Temporal Predictability Modulates Cortical Activity and Functional Connectivity in the Frontoparietal Network in 6-Month-Old Infants

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Abstract

■ Despite the abundance of behavioral evidence showing the interaction between attention and prediction in infants, the neural underpinnings of this interaction are not yet well-understood. The endogenous attentional function in adults have been largely localized to the frontoparietal network. However, resting-state and neuroanatomical investigations have found that this frontoparietal network exhibits a protracted developmental trajectory and involves weak and unmyelinated long-range connections early in infancy. Can this developmentally nascent network still be modulated by predictions? Here, we conducted the first investigation of infant frontoparietal network engagement as a function of the predictability of visual events. Using functional near-infrared spectroscopy, the hemodynamic response in the frontal, parietal, and occipital lobes was analyzed as infants watched videos of temporally predictable or unpredictable sequences. We replicated previous findings of cortical signal attenuation in the frontal and sensory cortices in response to predictable sequences and extended these findings to the parietal lobe. We also estimated background functional connectivity (i.e., by regressing out task-evoked responses) to reveal that frontoparietal functional connectivity was significantly greater during predictable sequences compared to unpredictable sequences, suggesting that this frontoparietal network may underlie how the infant brain communicates predictions. Taken together, our results illustrate that temporal predictability modulates the activation and connectivity of the frontoparietal network early in infancy, supporting the notion that this network may be functionally available early in life despite its protracted developmental trajectory. ■

INTRODUCTION

Prediction is an important cognitive mechanism that facilitates early learning. Many behavioral studies have demonstrated that young infants can engage in predictions (Emberson, Richards, & Aslin, 2015; Stahl & Feigenson, 2015; Van Giffen & Haith, 1984) and that these predictions affect attention in infancy (Tummeltshammer, Mareschal, & Kirkham, 2014; Kidd, Piantadosi, & Aslin, 2012; Kirkham, Slemmer, Richardson, & Johnson, 2007; Amso & Johnson, 2006; Doherty, Rao, Mesulam, & Nobre, 2005; Wentworth, Haith, & Hood, 2002; Baillargeon, 1987). A likely neural substrate of prediction is the frontoparietal network, which is a large-scale network that is composed of the dorsolateral pFC and posterior parietal cortex (Yeo et al., 2011). In adults, the frontoparietal network has been repeatedly implicated during predictive processing (Koban, Jepma, López-Solà, & Wager, 2019; Leong, Radulescu, Daniel, DeWoskin, & Niv, 2017; Corbetta, Kincade, Ollinger, McAvoy, & Shulman, 2000; Kastner, Pinsk, De Weerd, Desimone, & Ungerleider, 1999); for example, anticipatory shifts of attention to visual targets were found to be mediated by the frontoparietal network. Prior evidence thus suggests that predictive processes modulate attentional processes in both adults and infants, and that they engage the frontoparietal network in adults.

However, the neural basis of prediction in infancy remains unclear, as the frontoparietal network has been found to be immature in young infants. Several studies have reported limited and delayed development of white matter that supports long-range connections in the frontoparietal network (Lebel & Deoni, 2018; Kulikova et al., 2015; O'Muircheartaigh et al., 2014; Deoni et al., 2011). Some studies have also reported underdeveloped resting-state connectivity in infants' frontoparietal network and other long-range networks (Bulgarelli et al., 2020; Damaraju et al., 2014; Fransson, Åden, Blennow, & Lagercrantz, 2011). Yet, it is still possible that this immature frontoparietal network could be functionally available and modulated by predictability in young infants. Converging evidence from several studies has highlighted the importance of the frontal lobe during predictive processing in infancy (Emberson, Boldin, Robertson, Cannon, & Aslin, 2019; Jaffe-Dax et al., 2019; Boldin, Geiger, & Emberson, 2018; Kersey & Emberson, 2017). However, no prior study has investigated the engagement of the parietal lobe in these predictive tasks or functional connectivity across the frontoparietal network during prediction in infancy. Here, we investigated

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frontoparietal network engagement during predictive processing in infancy using functional near-infrared spectroscopy (fNIRS).

In addition, we also examined the occipital lobe during predictive processing. Our exploration of the frontal, parietal, and occipital lobes can clarify whether the predictability of a sequence can result in top–down attenuation of sensory cortices. Previous work in adults found that both predictably repetitive and predictably deviant stimuli attenuate neural responses in the sensory cortices (Summerfield & De Lange, 2014; Sussman & Steinschneider, 2011), suggesting that the attenuation of occipital lobe activity is induced by predictability rather than simple repetition. Research with infants also finds this kind of modulation in the sensory cortex (Jaffe-Dax, Herbolzheimer, Bejjanki, & Emberson, 2021). Whereas the current study will be able to further confirm these past findings regarding the occipital lobe, our focus is on the frontoparietal network as the potential network that supports such suppression in sensory cortices.

fNIRS is a particularly suitable neuroimaging method for this investigation because of its utility for infant research (Azhari et al., 2020), especially given its robust resistance to motion artifacts (Nishiyori, 2016; Wilcox & Biondi, 2015; Brigadoi et al., 2014). fNIRS can easily record lobe-level data that can be standardized through spatial registration methods (Tsuzuki & Dan, 2014) and localized anatomically (Ferradal, Eggebrecht, Hassanpour, Snyder, & Culver, 2014) with good reliability (Zhang et al., 2011; Plichta et al., 2006). Indeed, it has already been used successfully to localize specific anatomical regions (e.g., Emberson, Crosswhite, Richards, & Aslin, 2017). We used lobular measurements from the frontal and parietal lobes as a proxy for the frontoparietal network. This approach is similar to that of a number of prior studies that also used interlobular connectivity to examine large-scale networks (Bulgarelli et al., 2019; Rosenbaum et al., 2017; Liang, Chen, Shewokis, & Getchell, 2016; Durantin, Dehais, & Delorme, 2015; Sasai et al., 2012). Furthermore, we had three specific reasons for following this approach: First, given that it is an open question as to which regions are involved in prediction in infants, we decided that a broader definition to start with (frontal-parietal connectivity) was more prudent, rather than selecting specific sublobular networks. Second, we were limited by the practical constraints imposed by the spatial resolution of fNIRS, which in principle is sufficient to measure from subregions, but in practice, it is very challenging to localize small contiguous regions. Third, we would have to rely on a small number of channels per region rather than being able to average across multiple channels. Such use of singular channels rather than averages could result in decreased signal-to-noise ratio. Given these reasons, we opted to use lobular connectivity for the FPN. However, it will be important for future research to build upon our exploratory work and further refine this exploration by focusing on smaller sublobular networks.

Using fNIRS, we compared the cortical activity in, and functional connectivity between, the frontal, parietal, and occipital lobes as infants watched a predictable sequence (PS) or unpredictable sequence (UPS) of items (experimental design developed by Jaffe-Dax et al., 2021). Previous research has shown that predictability attenuates neural responses in adults (e.g., Sussman & Steinschneider, 2011; Summerfield, Trittschuh, Monti, Mesulam, & Egner, 2008) and in the frontal lobes of infants (Kouider et al., 2015; Basirat, Dehaene, & Dehaene-Lambertz, 2014). These findings are consistent with the predictive coding framework (Friston, 2005; Rao & Ballard, 1999), which posits that PSs would be associated with reduced prediction error and thus attenuated neural responses. Building on this prior work, we hypothesized an attenuation of cortical activation in the frontal, parietal, and occipital lobes in response to the PS compared to the UPS. Evidence in support of this hypothesis would confirm the predictability-driven attenuation of activity in the infant frontal cortex using fNIRS and extend the findings to the infant parietal lobe, an area that has been heavily implicated in predictive processes in adults.

We were also interested in examining the interactions among the frontal, parietal and occipital lobes that might underlie the predictability-driven attenuation of activity in the infant brain. Previous research in adults has found greater frontoparietal connectivity during prediction periods compared to neutral periods (Bollinger, Rubens, Zanto, & Gazzaley, 2010). Thus, we hypothesized greater frontoparietal functional connectivity in response to the PS compared to the UPS. Such a finding would provide crucial evidence that the frontoparietal network is engaged during predictive processes in infancy and suggests that feedback between the frontal and parietal lobes underlies the attenuation effect of predictability.

METHODS

Experimental Design

Data from 34 infants between the ages of 5 and 7 months (mean = 5.71, *SD* = 0.52 months old; 19 male; 15 female) were used in our analyses. Considering a paired *t* test (e.g., comparison of univariate activity between conditions), 34 is a sample size sufficient to detect an effect size of 0.5 (medium effect) with power of 80% at $p = .05$ (Dhand & Khatkar, 2014). Our sample size is also double the median sample size among infant fNIRS studies (Cristia et al., 2013). In total, we recruited 44 infants for this study; however, three infants were excluded because they did not want to wear the fNIRS cap; two were excluded because their head was too small for a good fit of the fNIRS cap; three were excluded because they were fussy and did not want to start the task; and two were excluded because of technical error and file corruption. Therefore, data from 34 out of 44 infants were analyzed, resulting in the total attrition rate of 22.72%, compared to the average of 54%

among infant studies with more than 20 optodes (Cristia et al., 2013). This experiment was approved by Princeton University's Institutional Review Board. Each infant's caregiver was given a description of the study, and they provided informed consent before starting the experiment. Infants and their caregivers received $10, a t-shirt, and a children's book as a compensation for their participation.

The visual stimuli developed in prior research (Jaffe-Dax et al., 2021) were used for this study. In each trial, four smiling shapes (green square, yellow crescent, pink star, or blue cloud) sequentially crossed the screen upward, downward, leftward, or rightward, whereas a sound of old windows startup, rattle, train, or chimes played for 10 sec (Movie 1). For each subject, each shape was always paired with one movement and one sound throughout the task, and participants were pseudorandomly assigned to particular shape–movement–sound pairings. In other words, the same shape was always associated with the same direction and sound for one infant, and this association was changed between infants. A video of dimmed fireworks accompanied by a nursery song was shown for 10–15 sec between each trial as an attention-grabbing period (Emberson et al., 2015). Within-subject design was used, such that each infant experienced both PS and UPS conditions. Each condition was composed of eight consecutive trials in a block design. In PS, the order of the shapes within each trial was consistently AAAB so that the order was predictable in each trial (Figure 1A). AAAB was chosen as the format for our PS for all trials because prior research has demonstrated that infants as young as 3 months old are able to represent regularities of this particular sequence, as well as detect violations (Basirat et al., 2014). In UPS, the order of the shapes within each trial was pseudorandomly chosen between AABA, ABAA, and BAAA so that the order was unpredictable in each trial (Figure 1B). The order of conditions was counterbalanced between infants. Infants sat on their caregiver's laps while they watched the stimuli on a screen that was placed about 60 cm away. Shapes moved across the screen for about 20 degrees of visual angle, and sounds were played through centrally positioned speakers at a comfortable volume.

The fNIRS cap was placed on each infant's head. There were 24 source optodes and 24 detector optodes placed in the frontal, parietal, and occipital regions of the cap. The same cap, optode arrangement, and placement procedure was used for all infants. However, despite these consistent procedures, the location of the optodes varied depending on the placement of the cap and the size of the infant's head and corresponding snugness of the fit of the cap (as is common in infant fNIRS research but rarely quantified). As such, we captured the natural variation in the optode placements across infants using optode localization and co-registration with an atlas. We recorded infants' cortical activity from 80 fNIRS channels at ~13.33 Hz (intersample interval of 75 msec) at three wavelengths (790, 805, and 830 nm) using custom-made infant fibers connected to Shimadzu LABNIRS.

Channel separation on the scalp was 25 mm. For each subject, the position of the fNIRS cap on the infant's head was estimated using a novel motion-resistant, video-based localization technique (Jaffe-Dax, Bermano, Erel, & Emberson, 2020). For this technique, we used a GoPro to capture a video of all views of each infant's head with

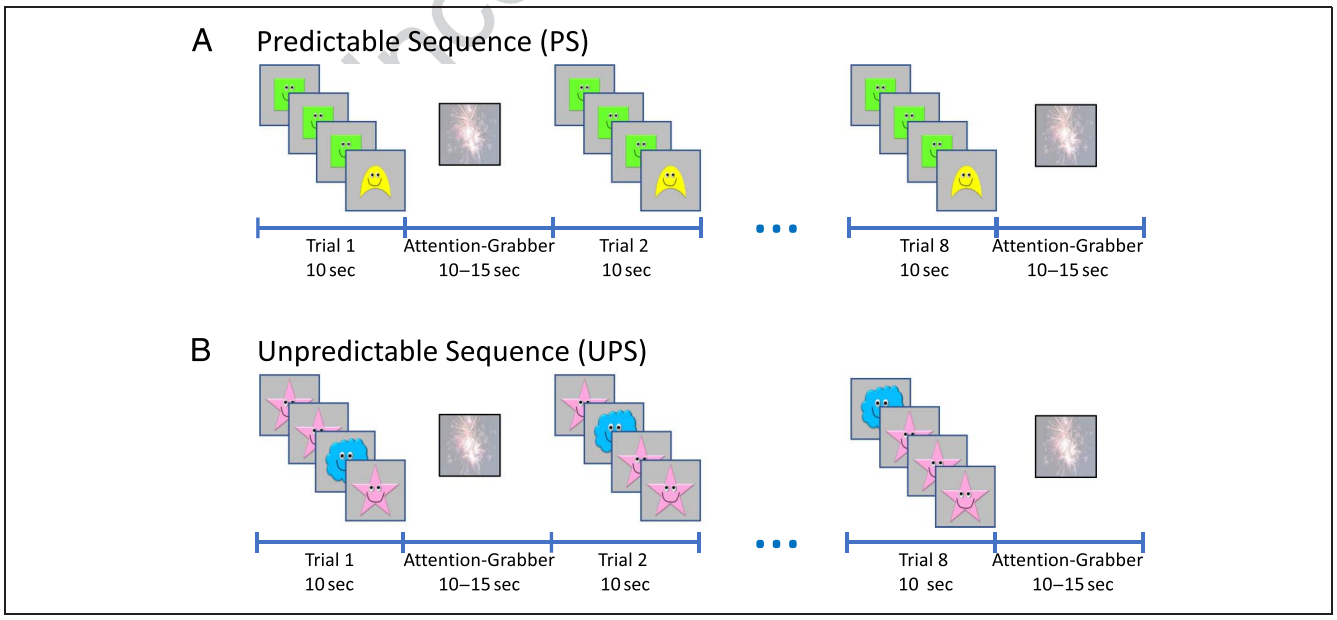

Figure 1. Experimental design of the PS and UPS conditions. PS was composed of eight consecutive trials, which displayed the same order of shapes (AAAB). UPS was composed of eight consecutive trials, which displayed varying orders of shapes (AABA, ABAA, or BAAA). Ten- to 15-sec clips of fireworks were shown between each trial.

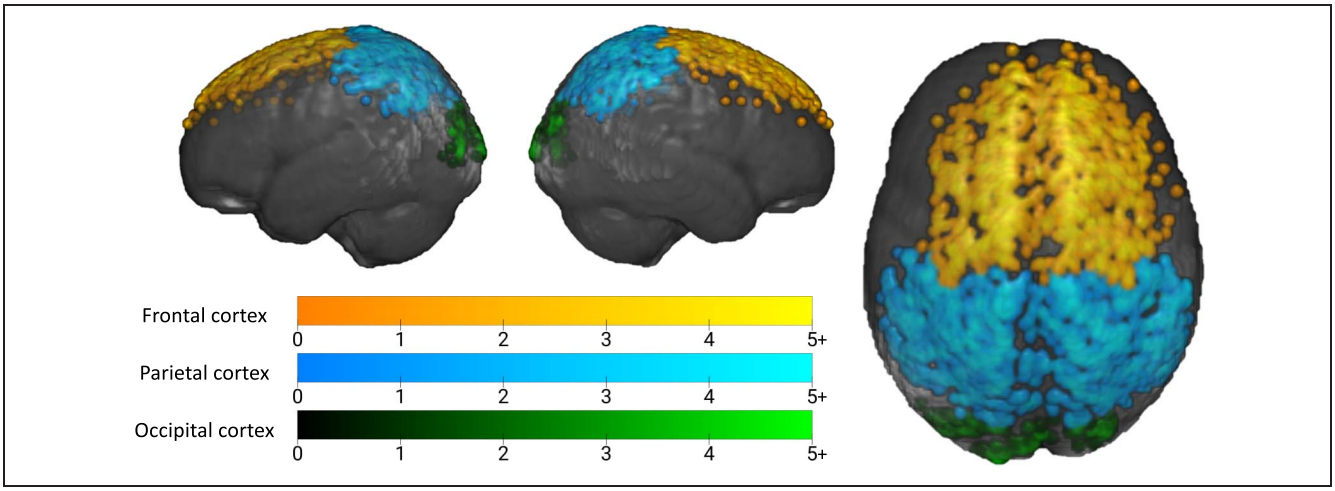

Figure 2. Localization of channels across participants. The channels were localized to the frontal cortex (dark yellow to light yellow) parietal cortex (dark blue to light blue), and occipital cortex (dark green to light green). The gradation of colors represents the number of participants with a channel in a given area. As is standard for fNIRS measurements, the range of head sizes and variation in cap placement (e.g., because of differences in head size and shape) both contribute to the scatter in channel placement. Here, we show the distribution of the channels that were used to aggregate lobe-level data for our analyses. For visualization purposes, all channels with data from five or more participants are represented in the brightest color to show the general range of the recording sites and as a marker that there are differences in the density of sampling between each subject. The maximum overlap for any single channel position is $n = 12$.

the fNIRS cap placed upon it. We then reconstructed a 3-D model of each infant's head with the fNIRS cap from this video using structure from motion (SfM), a popular computer vision technique for 3-D reconstruction. We extracted the coordinates of relevant fiducials (e.g., Nz, Cz, Iz, AL, AR, and cap edges) from this 3-D model, and the positions of all channels were interpolated and projected to Montreal Neurological Institute space (Tak, Uga, Flandin, Dan, & Penny, 2016). Based on the coordinates of each channel, we assigned each channel to lobes based on the coordinates listed in the Talairach Daemon database (Lancaster et al., 2000). Channels in the frontal, parietal, and occipital lobes were used in our analyses. Homologous lobes were aggregated together, and signals were averaged across all channels within each lobe for each subject. In each subject, we recorded between 28–37 channels in the frontal lobe (mean = 33, *SD* = 3 channels), 25–36 channels in the parietal lobe (mean = 34, *SD* = 2 channels), and 8–16 channels in the occipital lobe (mean = 11, *SD* = 3 channels), depending on the subject-specific placement of the fNIRS cap. The distribution of the channels across participants is shown below (Figure 2).

Statistical Analysis

The Homer2 toolbox for MATLAB (Huppert, Diamond, Franceschini, & Boas, 2009) was used to preprocess the raw data using the parameters recommended by Brigadoi et al. (2014). First, raw intensity data were converted to optical density using and filtered using the HOMER2 toolbox. Motion artifacts were detected using the following parameters: tMotion = 0.5, tMask = 1, STDEVthresh = 25, and AMPthresh = 1. Epochs containing detected artifacts were removed from the data and spline interpolated using $p = .99$. Data were then bandpass filtered between 0.01 and 0.5 Hz. Then, this filtered optical density was transformed to oxygenated hemoglobin (HbO_2) concentrations using a modified Beer-Lambert equation with partial path factor of 6 for all wavelengths. Any channel containing concentration changes beyond ±5e-5 μM were considered spurious and were omitted from further analysis.

We chose to use the finite impulse responses (FIR) as a basis function to approximate the hemodynamic response, particularly given that we do not have definitive knowledge about the shape of the hemodynamic response in infant participants. We defined our impulse response window as 20 sec to account for 10 sec of stimulus and 10 sec of intertrial baseline period. At one FIR regressor per second, we used 20 FIR regressors to model the neural response, and the weighted sum of those impulses were used to estimate the shape of the hemodynamic response. We used this estimate of hemodynamic response as the measure of task-evoked cortical activity in our following analyses. This technique is widely used in the field to model task-evoked hemodynamic response (see the works of Huppert et al. [2009] and Santosa, Zhai, Fishburn, & Huppert [2018] for more details on using an FIR model to analyze fNIRS data).

We removed the first trial of both conditions before performing our statistical analyses to offset the effect of initial acclimation period, as it was possible that the novelty of the task itself and its sounds, shapes, and sounds may

affect the infants' frontoparietal network engagement. Acclimating to simple novel tasks have been found to evoke frontoparietal engagement in adults (Cole, Braver, & Meiran, 2017). To calculate the differences between conditions in the task-based activations in the frontoparietal network, we aggregated the frontal, parietal, and occipital lobes' cortical activity measured during PS and UPS across all participants. Lobe-level analysis was appropriate for our level of specificity, given that our hypotheses were about the lobe-level frontoparietal engagement during our task. The mean level of cortical activity was calculated from the 5-sec time window from 0 to 5 sec before the trial onset to obtain the baseline for each lobe. Then, to obtain the activation for each lobe, the mean level of cortical activity was calculated from a window of 5 sec between 10 and 15 sec after trial onset. This 5-sec time window was selected a priori based on a previous finding of predictability-dependent differential activity in the frontal and sensory cortices within this time range (Jaffe-Dax et al., 2021). We performed within participants two-tailed t tests on baseline levels between PS versus UPS across all participants to test that there were no spurious differences between the conditions in any of the lobes. Then, we performed one-tailed t tests on activation levels to test the hypothesis that the activity in response to PS is more attenuated compared to the activity in response to UPS. All p values were corrected for multiple comparisons using the Benjamini-Hochberg procedure (Benjamini & Hochberg, 1995).

To assess task-based functional connectivity between the fontal, parietal, and occipital lobes, we used the "background connectivity" approach (Al-Aidroos, Said, & Turk-Browne, 2012; Norman-Haignere, McCarthy, Chun, & Turk-Browne, 2012). In the presence of external stimulation, hemodynamic responses in different neural areas are correlated not only because of the connectivity between them but also because of the synchronized task-evoked responses. If the task-evoked responses are not appropriately controlled for, the functional connectivity analysis can yield overinflated correlation estimates (Cole et al., 2019). The background connectivity approach to inferring functional connectivity models and linearly regresses stimulus-evoked responses out of the data, before measuring correlations in the residual spontaneous fluctuations. Specifically, we modeled task-evoked activations by fitting a generalized linear model using the FIR approach described above. The residuals from this model were used to measure background activity. After confirming that the residuals were normally distributed and therefore were suitable for Pearson correlation, we calculated the Pearson correlations over the residuals to infer the functional connectivity between the frontal, parietal, and occipital lobes. Similar techniques have been used for fMRI data (Al-Aidroos et al., 2012; Norman-Haignere et al., 2012), although, unlike with fMRI data, we did not regress out nuisance and global variables because of the lack of coverage of nonresponsive regions like brain stems and ventricles in an fNIRS recording. The correlation coefficients (Pearson's r) of each subject were Fisher transformed to z values to aggregate across all participants. We tested whether the background connectivity in the frontoparietal network was different in response to PS versus UPS using a two-tailed t test. We also calculated the same measure between the frontal and occipital lobes and between the parietal and occipital lobes for comparison. Then, the z values were Fisher transformed back to Pearson's r values.

RESULTS

Predictability Attenuates Cortical Activity

To test our first hypothesis that the frontal, parietal, and occipital lobe activities would be significantly lower during PS compared to UPS, cortical activity (measured by aggregated HbO_2 levels) in each lobe was averaged across all participants for each condition, and compared between the conditions (Figure 3).

In support of our hypothesis, the cortical response to PS was significantly attenuated compared to the cortical response to UPS in the frontal lobe, $t(32) = 3.3846$, adjusted $p = .006$; parietal lobe, $t(32) = 2.5057$, adjusted $p = .018$; and occipital lobe, $t(31) = 3.2597$, adjusted $p = .005$, in the activation period, defined as the 5-sec time window 10 sec after stimulus onset determined based on a previous study (Jaffe-Dax et al., 2021). These results showed that the differences found 10 sec after the trial onset were not because of spurious differences in cortical activity unrelated to the task.

The significantly lower cortical activity in the frontal and occipital cortices in response to PS compared to UPS closely replicates the previous findings of attenuated cortical activity in frontal cortex as a result of sequence learning (Jaffe-Dax et al., 2021). Furthermore, the significantly attenuated parietal lobe activity in PS compared to UPS importantly extends that finding to the parietal lobe. Thus, our univariate outcomes both replicate and extend existing research about the involvement of the frontoparietal and sensory cortices in predictive processes.

Predictability Selectively Modulates Frontoparietal Connectivity

To test our second hypothesis that frontoparietal functional connectivity would be significantly greater in response to PS compared to UPS, background functional connectivity between the frontal and parietal lobes was estimated across all participants, for each condition (Figure 4). Functional connectivity was also estimated between frontal and occipital lobes and between parietal and occipital lobes for comparison.

In support of our hypothesis, frontoparietal background connectivity was significantly different between the two

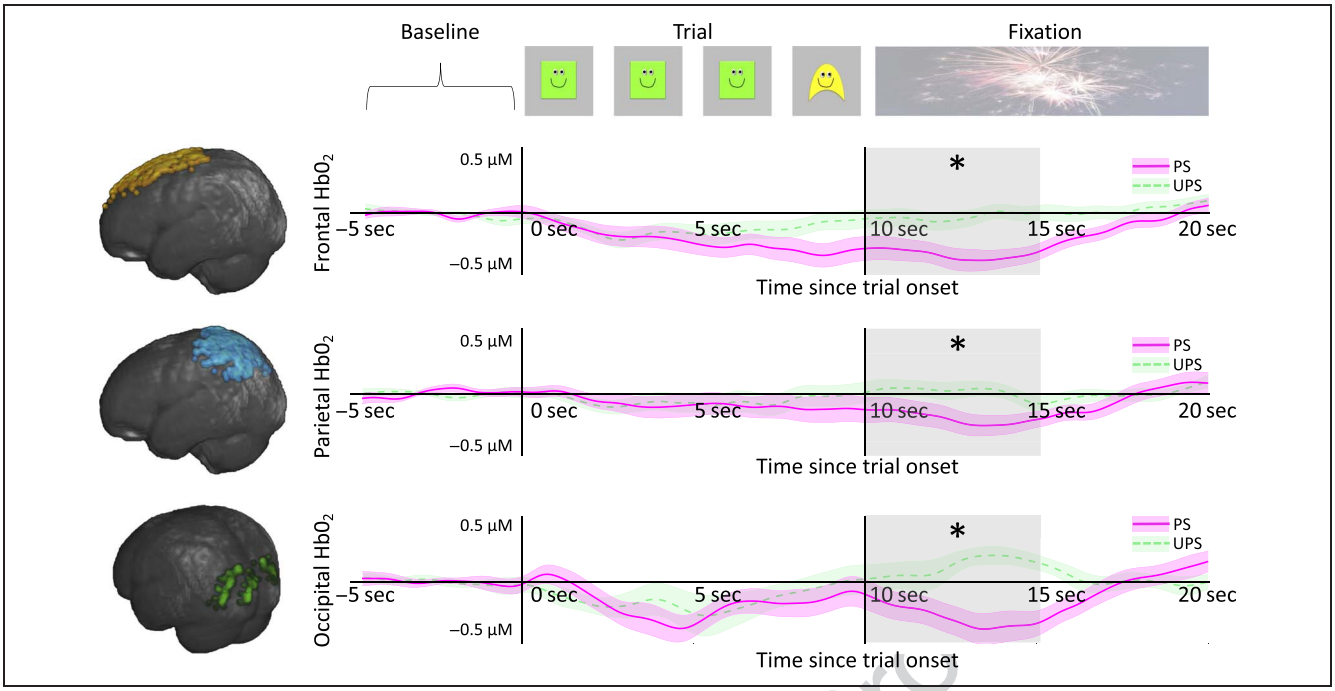

Figure 3. Concentration changes of HbO_2 as a function of time in seconds from stimulus onset. Cortical activity in the frontal (top), parietal (middle), and occipital lobes (bottom). In each graph, the mean (solid/dashed line) and standard error (shaded region) of activity in response to the PS condition is depicted in pink, whereas the mean and standard error of activity in response to the UPS condition is depicted in green. The gray box represents the time window of 10–15 sec after stimulus onset, which was a priori determined to be used for statistical testing based on previous finding of significant predictability-dependent differences in the frontal and sensory regions (Jaffe-Dax et al., 2021). The star located at the top of the gray box denotes that the cortical response to PS was significantly attenuated ($p < .05$) compared to the response to UPS in this time window.

conditions ($r_{PS} = 0.46$; $r_{UPS} = 0.35$; $p = .035$). In contrast, the fronto-occipital ($r_{PS} = 0.36$; $r_{UPS} = 0.27$; *ns*) and parieto-occipital background connectivity ($r_{PS} = 0.35$; $r_{UPS} = 0.35$; *ns*) was not significantly different between conditions. The significantly greater background connectivity between the frontal and parietal cortices in PS compared to UPS suggests that the frontoparietal network is modulated by the predictability of stimuli.

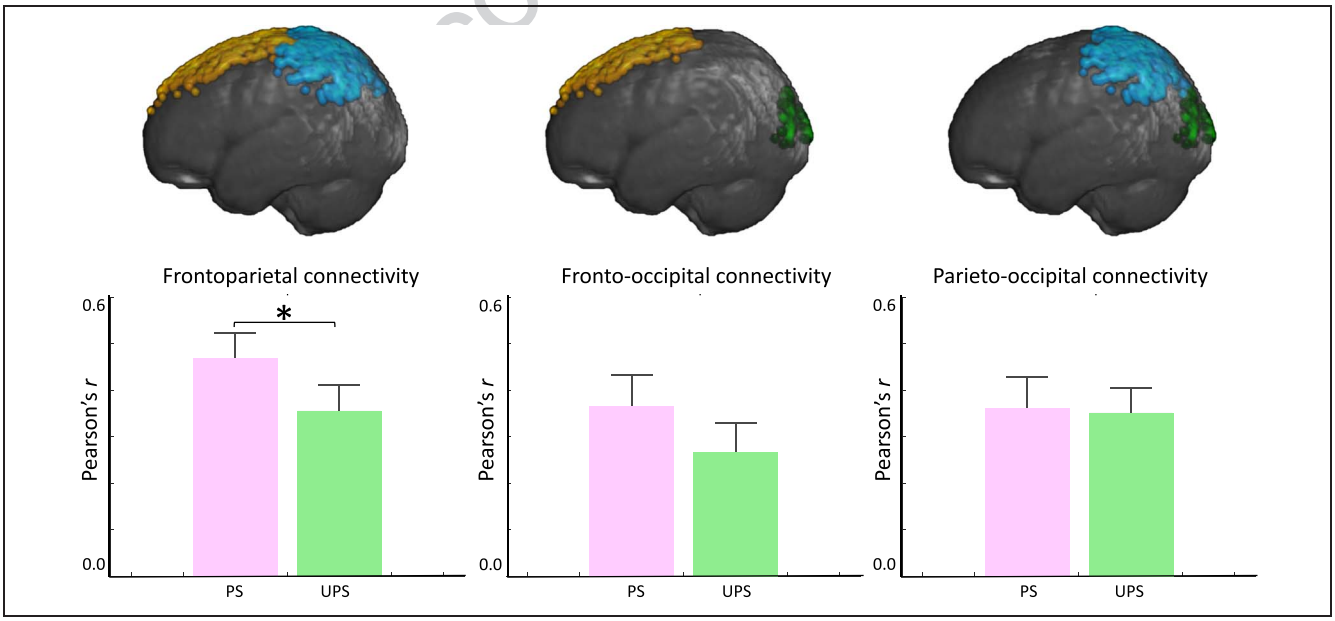

Figure 4. Background connectivity. Correlation between two lobes' cortical activity was used to estimate the interlobular connectivity. Frontoparietal connectivity (left), fronto-occipital connectivity (center), and parieto-occipital connectivity (right) during PS (pink bar) and UPS (green bar) are shown. There was a significant difference in frontoparietal connectivity between PS and UPS ($p < .05$), but no significant difference in fronto-occipital or parieto-occipital connectivity between the two conditions.

DISCUSSION

Although there is a wealth of behavioral evidence for the interaction between attention and prediction in infants, and abundant neural evidence for the interaction in adults, no study to date has examined prediction in the infant frontoparietal network. Using fNIRS, we recorded from the frontoparietal network and from a sensory cortex (i.e., the occipital lobe) while infants engaged with temporally predictable and UPSs. As hypothesized, we found markedly attenuated frontal, parietal, and occipital lobe activity in response to PSs compared to UPSs. We note that it is possible that there were temporal inconsistencies across the unpredictable trials (e.g., AABA, ABAA, and BAAA had different lengths of time until the time of unpredictability), and thus these individual stimuli may have elicited different hemodynamic responses. However, our research design is not optimized to further explore this possibility for two reasons. First, fNIRS is limited in its temporal resolution by the speed of the BOLD signal, making fNIRS less than ideal for examining such fine-grained temporal differences. Second, we lack statistical power for carrying out this within-condition analysis as we only presented up to two trials with each form of the unpredictable trial to our infant participants. Such temporal differences in unpredictability could, however, be an exciting avenue for future work using EEG, which offers a better temporal resolution.

The attenuated frontal, parietal, and occipital lobe activity in response to PSs replicated previous findings of attenuated frontal and occipital lobe responses to predictable temporal sequences (Jaffe-Dax et al., 2021), and extended the findings to the parietal lobe. Indeed, despite the theorized importance of the frontal and parietal lobes for mediating predictive processes in infants, no prior study had directly examined the engagement of the parietal lobe. Our findings help to establish that the parietal lobe is functionally available to support an infant's sensitivity to environmental predictability, which infants possess from a very young age (Stahl & Feigenson, 2015; Van Giffen & Haith, 1984). These findings of suppressed activity in response to PSs are consistent with the predictive coding framework (Friston, 2005; Rao & Ballard, 1999), which suggests that this suppression effect is because of reduced prediction error.

Also as hypothesized, we found different levels of functional connectivity in the frontoparietal network depending on the predictability of the visuo-temporal input. Specifically, we found that increased predictability of events was associated with greater functional connectivity between the frontal and parietal lobes, suggesting that the frontoparietal network is more strongly engaged when there were patterns in the environmental input, compared to when there were no discernible patterns. In contrast, no such differences were observed in the connectivity between either the frontal or the parietal lobe, and the occipital lobe. Thus, our results suggest that the frontoparietal network in infants is modulated by predictability. The increased functional connectivity potentially reflects the feedback processes as suggested by the predictive coding framework (Rao & Ballard, 1999).

Overall, these findings provide compelling evidence that infants as young as 6 months old can engage a rudimentary version of the frontoparietal network despite the relative anatomical immaturity of this network. On the surface, the functional engagement of this network may appear to be in contrast with the previously reported lack of myelination, and the protracted developmental trajectory of resting-state functional connectivity, in this network (Bulgarelli et al., 2020; Deoni et al., 2011). However, the relationship between anatomical measures of connectivity (white matter and resting-state functional connectivity) and task-based functional engagement is unknown, particularly in the developmental context. Moreover, it has been theorized that brain regions and networks become more selective and specialized with cognitive experiences (i.e., functional engagement) across development (Johnson, 2011). Thus, it is possible that the functional engagement of this network serves as a catalyst for the anatomical development of the sophisticated attention network seen in adults.

There are several avenues for future research. First, the PS utilized in our study was AAAB for all participants; although not using an exhaustive counterbalancing procedure is in line with previous research on learning with temporal sequences (Basirat et al., 2014; Saffran, Aslin, & Newport, 1996), future replication of our results using counterbalanced PSs may further support our findings. Secondto examine changes in infant neural responses as learning progresses. In studies using more simple learning paradigms, changes in fNIRS responses has been reported (e.g., Lloyd-Fox et al., 2019; Kersey & Emberson, 2017). Although these temporal changes were not our focus, an exploratory analysis did not reveal any statistically significant differences in univariate responses. However, we emphasize that our analysis here was exploratory in nature; one possibility for this null result is that our experiment did not have enough trials to meaningfully conduct such an analysis, given the constraints of working with infants who are prone to losing interest and becoming fidgety, and the use of two types of trials for a condition-based comparison. Another reason may be that such tasks involve substantial variability in the trajectory of learning across infants. Finally, other experimental designs can be used to accommodate other analytical methods, such as the use of psychophysiological interaction to estimate task-based connectivity. Convergence of results based on diverse analytical methods would further strengthen our results.

Our findings meaningfully advance our knowledge in several directions. First, this study provides neural evidence that complements existing behavioral evidence for the interaction between attention and prediction in infants. In particular, we point to a particular neural substrate by which this interaction can occur: the frontoparietal network, the same general network as would be implicated in adults. Second, our results indicate that, despite the evidence from anatomical scans and resting-state functional

connectivity that there may be limited connectivity in the infant brain, and in higher-level cognitive networks in particular, 6-month-old infants functionally engage their frontoparietal network during predictive tasks. As the first study to examine task-based functional connectivity of the frontoparietal network in infancy, our findings suggest that long-range functional connectivity during cognition may be more functionally capable than previously estimated via resting-state research. This finding has important theoretical implications regarding the interaction of functional and anatomical development in the brain that will need to be tested in future work. Finally, our study shows the engagement of both higher-order associative and lower-level perceptual regions in a predictive context. This pattern of results reveals that the infant brain is capable of sophisticated, large-scale neural coordination despite having relatively immature long-range connectivity. Overall, this study provides neural evidence that significantly advances our knowledge about prediction in infancy.

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Author Contributions

Vikranth R. Bejjanki: Conceptualization; Formal analysis.

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Diversity in Citation Practices

Retrospective analysis of the citations in every article published in this journal from 2010 to 2021 reveals a persistent pattern of gender imbalance: Although the proportions of authorship teams (categorized by estimated gender identification of first author/last author) publishing in the *Journal of Cognitive Neuroscience* (*JoCN*) during this period were M(an)/M = .407, W(oman)/M = .32, M/W = .115, and W/W = .159, the comparable proportions for the articles that these authorship teams cited were M/M = .549, W/M = .257, M/W = .109, and W/W = .085 (Postle and Fulvio, *JoCN*, 34:1, pp. 1–3). Consequently, *JoCN* encourages all authors to consider gender balance explicitly when selecting which articles to cite and gives them the opportunity to report their article's gender citation balance.

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