch. Version.

Goldsmith, H.H., Rothbart, M.K., 1999. The laboratory temperament assessment battery. Locomot. Version 3 (1) (Unpublished Manuscript).

Hakuno, Y., Hata, M., Naoi, N., Hoshino, E., Minagawa, Y., 2020. Interactive live fNIRS reveals engagement of the temporoparietal junction in response to social contingency in infants. NeuroImage 218, 116901. https://doi.org/10.1016/j.neuroimage.2020.116901.

Hardee, J.E., Benson, B.E., Bar-Haim, Y., Mogg, K., Bradley, B.P., Chen, G., Britton, J.C., Ernst, M., Fox, N.A., Pine, D.S., Pérez-Edgar, K., 2013. Patterns of neural connectivity during an attention bias task moderate associations between early childhood temperament and internalizing symptoms in young adulthood. Biol. Psychiatry 74 (4), 273–279. https://doi.org/10.1016/j.biopsych.2013.01.036.

Hirshfeld-Becker, D.R., Biederman, J., Henin, A., Faraone, S.V., Davis, S., Harrington, K., Rosenbaum, J.F., 2007. Behavioral inhibition in preschool children at risk is a specific predictor of middle childhood social anxiety: a five-year follow-up. J. Dev. Behav. Pediatr. 28 (3), 225. https://doi.org/10.1097/01.DBP.0000268559.34463.d0.

Hudson, J.L., Dodd, H.F., Lyneham, H.J., Bovopoulous, N., 2011. Temperament and family environment in the development of anxiety disorder: two-year follow-up. J. Am. Acad. Child Adolesc. Psychiatry 50 (12), 1255–1264.e1. https://doi.org/10.1016/j.jaac.2011.09.009.

Japee, S., Holiday, K., Satyshur, M.D., Mukai, I., Ungerleider, L.G., 2015. A role of right middle frontal gyrus in reorienting of attention: a case study. Front. Syst. Neurosci. 9. https://doi.org/10.3389/fnsys.2015.00023.

Jarcho, J.M., Guyer, A.E., 2018. The neural mechanisms of behavioral inhibition. In: Pérez-Edgar, In.K., Fox, N.A. (Eds.), Behavioral Inhibition: Integrating Theory, Research, and Clinical Perspectives. Springer International Publishing, pp. 59–90. 〈https://doi.org/10.1007/978-3-319-98077-5_4〉.

Jasper, H.H., 1958. The ten-twenty electrode system of the international federation. Electroencephalogr. Clin. Neurophysiol. 10, 371–375.

Kagan, J., Reznick, J.S., Gibbons, J., 1989. Inhibited and uninhibited types of children. Child Dev. 60 (4), 838–845. https://doi.org/10.2307/1131025.

Kagan, J., Reznick, J.S., Clarke, C., Snidman, N., Garcia-Coll, C., 1984. Behavioral Inhibition to the Unfamiliar. Child Dev. 55 (6), 2212–2225. https://doi.org/10.2307/1129793.

Kerr-German, A., White, S.F., Santosa, H., Buss, A.T., Doucet, G.E., 2022. Assessing the relationship between maternal risk for attention deficit hyperactivity disorder and functional connectivity in their biological toddlers. Eur. Psychiatry 65 (1), e66. https://doi.org/10.1192/j.eurpsy.2022.2325.

Kiel, E.J., Buss, K.A., 2011. Prospective relations among fearful temperament, protective parenting, and social withdrawal: the role of maternal accuracy in a moderated mediation framework. J. Abnorm. Child Psychol. 39 (7), 953–966. https://doi.org/10.1007/s10802-011-9516-4.

Kim, J., Klein, D.N., Olino, T.M., Dyson, M.W., Dougherty, L.R., Durbin, C.E., 2011. Psychometric properties of the behavioral inhibition questionnaire in preschool children. J. Personal. Assess. 93 (6), 545–555. https://doi.org/10.1080/00223891.2011.608756.

Kochanska, G., 1991. Patterns of inhibition to the unfamiliar in children of normal and affectively ill mothers. Child Dev. 62 (2), 250–263. https://doi.org/10.2307/1131001.

Kochanska, G., Knaack, A., 2003. Effortful control as a personality characteristic of young children: antecedents, correlates, and consequences. J. Personal. 71 (6), 1087–1112. https://doi.org/10.1111/1467-6494.7106008.

Li, S., Xie, H., Zheng, Z., Chen, W., Xu, F., Hu, X., Zhang, D., 2022. The causal role of the bilateral ventrolateral prefrontal cortices on emotion regulation of social feedback. Hum. Brain Mapp. 43 (9), 2898–2910. https://doi.org/10.1002/hbm.25824.

Liu, R., Calkins, S.D., Bell, M.A., 2021. Frontal EEG asymmetry moderates the associations between negative temperament and behavioral problems during childhood. Dev. Psychopathol. 22, 1016–1025. https://doi.org/10.1017/S0954579420000309.

Lloyd-Fox, S., Blasi, A., Elwell, C.E., 2010. Illuminating the developing brain: the past, present and future of functional near infrared spectroscopy. Neurosci. Biobehav. Rev. 34 (3), 269–284. https://doi.org/10.1016/j.neubiorev.2009.07.008.

Monk, C.S., Telzer, E.H., Mogg, K., Bradley, B.P., Mai, X., Louro, H.M.C., Chen, G., McClure-Tone, E.B., Ernst, M., Pine, D.S., 2008. Amygdala and ventrolateral prefrontal cortex activation to masked angry faces in children and adolescents with generalized anxiety disorder. Arch. Gen. Psychiatry 65 (5), 568–576. https://doi.org/10.1001/archpsyc.65.5.568.

Morgan, J.K., Santosa, H., Conner, K.K., Fridley, R.M., Forbes, E.E., Iyengar, S., Joseph, H.M., Huppert, T.J., 2023. Mother–child neural synchronization is time linked to mother–child positive affective state matching. Soc. Cogn. Affect. Neurosci. 18 (1), nsad001. https://doi.org/10.1093/scan/nsad001.

Okamoto, M., Dan, H., Sakamoto, K., Takeo, K., Shimizu, K., Kohno, S., Oda, I., Isobe, S., Suzuki, T., Kohyama, K., Dan, I., 2004. Three-dimensional probabilistic anatomical cranio-cerebral correlation via the international 10–20 system oriented for transcranial functional brain mapping. NeuroImage 21 (1), 99–111. https://doi.org/10.1016/j.neuroimage.2003.08.026.

Paulus, F.W., Backes, A., Sander, C.S., Weber, M., von Gontard, A., 2015. Anxiety disorders and behavioral inhibition in preschool children: a population-based study. Child Psychiatry Hum. Dev. 46 (1), 150–157. https://doi.org/10.1007/s10578-014-0460-8.

Pfeifer, M., Goldsmith, H.H., Davidson, R.J., Rickman, M., 2002. Continuity and change in inhibited and uninhibited children. Child Dev. 73 (5), 1474–1485. https://doi.org/10.1111/1467-8624.00484.

Planalp, E.M., Van Hulle, C., Gagne, J.R., Goldsmith, H.H., 2017. The infant version of the Laboratory Temperament Assessment Battery (Lab-TAB): measurement properties and implications for concepts of temperament. Front. Psychol. 8, 846. https://doi.org/10.3389/fpsyg.2017.00846.

Quiñones-Camacho, L.E., Hoyniak, C.P., Wakschlag, L.S., Perlman, S.B., 2022. Getting in synch: Unpacking the role of parent-child synchrony in the development of internalizing and externalizing behaviors. Dev. Psychopathol. 24, 1901–1913. https://doi.org/10.1017/S0954579421000468.

Reznick, J.S., Kagan, J., Snidman, N., Gersten, M., Baak, K., Rosenberg, A., 1986. Inhibited and uninhibited children: a follow-up study. Child Dev. 57 (3), 660–680. https://doi.org/10.2307/1130344.

Ridderinkhof, K.R., Ullsperger, M., Crone, E.A., Sander, N., 2004. The role of the medial frontal cortex in cognitive control. Science 306 (5695), 443–447. ⟨https://www.jstor.org/stable/3839313⟩.

Robins, D.L., Hunyadi, E., Schultz, R.T., 2009. Superior temporal activation in response to dynamic audio-visual emotional cues. Brain Cogn. 69 (2), 269–278. https://doi.org/10.1016/j.bandc.2008.08.007.

Rubin, K.H., Hastings, P.D., Stewart, S.L., Henderson, H.A., Chen, X., 1997. The consistency and concomitants of inhibition: some of the children, all of the time. Child Dev. 68 (3), 467–483. https://doi.org/10.2307/1131672.

Santosa, H., Aarabi, A., Perlman, S.B., Huppert, T.J., 2017. Characterization and correction of the false-discovery rates in resting state connectivity using functional near-infrared spectroscopy. J. Biomed. Opt. 22, 055002. https://doi.org/10.1117/1.JBO.22.5.055002.

Santosa, H., Zhai, X., Fishburn, F., Huppert, T., 2018. The NIRS brain AnalyzIR toolbox. Algorithms 11 (5). https://doi.org/10.3390/a11050073. Article 5.

Spence, S.H., Rapee, R., McDonald, C., Ingram, M., 2001. The structure of anxiety symptoms among preschoolers. Behav. Res. Ther. 39 (11), 1293–1316. https://doi.org/10.1016/S0005-7967(00)00098-X.

Spence, S.H., Rapee, R., 1999. Preschool Anxiety Scale (Parent Report). University of Queensland, Brisbane, Australia.

Sylvester, C.M., Smyser, C.D., Smyser, T., Kenley, J., Ackerman, J.J., Shimony, J.S., Petersen, S.E., Rogers, C.E., 2018. Cortical functional connectivity evident after birth and behavioral inhibition at age 2. Am. J. Psychiatry 175 (2), 180–187. https://doi.org/10.1176/appi.ajp.2017.17010018.

Tan, E., Zeytinoglu, S., Morales, S., Buzzell, G.A., Almas, A.N., Degnan, K.A., Chronis-Tuscano, A., Henderson, H., Pine, D.S., Fox, N.A., 2024. Social versus non-social behavioral inhibition: Differential prediction from early childhood of long-term psychosocial outcomes. Dev. Sci. 27 (1), e13427. https://doi.org/10.1111/desc.13427.

Tzourio-Mazoyer, N., Landeau, B., Papathanassiou, D., Crivello, F., Étard, Delcroix, O., N., Mazoyer, B., Joliot, M., 2002. Automated anatomical labeling of activations in SPM using a macroscopic anatomical parcellation of the MNI MRI single-subject brain. NeuroImage 15, 273–289. https://doi.org/10.1006/nimg.2001.0978.

Van Hoeck, N., Begtas, E., Steen, J., Kestemont, J., Vandekerckhove, M., Van Overwalle, F., 2014. False belief and counterfactual reasoning in a social environment. NeuroImage 90, 315–325. https://doi.org/10.1016/j.neuroimage.2013.12.043.

Wang, J., Dong, Q., Niu, H., 2017. The minimum resting-state fNIRS imaging duration for accurate and stable mapping of Brain Connectivity Network in children. Sci. Rep. 7 (1). https://doi.org/10.1038/s41598-017-06340-7.

Whalen, D.J., Gilbert, K.E., Kelly, D., Hajcak, G., Kappenman, E.S., Luby, J.L., Barch, D. M., 2020. Preschool-onset major depressive disorder is characterized by electrocortical deficits in processing pleasant emotional pictures. Res. Child Adolesc. Psychopathol. 48, 91–108. https://doi.org/10.1007/s10802-019-00585-8.

Wilcox, T., Biondi, M., 2015. fNIRS in the developmental sciences. WIREs Cogn. Sci. 6 (3), 263–283. https://doi.org/10.1002/wcs.1343.

Zhai, X., Santosa, H., Huppert, T.J., 2020. Using anatomically defined regions-of-interest to adjust for head-size and probe alignment in functional near-infrared spectroscopy. Neurophotonics 7 (3), 035008. https://doi.org/10.1117/1.NPh.7.3.035008.

Zhou, S., Creswell, C., Spence, S.H., Reardon, T., 2024. Measurement invariance of the higher-order model of the Preschool Anxiety Scale (PAS) across child age, gender, parental anxiety, and pandemic period in England. Psychol. Assess. 36 (9), 526–537. https://doi.org/10.1037/pas0001325.