

# A Computational Role for Top-Down Modulation from Frontal Cortex in Infancy

Sagi Jaffe-Dax, Alex M. Boldin, Nathaniel D. Daw, and Lauren L. Emberson

## Abstract

Recent findings have shown that full-term infants engage in top-down sensory prediction, and these predictions are impaired as a result of premature birth. Here, we use an associative learning model to uncover the neuroanatomical origins and computational nature of this top-down signal. Infants were exposed to a probabilistic audiovisual association. We find that both groups (full term, preterm) have a comparable stimulus-related response in sensory and frontal lobes and track prediction error in their frontal lobes.

However, preterm infants differ from their full-term peers in weaker tracking of prediction error in sensory regions. We infer that top-down signals from the frontal lobe to the sensory regions carry information about prediction error. Using computational learning models and comparing neuroimaging results from full-term and preterm infants, we have uncovered the computational content of top-down signals in young infants when they are engaged in a probabilistic associative learning.

## INTRODUCTION

Decades of work have argued that infants are able to use their bottom-up sensory experience to drive learning and increase perceptual specificity (e.g., Saffran & Kirkham, 2018; Maurer & Werker, 2014). Extending this view, recent theoretical pieces have proposed that infants may start to engage in top-down processing using long-range cortical connections late in the first year of life (Markant & Scott, 2018; Emberson, 2017; Amso & Scerif, 2015; Hadley, Pickron, & Scott, 2015). In this study, we investigate top-down modulation of perceptual cortices based on learning and specifically modulation of the occipital lobe by the frontal lobe. To this end, we investigate the trial-by-trial modulation of neural signals, as measured using functional near-infrared spectroscopy (fNIRS; Aslin, Shukla, & Emberson, 2015; Blasi, Lloyd-Fox, Johnson, & Elwell, 2014) during a task designed to reveal differences in top-down modulation between premature and full-term infants (Emberson, Boldin, Riccio, Guillet, & Aslin, 2017).

Previous neuroimaging work has uncovered evidence of top-down neural signals in infancy (Emberson, Richards, & Aslin, 2015; Kouider et al., 2015). Infants at 6 months of age were presented with a consistent association of audiovisual events while their cortical responses were recorded from occipital, temporal, and frontal lobes. As expected, following an event, a sustained cortical response was recorded from sensory cortices. After a short exposure, the visual component was unexpectedly omitted in 20% of trials. A sustained response was still recorded from

the occipital lobe, even in these auditory-only trials. These findings led the researchers to conclude that the occipital lobe received an input from a different source—a higher order, associative neural region, which reflected an expectation violation, or prediction error. Using a computational modeling approach, we investigate whether the activity in the infant frontal lobe reflects prediction error, and thus, this region is a possible source of these top-down signals.

Using a design identical to that used in Emberson et al. (2015), top-down signals were found to be weaker in preterm infants (Emberson et al., 2017), likely related to the weaker long-range connectivity found in this population (Smyser et al., 2010), which is not recovered even later in the course of development (Thompson et al., 2016). Preterm infants are at risk for developing a wide range of cognitive and developmental difficulties (van Noort-van der Spek, Franken, & Weisglas-Kuperus, 2012). Thus, these top-down signals might be a key feature of development, which serves an important role in the developmental trajectory from an early stage in infancy. However, the content and function of these top-down connections are still unclear. Comparing across these populations and employing a computational learning model, we now ask, what is the computational role of these top-down signals and what content do they convey? The use of computational modeling allowed us to move beyond condition comparison and to compare cortical responses, on a trial-by-trial basis, to well-defined computational roles. The learning model allowed us to interpret the cognitive role of frontal activity, which was not reported earlier (Emberson et al., 2015, 2017).

Infants' frontal lobe has been classically thought to have protracted development (Paredes et al., 2016), and yet the field of developmental neuroimaging has revealed the involvement of the frontal lobe starting early in life (Grossmann, Lloyd-Fox, & Johnson, 2013; Gervain, Berent, & Werker, 2012; Gervain, Macagno, Cogoi, Peña, & Mehler, 2008). Neuroimaging studies have shown that, already at 4 months of age, infants' frontal lobe is involved in processing novelty of unfamiliar (Nakano, Watanabe, Homae, & Taga, 2009) and out-of-order (Basirat, Dehaene, & Dehaene-Lambertz, 2014) stimuli. At 8 months, infants' frontal lobe is involved in processing congruency between audio and visual domains (Grossmann, Striano, & Friederic, 2006) and processing complex hierarchical rules (Werchan, Collins, Frank, & Amso, 2016). In adults, activity in the dorsolateral pFC was found correlated with prediction error in a paradigm similar to the one we employed (den Ouden, Friston, Daw, McIntosh, & Stephan, 2009). Other candidate regions for processing prediction error include the BG (O'Doherty et al., 2004), but these brain regions are not accessible to our neuroimaging methods with infants.

Our probabilistic audiovisual association paradigm taps cross-modal prediction. As such, we should track the processing of prediction error in associative cortex beyond sensory-specific regions. Because predictions of upcoming visual stimulus in this paradigm were based on preceding auditory cue and tracking complex statistical information across trials often involves frontal lobe activity (Dürschmid et al., 2016; Basirat et al., 2014), we infer that finding a correlate of prediction error in visual cortices could imply top-down propagation of prediction error back from higher order, associative to sensory regions (Emberson et al., 2015).

Following this logic, we employed an established learning model, which calculates trial-by-trial prediction error, to uncover which cortical regions processed prediction error in our associative learning paradigm (Rescorla & Wagner, 1972). Computational associative learning models have been extensively used to characterize the functional role of neural responses in various learning tasks in adults (Li, Schiller, Schoenbaum, Phelps, & Daw, 2011; Seymour et al., 2004) and in non-human animals (Schultz, Dayan, & Montague, 1997). We now employ a computational learning model to tap the possible computational cognitive roles of neural activities that were recorded during an associative learning paradigm in early infancy.

We hypothesized that (1) in full-term infants, sensory information and prediction error would be reflected in all measured cortical regions—frontal and posterior revealing both the processing of the frontal lobe to prediction error and the propagation of this information to posterior cortices through feedback or top-down connections—and that (2) in preterm infants, their frontal associative activity would reflect processing of prediction error indicating an intact audiovisual associative learning ability in

this task; but that (3) in those preterm infants, prediction error would not propagate backward to posterior sensory regions. Such a pattern of results would imply that, indeed, premature birth is related selectively to weaker top-down projection of prediction error.

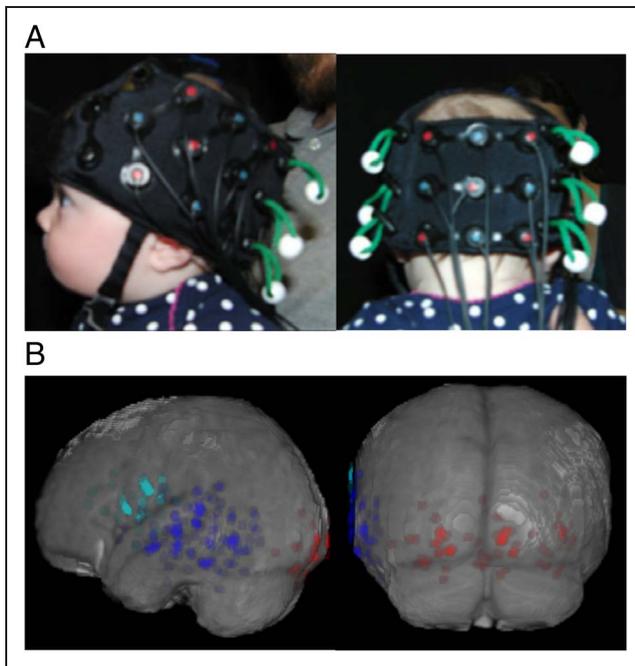
In summary, this study investigates whether the infant brain is more interactive and interconnected than previously theorized. Specifically, we combine computational modeling with infant neuroimaging across two populations of infants—typical developing and preterm infants—to examine whether even tracking simple cross-modal association, at 6 months, can involve prediction-related activity in both sensory and the frontal lobe.

## METHODS

We analyzed fNIRS data from 36 infants, born at full term (full-terms), and 43 infants, born extremely or very prematurely (<33 weeks of gestation; preterms), who were presented with a sequence of audiovisual trials (80% of the trials) interleaved with audio-only trials (visual omission trials that violate the audiovisual association; 20% of the trials). Infants were tested at 6 months of corrected age and had no identified risk factors for disrupted cognitive development other than premature birth. The majority of our preterm infant sample were born in a tight range between 28 and 32 weeks; thus, following our previous analysis that found no effect of gestational age within this group, we did not add gestational age at birth as a covariate in our analysis. For detailed information of the demographics and lack of gestational age effect, see Emberson et al. (2017).

Before the first introduction of audio-only trials, there was a familiarization phase of 18 audiovisual trials. After this familiarization phase, the order of the trials was randomly assigned such that, in every 10 trials, there were two audio-only trials. For a detailed description of the experimental procedures and preprocessing of fNIRS results, see Emberson et al. (2015). We measured oxy-Hb concentration changes in occipital, left temporal, and left frontal lobes (three, five, and two channels per lobe, respectively; Hitachi ETG-4000; Figure 1). For each trial, we extracted the mean baseline-corrected amplitude of oxy-Hb change during 5–9 sec after visual stimulus onset (or omitted onset), where the hemodynamic response peaks in infants (Nakano et al., 2009).

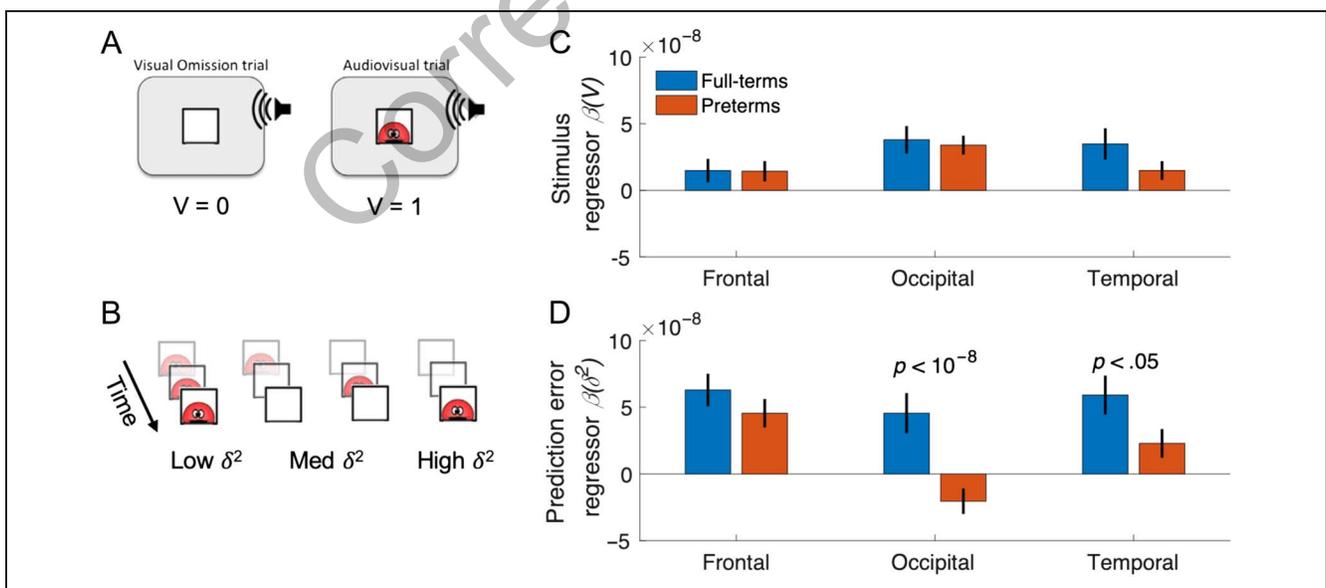
We analyzed trial-by-trial results of individual infants, using a linear mixed-effects approach (MATLAB, The MathWorks, Inc.). For each infant, for each trial, we determined the nature of visual presentation ( $V$ ; stimulus-evoked, present/omitted [ $V = 1/0$ ]; Figure 2A) and, using the learning model, determined the prediction error magnitude ( $\delta^2$ ; Figure 2B). The model was generated based on all the trials that were administered to each infant. We then regressed oxy-Hb responses for each lobe against these regressors ( $V$  and  $\delta^2$ ) to find the



**Figure 1.** (A) Each infant who participated in the study was photographed to help determine the relation between the NIRS optodes and anatomical markers. (B) Three ROIs. Each semitransparent spot represents a single-channel location for an individual infant. Opacity represents channel density across individual infants. The frontal ROI (cyan) comprised two channels. The temporal ROI (blue) comprised five channels. The occipital ROI (red) comprised three channels. For details on the NIRS–MR coregistration supporting the creation of these ROIs, see Emberson et al. (2015). Reproduced with permission from Kersey and Emberson (2017).

contribution of these two factors in driving the neural response.

Associative learning was formulated into a computational model by Rescorla and Wagner (RW model; Rescorla & Wagner, 1972). In the RW model, association ( $P$ ) is learned by comparing the predicted association at each time step ( $t$ ) with the current observation ( $V$ ; the stimulus-related response; Figure 2A). The result of this comparison is prediction error:  $\delta(t) = V(t) - P(t)$ . This prediction error is then used to update the association through a learning rate ( $\alpha$ ):  $P(t + 1) = P(t) + \alpha(t)\delta(t)$ . The stimulus-related response ( $V$ ) and the magnitude of prediction error ( $\delta^2$ ) were used to regress the cortical response. The latter regressor arises in a family of elaborations of this model, which have been used in a number of different applications in behavioral neuroscience. These posit a role for the unsigned error magnitude (often measured by  $\delta^2$ ) in tracking the volatility of the environment in a hierarchical model and using it, top-down, to modulate the rate of learning predictions (Piray & Daw, 2019; Li et al., 2011; Behrens, Woolrich, Walton, & Rushworth, 2007; Pearce & Hall, 1980). We used the model parameters that were reported previously for a hybrid of RW and Pearce-Hall (Pearce & Hall, 1980) models (Li et al., 2011) to generate the trial-by-trial prediction error and its magnitude for each infant according to the specific sequence of trials administered. We also used a lower learning rate, as assessed in a previous infant pupillometry work (Zhang, Jaffe-Dax, Wilson, & Emberson, 2018) and found similar pattern of results (Supplementary Figure S1 and Supplementary Table S1<sup>1</sup>). In addition, we used individually



**Figure 2.** Regressor coefficients by lobe. (A) Trial types and respective stimulus regressor value. Visual omissions are assigned with stimulus regressor value  $V = 0$ , and audiovisual trials are assigned with stimulus regressor value  $V = 1$ . (B) Examples of trial sequences and the respective prediction error value of the last trial. Prediction error regressor value is assigned to each trial according to the trials that preceded it. Trials that match previous trials have low prediction error regressor values. Trials that do not match their preceding trials have high prediction error regressor values. (C) Response for the presentation of a visual stimulus (stimulus-evoked;  $V$ ). In both populations, all three lobes responded to the appearance of a visual stimulus on the screen. (D) Response to prediction error ( $\delta^2$ ). In full-term infants, all three lobes responded to prediction error. In preterm infants, the response to prediction error was limited to the frontal and temporal lobes. See Table 1 for statistics.

fitted learning rate ( $\alpha$ ) and found similar results to using a predetermined learning rate (Supplementary Figure S2 and Supplementary Table S2). We also tested the effects in a model that explicitly includes a second learning layer (using  $\delta^2$  to guide a dynamic learning rate; known as the hybrid RW/Pearce–Hall model; Pearce & Hall, 1980; Li et al., 2011) and find qualitatively the same results to using the simpler RW model alone (Supplementary Figure S3 and Supplementary Table S3).

## RESULTS

The contribution of prediction error magnitude ( $\delta^2$ ) to the response of the occipital lobe was significantly smaller among preterm compared with full-term infants (Group  $\times$   $\delta^2$  interaction;  $F(1, 1081) = 29.6, p < 10^{-8}$ ; Figure 2D; see Table 1 for all statistics). Importantly, bottom–up pro-

cessing was found to be intact in preterm infants: All lobes responded to the appearance of visual stimuli similarly in both groups (no significant Group  $\times$  V effects: all  $ps > .1$ ; Figure 2C), and their frontal lobe tracked prediction error similarly to full-term infants (no significant Group  $\times$   $\delta^2$  effect:  $p > .7$ ). However, specifically in the occipital lobe, we found that the Group  $\times$   $\delta^2$  effect was larger than the Group  $\times$  V effect,  $F(1, 1134) = 10.5, p < .005$ .

In line with previous findings (Taga & Asakawa, 2007), we also found evidence of cross-modal processing in the temporal lobe: An auditory stimulus is presented with each trial, and the temporal lobe responded to the addition of a visual stimulus (all  $ps < .05$ ; no Group  $\times$  V effect). We also found a Group  $\times$   $\delta^2$  effect,  $F(1, 1087.3) = 3.9, p < .05$ , in the temporal lobe suggesting these top–down signals are not specific to the modality of violation or the occipital lobe. However, we interpret this finding

**Table 1.** Mixed-effects Statistics of RW Model for Response from Each Lobe with Fixed Learning Rate of  $\alpha = .5$

Lobe	Effect	F	DF2	p
Frontal	Group $\times$ V	0.7	1076.5	.4
	Group $\times$ $\delta^2$	0.1	1088.5	.7
	(Group $\times$ V) vs. (Group $\times$ $\delta^2$ )	0.5	1134	.5
	Full-terms' V	2.9	74.1	.1
	Preterms' V	3.5	101.8	.1
	<b>Full-terms' <math>\delta^2</math></b>	<b>26.6</b>	<b>98.6</b>	<b>&lt;10<sup>-6</sup></b>
	<b>Preterms' <math>\delta^2</math></b>	<b>18.3</b>	<b>111.2</b>	<b>&lt;10<sup>-5</sup></b>
Occipital	Group $\times$ V	1.7	1073	.2
	<b>Group <math>\times</math> <math>\delta^2</math></b>	<b>29.6</b>	<b>1081</b>	<b>&lt;10<sup>-8</sup></b>
	<b>(Group <math>\times</math> V) vs. (Group <math>\times</math> <math>\delta^2</math>)</b>	<b>10.5</b>	<b>1134</b>	<b>&lt;0.005</b>
	<b>Full-terms' V</b>	<b>13.6</b>	<b>47.9</b>	<b>&lt;.001</b>
	<b>Preterms' V</b>	<b>22.9</b>	<b>67.9</b>	<b>&lt;10<sup>-6</sup></b>
	<b>Full-terms' <math>\delta^2</math></b>	<b>9.1</b>	<b>47.9</b>	<b>&lt;.001</b>
	<b>Preterms' <math>\delta^2</math></b>	<b>4.7<sup>a</sup></b>	<b>81.8</b>	<b>&lt;.05</b>
Temporal	Group $\times$ V	2.7	1079.4	.1
	<b>Group <math>\times</math> <math>\delta^2</math></b>	<b>3.9</b>	<b>1087.3</b>	<b>&lt;.05</b>
	(Group $\times$ V) vs. (Group $\times$ $\delta^2$ )	0.3	1134	.6
	<b>Full-terms' V</b>	<b>8.8</b>	<b>35.8</b>	<b>&lt;.01</b>
	<b>Preterms' V</b>	<b>4.5</b>	<b>109.1</b>	<b>&lt;.05</b>
	<b>Full-terms' <math>\delta^2</math></b>	<b>16.5</b>	<b>45.9</b>	<b>&lt;.001</b>
	<b>Preterms' <math>\delta^2</math></b>	<b>4.6</b>	<b>84.5</b>	<b>&lt;.05</b>

In each lobe, we used the mixed-effect formula: Response  $\sim V + \delta^2 + \text{Group} : V + \text{Group} : \delta^2 + (V + \delta^2 \mid \text{subject})$ . DF = degrees of freedom. Significant effects are highlighted in **bold**.

<sup>a</sup>Negative response.

with caution for two reasons: (1) The Group  $\times$   $\delta^2$  effect was not larger than the Group  $\times$   $V$  effect (as was the case for the occipital lobe finding), and (2) the Group  $\times$   $\delta^2$  effect was not replicated in the alternative model analyses that are described in the supplementary materials, suggesting it is not a robust effect or as robust as these effects in the occipital lobe. Future research is needed to determine whether this result arose from the superior time domain processing in the temporal lobe (Jaffe-Dax, Kimel, & Ahissar, 2018), or earlier developing white matter connections to the frontal lobe (Leroy et al., 2011), or involvement of higher level visual areas in the temporal lobe.

## DISCUSSION

We infer that top-down signals from the frontal lobe propagate prediction error content in young infants: (1) premature infants have impaired top-down communication to the occipital lobe during this audiovisual associative learning paradigm (Emberson et al., 2017), (2) the stimulus-related response was similar across populations, and prediction error ( $\delta^2$ ) was comparably tracked in the frontal lobe in both populations, but (3) weaker prediction error tracking was observed in preterm infants' occipital lobe. The work presented here assigns a well-defined computational role for the functional connections between frontal and sensory cortices: to supply sensory-specific cortices with essential information regarding the surprising nature of the perceived events. However, it is also plausible that both the frontal and occipital lobes share a common source that propagates prediction error. Such a common source can be the BG (O'Doherty et al., 2004) or other brain region that was beyond the scope of the imaging methods that we employed.

An alternative account for our finding would be that the response on the occipital lobe undergoes local habituation to visual stimuli and that the omission of visual stimuli elicits a recovery from habituation response in full-term but not preterm infants. A previous study reports a behavioral control experiment in this population to assess looking time preference to the visual stimuli after exposure and found no evidence for such habituation. By contrast, this study reports that, in both groups of infants, after a familiarization period, the presentation of visual stimuli attracts more attention than the omission of these stimuli (Emberson et al., 2017).

We present two notable findings that extend our current understanding of the frontal lobe in infancy: First, we find that by 6 months after birth, the frontal lobe processed prediction error in a relatively simple task (tracking visual predictability in an audiovisual association). Our use of computational modeling has revealed a specific computational role for the frontal lobe: tracking prediction error.

We find evidence of this functionality of the frontal lobe in both preterm and full-term infants. Second, we propose the interpretation that the frontal lobe uses feedback or top-down connections to modulate sensory cortices according to prediction error. Thus, we propose by 6 months after birth that the frontal lobe has a role in shaping the response of the sensory cortices to events according to their predictability.

Furthermore, this work exemplifies the distinction between activity in the frontal lobe and top-down activity. In our preterm population, the first (frontal lobe activity) was found intact compared with full-term infants, but the latter was found to be substantially weaker. The processing of prediction error in this task depends on cross-modal integration of information from auditory cues and the tracking of complex statistical information trial-by-trial. None of these functions are believed to be supported by the occipital lobe alone. However, these functions are in line with frontal lobe (see above). Thus, we infer weaker prediction error-related activity in the occipital lobe was interpreted as weaker top-down activity, despite comparable prediction error-related activity in the frontal lobe.

This current study extends the framework of "predictive coding" (Friston, 2005; Rao & Ballard, 1999), beyond the scope of the consolidated developed brain back to development. A recent ERP study found that at 12–24 months of age, contextual predictability affected the responses to words (Ylinen, Bosseler, Junttila, & Huotilainen, 2017). We now show that, as early as 6 months after birth, the frontal lobe processed prediction error and, in full-term infants, affected the processing of perceived stimuli in the respective sensory lobe in the same manner that was hypothesized by the predictive coding theory—stronger response for less predicted stimuli. Preterm infants did not exhibit top-down modulation of sensory cortices according to prediction error. Namely, these infants differed from the general hypothesized framework of predictive coding—a well-defined theory that has clear predictions for neuroimaging results.

We could not, in the scope of this study, assess whether prediction and prediction error in early infancy depends on the specific content of the stimuli that are presented. For example, we did not alternate the pairing between auditory and visual stimuli between trials. Furthermore, we did not assess whether prediction and prediction error could be processed from visual cue toward auditory stimulus or toward other modalities. Follow-up studies should assess the nature of these predictions and prediction errors that are available in early infancy. Future studies should also examine whether results from preterm infants exhibit a more general divergence from the predictions of predictive coding by examining other neuroimaging paradigms. More broadly, this divergence could be diagnostic of preterm infants' risk status and predictive of their later cognitive abilities.

## Acknowledgments

This work was funded by Eunice Kennedy Shriver National Institute of Child Health and Human Development Grant/award number 4R00HD076166, the McDonnell Foundation (220020505), and the Bill & Melinda Gates Foundation Modeling Neurodevelopment Initiative.

Reprint requests should be sent to Sagi Jaffe-Dax, Psychology Department, Peretsman Scully Hall, Princeton, NJ 08540, or via e-mail: jaffedax@princeton.edu.

## Note

1. Supplementary materials for this paper are available on: [github.com/sagijaffedax/pretermRL](https://github.com/sagijaffedax/pretermRL).

## REFERENCES

- Amso, D., & Scerif, G. (2015). The attentive brain: Insights from developmental cognitive neuroscience. *Nature Reviews Neuroscience, 16*, 606–619.
- Aslin, R. N., Shukla, M., & Emberson, L. L. (2015). Hemodynamic correlates of cognition in human infants. *Annual Review of Psychology, 66*, 349–379.
- Basirat, A., Dehaene, S., & Dehaene-Lambertz, G. (2014). A hierarchy of cortical responses to sequence violations in three-month-old infants. *Cognition, 132*, 137–150.
- Behrens, T. E., Woolrich, M. W., Walton, M. E., & Rushworth, M. F. (2007). Learning the value of information in an uncertain world. *Nature Neuroscience, 10*, 1214–1221.
- Blasi, A., Lloyd-Fox, S., Johnson, M. H., & Elwell, C. (2014). Test–retest reliability of functional near infrared spectroscopy in infants. *Neurophotonics, 1*, 025005.
- den Ouden, H. E., Friston, K. J., Daw, N. D., McIntosh, A. R., & Stephan, K. E. (2009). A dual role for prediction error in associative learning. *Cerebral Cortex, 19*, 1175–1185.
- Dürschmid, S., Edwards, E., Reichert, C., Dewar, C., Hinrichs, H., Heinze, H. J., et al. (2016). Hierarchy of prediction errors for auditory events in human temporal and frontal cortex. *Proceedings of the National Academy of Sciences, U.S.A., 113*, 6755–6760.
- Emberson, L. L. (2017). Chapter one - How does experience shape early development? Considering the role of top-down mechanisms. In J. B. Benson (Ed.), (Vol. 52, pp. 1–41). <https://doi.org/10.1016/bs.acdb.2016.10.001>.
- Emberson, L. L., Boldin, A. M., Riccio, J. E., Guillet, R., & Aslin, R. N. (2017). Deficits in top–down sensory prediction in infants at risk due to premature birth. *Current Biology, 27*, 431–436.
- Emberson, L. L., Richards, J. E., & Aslin, R. N. (2015). Top–down modulation in the infant brain: Learning-induced expectations rapidly affect the sensory cortex at 6 months. *Proceedings of the National Academy of Sciences, U.S.A., 112*, 9585–9590.
- Friston, K. (2005). A theory of cortical responses. *Philosophical Transactions of the Royal Society of London: Series B: Biological Sciences, 360*, 815–836.
- Gervain, J., Berent, I., & Werker, J. F. (2012). Binding at birth: The newborn brain detects identity relations and sequential position in speech. *Journal of Cognitive Neuroscience, 24*, 564–574.
- Gervain, J., Macagno, F., Cogoi, S., Peña, M., & Mehler, J. (2008). The neonate brain detects speech structure. *Proceedings of the National Academy of Sciences, U.S.A., 105*, 14222–14227.
- Grossmann, T., Lloyd-Fox, S., & Johnson, M. H. (2013). Brain responses reveal young infants' sensitivity to when a social partner follows their gaze. *Developmental Cognitive Neuroscience, 6*, 155–161.
- Grossmann, T., Striano, T., & Friederic, A. D. (2006). Crossmodal integration of emotional information from face and voice in the infant brain. *Developmental Science, 9*, 309–315.
- Hadley, H., Pickron, C. B., & Scott, L. S. (2015). The lasting effects of process-specific versus stimulus-specific learning during infancy. *Developmental Science, 18*, 842–852.
- Jaffe-Dax, S., Kimel, E., & Ahissar, M. (2018). Shorter cortical adaptation in dyslexia is broadly distributed in the superior temporal lobe and includes the primary auditory cortex. *ELife, 7*, e30018.
- Kersey, A. J., & Emberson, L. L. (2017). Tracing trajectories of audio-visual learning in the infant brain. *Developmental Science, 20*, e12480. <http://doi.org/10.1111/desc.12480>.
- Kouider, S., Long, B., Le Stanc, L., Charron, S., Fievet, A. C., Barbosa, L. S., et al. (2015). Neural dynamics of prediction and surprise in infants. *Nature Communications, 6*, 8537.
- Leroy, F., Glasel, H., Dubois, J., Hertz-Pannier, L., Thirion, B., Mangin, J. F., et al. (2011). Early maturation of the linguistic dorsal pathway in human infants. *Journal of Neuroscience, 31*, 1500–1506.
- Li, J., Schiller, D., Schoenbaum, G., Phelps, E. A., & Daw, N. D. (2011). Differential roles of human striatum and amygdala in associative learning. *Nature Neuroscience, 14*, 1250–1252.
- Markant, J., & Scott, L. S. (2018). Attention and perceptual learning interact in the development of the other-race effect. *Current Directions in Psychological Science, 27*, 163–169.
- Maurer, D., & Werker, J. F. (2014). Perceptual narrowing during infancy: A comparison of language and faces. *Developmental Psychobiology, 56*, 154–178.
- Nakano, T., Watanabe, H., Homae, F., & Taga, G. (2009). Prefrontal cortical involvement in young infants' analysis of novelty. *Cerebral Cortex, 19*, 455–463.
- O'Doherty, J., Dayan, P., Schultz, J., Deichmann, R., Friston, K., & Dolan, R. J. (2004). Dissociable roles of ventral and dorsal striatum in instrumental conditioning. *Science, 304*, 452–454.
- Paredes, M. F., James, D., Gil-Perotin, S., Kim, H., Cotter, J. A., Ng, C., et al. (2016). Extensive migration of young neurons into the infant human frontal lobe HHS public access. *Science, 354*, 1–6.
- Pearce, J. M., & Hall, G. (1980). A model for Pavlovian learning: Variations in the effectiveness of conditioned but not of unconditioned stimuli. *Psychological Review, 87*, 532–552.
- Piray, P., & Daw, N. D. (2019). A transparent model for learning in volatile environments. *BioRxiv, 701466*. <https://doi.org/10.1101/701466>.
- Rao, R. P., & Ballard, D. H. (1999). Predictive coding in the visual cortex: A functional interpretation of some extra-classical receptive-field effects. *Nature Neuroscience, 2*, 79–87.
- Rescorla, R. A., & Wagner, A. R. (1972). A theory of Pavlovian conditioning: Variations in the effectiveness of reinforcement and nonreinforcement. *Classical Conditioning II Current Research and Theory, 21*, 64–99.
- Saffran, J. R., & Kirkham, N. Z. (2018). Infant statistical learning. *Annual Review of Psychology, 69*, 181–203.
- Schultz, W., Dayan, P., & Montague, P. R. (1997). A neural substrate of prediction and reward. *Science, 275*, 1593–1599.
- Seymour, B., O'Doherty, J. P., Dayan, P., Koltzenburg, M., Jones, A. K., Dolan, R. J., et al. (2004). Temporal difference models describe higher-order learning in humans. *Nature, 429*, 664–667.

- Smyser, C. D., Inder, T. E., Shimony, J. S., Hill, J. E., Degnan, A. J., Snyder, A. Z., et al. (2010). Longitudinal analysis of neural network development in preterm infants. *Cerebral Cortex*, *20*, 2852–2862.
- Taga, G., & Asakawa, K. (2007). Selectivity and localization of cortical response to auditory and visual stimulation in awake infants aged 2 to 4 months. *Neuroimage*, *36*, 1246–1252.
- Thompson, D. K., Chen, J., Beare, R., Adamson, C. L., Ellis, R., Ahmadzai, Z. M., et al. (2016). Structural connectivity relates to perinatal factors and functional impairment at 7 years in children born very preterm. *Neuroimage*, *134*, 328–337.
- van Noort-van der Spek, I. L., Franken, M. C., & Weisglas-Kuperus, N. (2012). Language functions in preterm-born children: A systematic review and meta-analysis. *Pediatrics*, *129*, 745–754.
- Werchan, D. M., Collins, A. G., Frank, M. J., & Amso, D. (2016). Role of prefrontal cortex in learning and generalizing hierarchical rules in 8-month-old infants. *Journal of Neuroscience*, *36*, 10314–10322.
- Ylinen, S., Bosseler, A., Junttila, K., & Huotilainen, M. (2017). Predictive coding accelerates word recognition and learning in the early stages of language development. *Developmental Science*, *20*, e12472.
- Zhang, F., Jaffe-Dax, S., Wilson, R., & Emberson, L. (2018). Prediction in infants and adults: A pupillometry study. *Developmental Science*, *22*, e12780.

Corrected Proof