Prediction in infants and adults: A pupillometry study

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Abstract

Adults use both bottom-up sensory inputs and top-down signals to generate predictions about future sensory inputs. Infants have also been shown to make predictions with simple stimuli and recent work has suggested top-down processing is available early in infancy. However, it is unknown whether this indicates that top-down prediction is an ability that is continuous across the lifespan or whether an infant's ability to predict is different from an adult's, qualitatively or quantitatively. We employed pupillometry to provide a direct comparison of prediction abilities across these disparate age groups. Pupil dilation response (PDR) was measured in 6-month olds and adults as they completed an identical implicit learning task designed to help learn associations between sounds and pictures. We found significantly larger PDR for visual omission trials (i.e. trials that violated participants' predictions without the presentation of new stimuli to control for bottom-up signals) compared to visual present trials (i.e. trials that confirmed participants' predictions) in both age groups. Furthermore, a computational learning model that is closely linked to prediction error (Rescorla-Wagner model) demonstrated similar learning trajectories suggesting a continuity of predictive capacity and learning across the two age groups.

Keywords

1 | INTRODUCTION

To function efficiently in a changing environment, cognitive systems of adults use past experiences to make predictions about future sensory input. Correct predictions allow efficient processing of incoming stimuli (Kersten & Yuille, 2003; Kutas, DeLong, & Smith, 2011). Inaccurate predictions can elicit a prediction error (Friston, 2005; Hollerman &

Schultz, 1998; Rao & Ballard, 1999) which promote learning through updating of an internal model (Den Ouden, Friston, Daw, McIntosh, & Stephan, 2009; Nassar et al., 2012).

While research has provided neural (Emberson, Richards, & Aslin, 2015; Kouider et al., 2015) and behavioral evidence (Canfield & Haith, 1991; Gredebäck, von Hofsten, & Boudreau, 2002; Hespos, Gredebäck, Von Hofsten, & Spelke, 2009; Lew-Williams & Fernald, 2007; Romberg & Saffran, 2013) that infants also make predictions, there are reasons to believe infant's predictive capacity is different from an adult's. For example, the infant brain lacks the neural connections found in the adult brain (Nagy, Westerberg, & Klingberg, 2004; Smyser et al., 2010), which are used to compare predictions to sensory inputs. Moreover, research on statistical learning, an ability closely related to prediction,[1] has shown mixed results when comparing infant and adult performance (differences: Arciuli & Simpson, 2011; Raviv & Arnon, 2018; L. Emberson, J. B. Misyak, J. Schwade, M. H. Christiansen, & M. H. Goldstein, unpublished data; no differences: Kirkham, Slemmer, & Johnson, 2002; Saffran, Newport, Aslin, Tunick, & Barrueco, 1997).

This past work leads to a question: Does an infant's predictive capacity represent an ability that is continuous across the life-span or is it different from an adult's? A discontinuous perspective suggests studies reporting prediction in infancy is fundamentally different than prediction in adults, due to differences in neuroanatomy and knowledge. From a continuous perspective, both infants and adults have highly similar capacities to generate predictions. Continuity suggests that prediction is a part of the mechanism we use to build our initial models of the world and not simply update existing models in adulthood.

The goal of this study is to provide the first direct comparison of prediction and prediction error across infants and adults using pupillometry, the measurement of pupil diameter, and identical behavioral paradigms, to begin to answer these broader theoretical questions. The question of how prediction compares across infants and adults has been investigated in other domains. Hespos et al. (2009) compared infant and adult performance during a predictive reaching task; They found that infants and adults performed poorly when the object was occluded. While this work suggests similarity of prediction, a limitation of this paper is the use of different paradigms across the age groups (necessary to prevent adults from performing at ceiling). Using the same paradigm for infants and adults and eye movements, Gredebäck et al. (2002) found that both groups made accurate spatial and temporal predictions for an occluded object. Our current experiment allows a more mechanistic comparison of prediction and prediction error through using a novel task, pupillometry, and computational modeling to examine predictive capacities in infants and adults. Importantly, pupillometry allows for the recording of the *same* physiological response in an *identical* behavioral paradigm across these disparate age groups and more closely index prediction error compared to eye movements.

The pupil dilation response (PDR) has been shown to reflect cognitive surprise and prediction error. For example, Nassar et al. (2012) told adults to minimize errors in

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[1]Statistical learning, an ability related to the extraction of statistical regularities in the environment, is thought to be closely related to prediction both in the purported use of prediction to learn in these tasks and for the ability to use statistically-learned information to generate predictions.

predicting the next number in a series and revealed that the larger the prediction error, the larger the PDR (see also Braem, Coenen, Bombeke, van Bochove, & Notebaert, 2015; Raisig, Welke, Hagendorf, & van der Meer, 2010; Scheepers, Mohr, Fischer, & Roberts, 2013).

While PDR of infants has been linked to cognitive surprise (Gredebäck & Melinder, 2010; Jackson & Sirois, 2009; Wetzel, Buttlemann, Schieler, & Widmann, 2015), no work has directly linked the PDR and prediction or prediction error. For example, using the expectation-of-violation paradigm, Jackson and Sirois (2009) found that 8-month-old and 10-month-old infants have larger PDR for unexpected events that violate object permanence. Another study found similar PDRs in infants and adults when unexpected sounds involuntarily captured attention in an odd-ball task (Wetzel et al., 2015). While odd-ball studies require some aspect of memory for the detection of unusual sounds, this design cannot isolate contributions of predictive processes *per se*. However, predictions can occur without our awareness (DeLong, Urbach, & Kutas, 2005; Van Berkum, Brown, Zwitserlood, Kooijman, & Hagoort, 2005). Thus, we employed a learning task to study the relationship between prediction error and PDR in infants and directly compare infants' and adults' performance.

We modeled the current task after Emberson et al. (2015) which was designed to investigate predictions, specifically those initiated by top-down neural signals. During familiarisation, participants learn to associate audiovisual pairs such that after hearing the auditory cue, they expect to see a visual stimulus. After familiarisation, we introduced unexpected omission trials where the auditory cue was followed by a blank screen. This violation of participants' visual predictions should elicit a prediction error. Showing a blank screen instead of a novel visual stimulus allowed us to rule out the possibility that infants are simply experiencing an error signal reflecting the low-level perceptual features of a different visual stimulus, rather than violation of a prediction for upcoming visual input. Using this paradigm, Emberson et al. (2015) reported that 6-month-old infants exhibited significant visual system activity during an unexpected visual omission. In other words, top-down signals from the auditory system to the visual system resulted in a visual prediction. Thus, both the learning task and the type of violations employed were specifically designed to tap into predictions as opposed to other cognitive processes or types of error.

We investigated three questions:

1. Is prediction error in infants linked to larger PDR? Behavioral and neurodevelopmental research suggest early availability of predictive processing (Emberson et al., 2015; Kouider et al., 2015; Lew-Williams & Fernald, 2007; Romberg & Saffran, 2013). Here we use PDR to index prediction error in infants in an associative learning task (Gredebäck, Lindskog, Juvrud, Green, & Marciszko, 2018). We hypothesize that 6-month-old infants will show larger PDR in response to omission compared to present trials.

2. How does prediction error (measured using PDR) compare between infants and adults? The current study is the first to use the same paradigm and pupillometry to compare prediction error across developmental time.

3. Is the time-course of learning and prediction similar in infants and adults? There's a lack of research focusing on infants' learning trajectory due to methodological constraints. We combined the PDR collected on each trial and computational modeling to examine learning trajectories across age groups. Specifically, we used the Rescorla-Wagner (RW) model (Rescorla & Wagner, 1972), a well-established associative learning theory that explicitly includes prediction and prediction error, to uncover the trial-by-trial dynamics of learning and prediction.

2 | METHODS

2.1 | Participants

2.1.1 | Adults
We collected data from 44 adults. One participant was excluded due to age (51), eight were excluded due to technical errors, and three were excluded due to experimenter error. Our final adult sample included 32 healthy adults ($M = 21$ years; $SD = 2.5$; 27 females). We did not collect demographics for one participant but they fall within the standard range for the population.

2.1.2 | Infants
We collected data from 43 infants: Four infants were excluded due to insufficient number of good trials (see Supporting Information 2.4); Two were excluded because they were later identified as preterm; Ten were excluded due to technical errors. Our final infant sample included 27 infants ($M = 5.7$ months; $SD = 0.60$ months; ten females). Experiments were approved by the university's Institutional Review Board and informed consent was obtained before beginning the study from the adult participant or legal guardian of the infant. Adults received a course credit or $6 for their participation. Families received $10, a t-shirt, and a children's book for their participation.

2.2 | Stimuli

Two auditory stimuli and two visual stimuli formed two audiovisual pairs (A1V1, A2V2). Participants learned that A1 and A2 (i.e. the predicting sounds, xylophone and trill) predicted V1 and V2 (i.e. the predicted visual stimuli), respectively. We had two additional auditory stimuli (twinkle, doorbell), which were presented simultaneously with the visual stimuli and indicated when the visual stimulus should appear. Baseline videos (5) were presented to give the pupil enough time to fully evolve. To prevent luminance-related changes in pupil size, all visual stimuli were made isoluminant to the background color of the experiment and to the experimental room (see Supporting Information 2.2).

2.3 | Design and procedure

Participants sat approximately 60 cm from the monitor and eye tracker (Eyelink 1000, SR Research, Ontario, Canada, see Supporting Information 2.3 for details on eye tracking procedure).

There were two trial types (Figure 1): Present and omission. During a present trial, the predicting sound (A1/A2) and fixation cross appeared for 1,000 ms followed by a visual stimulus for 1,000 ms that appeared with a coincident sound. The visual stimulus appeared

in the center of the screen, and after 500 ms slid towards the bottom of the screen and disappeared at 1,000 ms. Then, participants saw a blank screen from 900 to 1,500 ms, designed to capture the pupil response and make an omission clearer. Next, one of five videos played for a jittered interstimulus interval (ISI) of 4.4–5 s. Each video was shown once before they were shuffled and presented again. The next trial followed the conclusion of video. The arrangement of an omission trial was identical to the present trial, except the predicted visual stimulus was omitted. Stimuli were presented using MATLAB for Mac (R2015b) and Psychtoolbox (3.0.12 Beta, SVN revision 6399).

The experiment began with a familiarization phase of 12 present trials to allow participants to learn the two audiovisual pairs (A1V1, A2V2). After familiarization, participants saw four present trials (two each A1V1, A2V2) and two omission trials (one A1–, one A2–) presented in a randomized order, and then repeated with new random orders for a total of 114 trials. Adults completed all 114 trials, and infants participated until they became consistently fussy or inattentive. This design ensured that participants only saw unexpected visual omissions 33% of the time. This percentage balances the need for as many visual omission trials as possible while at the same time allowing participants to maintain association of the two audiovisual pairs. Previous studies examining the visual omission design have used a 20% visual omission rate and found very robust responses with no decline over the course of the experiment (Emberson et al., 2015).

2.4 | Preprocessing

Details of the preprocessing steps can be found in Supporting Information 2.4. As a result of preprocessing, we removed 44% or 808 trials for infants and 1.2% or 45 trials for adults. Excluding this number of trials is common for infants. It is preferable to be conservative as trials with blinks, large amount of data missing, etc. can introduce outliers and bias results. For similar exclusion rate see Fawcett, Wesevich, and Gredebäck (2016). We calculated the PDR as percentage change from baseline to accommodate variations in pupil diameter due to individual differences, which is a standard approach for pupillometry data (Lavin, San Martín, & Rosales Jubal, 2014; Mill, O'Connor, & Dobbins, 2016; Preuschoff, Marius't Hart, & Einhäuser, 2011). We defined baseline as the average pupil diameter during the period after the predicting sound was played and before the visual stimulus appeared, which was 1,000 ms (Figure 1). This baseline measure was subtracted from each pupil diameter measurement and divided by baseline to get the PDR and then multiplied by 100 to convert the decimal number to percentage.

2.5 | Modeling PDR response using a learning model

We used a learning model to examine the trial-by-trial changes of prediction and prediction error in the task. We chose the RW learning model because it measures how prediction error affects the strength of predictions. Therefore, the model will be sensitive to the strength of the predictions our participants have for the visual stimuli, as they view present trials (designed to strengthen predictions) and omission trials (designed to generate prediction error).

We assumed individual PDR at each trial reflects the magnitude of prediction error or surprise in that trial (Kloosterman et al., 2015; Lavin et al., 2014; O'Reilly et al., 2013; Preuschoff et al., 2011; Sirois & Jackson, 2012). For each participant, we fitted a generative implementation of a learning model to their PDR response. The model asserts that prediction error is calculated for each trial, t:

$$\delta(t) = O(t) - P(t)$$

where: $O(t)$ is the appearance (or omission) of visual stimulus at trial t and $P(t)$ is the predicted probability of that appearance. In addition, predictions are updated for each trial based on the prediction error and learning rate, where α is the learning rate:

$$P(t + 1) = P(t) + \alpha\delta(t)$$

We fitted the individual models by minimizing the Mean Square Error (MSE) between the PDR and δ^2 (level of surprise or magnitude of prediction error regardless of the direction of the error) throughout the experiment for each participant (see Supporting Information 2.5). Furthermore, fitting the model revealed each participant's learning rate, α, and initial prediction, $P(0)$.

3 | RESULTS

3.1 | PDR to unexpected visual omissions

We examined the PDR of present versus omission trials for both age groups using two-tailed t tests across successive time points and corrected for multiple comparison using a conservative method (the Benjamini & Hochberg, 1995; procedure controlled for the rate of false discovery; Lavin et al., 2014; Mill et al., 2016). We used multiple t tests to analyze the time-course because we wanted to compare every single time point to identify where the prediction error signal starts and ends. As hypothesized, we found differences in the PDR across trial types for both age groups (Figure 2). In adults, the PDR varies across trial type (pFDR < 0.05) for two sustained periods from 1,726 to 3,250 ms and 3,620 to 4,000 ms. In infants, PDR vary across trial type (pFDR < 0.05) for a sustained period from 2,144 to 2,948 ms and two brief periods from 3,152 to 3,308 ms and 3,804 to 3,976 ms. Majority of participants from both age groups showed a larger pupil change to omission trials compared to present trials (Figure 3) where pupil change is an average calculated from after the visual stimulus appears/supposed to appear (i.e. from the second line of Figure 2) to 4,000 ms. Overall, these results demonstrate both infants and adults exhibit larger PDR to omission trials compared to present trials with a similar period[2]; Though, infants exhibit a differential PDR ~400 ms later than adults.

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[2]Prior work has found that the presentation of a visual stimulus can lead to a decreased PDR (e.g. updating response in O'Reilly et al., 2013). However, this is not likely to be driving the difference between the visual present and visual omission trials in the current design. In the current paradigm, after familiarization, the trial type that is most likely to drive an updating response in the omission rather than the present trials since the present trials are highly familiar and most frequent. Furthermore, anecdotally, we do find a negative response upon visual presentation but it is only found in the first trial of the task (the first familiarization trial). This negative response is quite pronounced and never observed for any other trial.

3.2 | Learning model

We calculated the average number of trials infants completed (37 trials) and used only the first 37 trials of adult data to make sure the exposure to the experiment was as close as possible for both age groups. Before interpreting the results, we determined model fit by correlating PDR and prediction error magnitude (δ^2) from the model for every trial of every subject (Figure 4). Results revealed significantly positive correlation for both infants and adults (adults: $r = 0.19$, $p < 0.001$; infants: $r = 0.16$, $p < 0.001$), suggesting the larger the prediction error, the larger the PDR. Therefore, PDR is a good index of prediction error.

Comparing adults and infants, we found the two groups did not differ on the goodness of fit, as measured by the MSE (adults: 1.44 ± 0.054; infants: 1.41 ± 0.042; $U = 413$, $p = 0.78$). Comparing the parameters (Figure 5), a Mann-Whitney test indicated adults had significantly higher initial predictions, $P(0)$, of a visual stimulus than infants (adults: 0.88 ± 0.044; infants: 0.48 ± 0.052; $U = 107$, $p < 0.0001$). In other words, adults came into the experiment with higher expectation of audio-visual association or the presentation of a visual stimulus than infants. Additionally, adults had significantly higher learning rate, α (adults: 0.31 ± 0.068; infants: $M = 0.055 \pm 0.032$; $U = 265.5$, $p < 0.05$. Mean $\pm$ *SEM*. Mann-Whitney tests), which is likely due to adults beginning the experiment with a strong prediction for the presentation of a visual stimulus that they needed a larger learning rate to update their predictions when encountering their first omission, whereas infants do not. However, a comparison of the infant learning rate to zero confirmed that infants are indeed learning ($Z = 4.53$, $p < 0.0001$; Wilcoxon signed-rank test).

Once the parameters (learning rate and initial prediction) were estimated, we examined prediction and prediction error on a trial-by-trial basis (Figure 6) which revealed that, although infants and adults start off distant from one another, they quickly converge. The divergence at the beginning of the experiment for δ^2 and P can be explained by the significant difference in initial prediction or $P(0)$ between infants and adults. However, as the experiment continued, both groups eventually experienced similar level of surprise and generated similar prediction. Importantly, the predictions converged accurately (i.e. a visual stimulus shows up 66% of the time and their predictions converge on this probability).

4 | DISCUSSION

In this study, we investigated continuity of predictive processing in young infants and adults. While studies have compared prediction across these ages, no study has used pupillometry and computational modelling to examine predictive capacity over developmental time. Consistent with the continuous perspective, we found larger PDR during omission trials compared to present trials in both age groups, with the exception that the divergence of the PDR between trials was slightly delayed in infants (Figure 2). Furthermore, both groups generate prediction errors (δ^2) and use it to adjust their prediction (P) to the correct stimulus probability as revealed through modeling trial-by-trial PDRs with the RW model (Figure 6). Moreover, results from our task, which has been shown to elicit top-down signals (Emberson et al., 2015), suggest infant prediction error might be generated from top-down signals, similar to adults. Thus, using the same learning task and recording the same physiological

response, we find that prediction abilities in young infants are continuous with the prediction abilities present in adults.

While our results also reveal differences between infants and adults, we believe they do not suggest discontinuity of predictive processing. The modelling results for predictions on trial 1 (and by consequence their learning rates) are different between the two groups. Despite our efforts to create a novel learning context for both infants and adults, we believe the differences are result of the different experiences infants and adults have about the world (i.e. about sitting in front of a computer screen). Moreover, in Figure 2, after the first significant PDR period (adults: 1,726–3,250 ms, infants: 2,144–2,948 ms), the time-course graph has other significant PDR periods (adults: 3,350–3,378 ms and 3,620–4,000 ms, infants: 3,028–3,056 ms, 3,152–3,308 ms, 3,340–3,348 ms, and 3,804–3,976 ms), which are different for infants and adults. These differences are likely due to the protracted PDR, which likely varies within and across age groups. These individual differences will manifest itself statistically as intermittent periods of significant difference. Despite these differences, this doesn't constitute prediction or prediction error being discontinuous across these age groups. The similarities between groups are in the time-course of the PDR, the fit of the RW learning model to the PDR response and the convergence of expectations towards the probability of the visual event. These measures are directly related to prediction and, given their continuity across the two groups, we conclude there is continuity of predictive processing despite differences in initial expectations. However, future research should extend investigation to other age groups as there could be developmental changes before 6 months and a non-linear trajectory between 6 months and adulthood.

As always, it is important to consider whether results could be due to other processes that give rise to a behavior that looks like prediction. Given the clear correspondences between the PDR on each trial and the prediction error parameter of a foundational learning model (RW model), this isn't a parsimonious explanation. Moving forward, we can start to ask more specific questions about the use of prediction to construct initial models of the world. For example, how stable are infants' predictions and models of the world compared to adults?

Our study adds to the growing field of literature examining predictive capacities between infants and adults (Gredebäck et al., 2002; Hespos et al., 2009) as well as the nature of the PDR. We provide the first evidence that the infant PDR can index predict processes and therefore is not only reactive (see Nassar et al., 2012; O'Reilly et al., 2013 for evidence in adults; Gredebäck & Melinder, 2010; Gredebäck & Daum, 2015 for information about the distinction). This contrasts with studies that have found that the PDR is not reflective of prediction in the context of action perception (Gredebäck & Melinder, 2010; Gredebäck & Daum, 2015). We find that the PDR can provide fruitful information regarding predictive abilities in other domains. Future work should continue to investigate this predictive PDR making sure to dissociate it from processes such as cognitive load and memory retrieval.

In sum, using the same learning task for both adults and infants, we found significantly larger pupil dilation (PDR) during trials that violate predictions compared to trials that met predictions. Specifically, the strong parallels in time-course and magnitude of the PDR,

along with modelling results, suggest a continuity of predictive abilities across these ages. Taken together, our data suggest that research documenting prediction in young infants (Emberson et al., 2015; Kouider et al., 2015; Lew-Williams & Fernald, 2007; Romberg & Saffran, 2013) is uncovering a life-span ability and not simply a nascent form of prediction that isn't yet comparable to adults.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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Research Highlights

- The first study to use an identical learning task to compare prediction and prediction error for infants and adults.

- Infants and adults exhibit strong parallels in time-course and magnitude of prediction error, as indexed by the pupil dilation response.

- Computational modelling reveals that infants and adults experience and use prediction error to help them make more accurate predictions in similar ways.

- These findings suggest a continuity of predictive processing between infancy and adulthood.
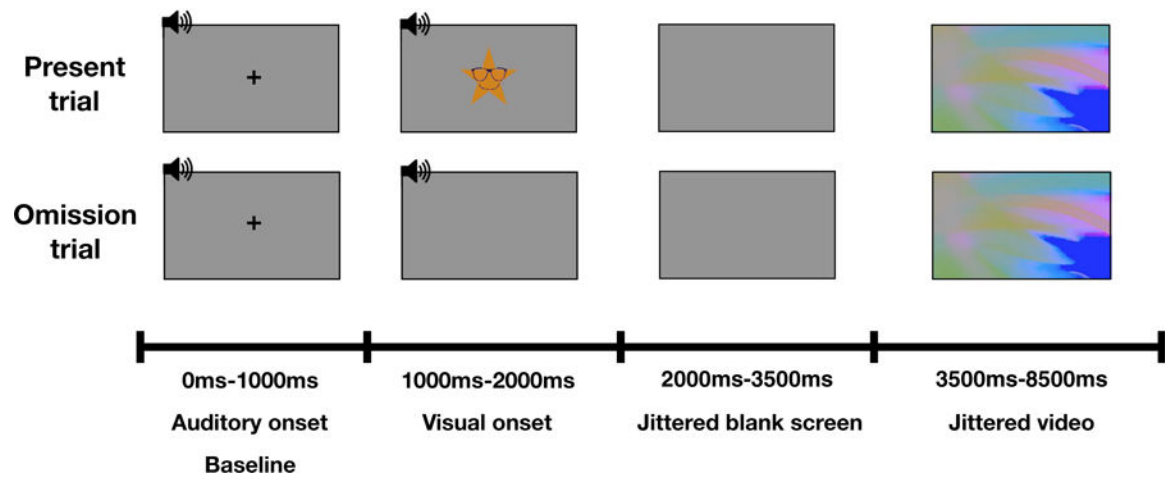
FIGURE 1.

Trial procedure. Arrangement of a present trial and an omission trial. Both trials started with an auditory stimulus that is presented for 1000ms, followed by either a visual stimulus (present trial) or blank screen (omission trial) for another 1000ms, followed by a jittered blank screen and a jittered video
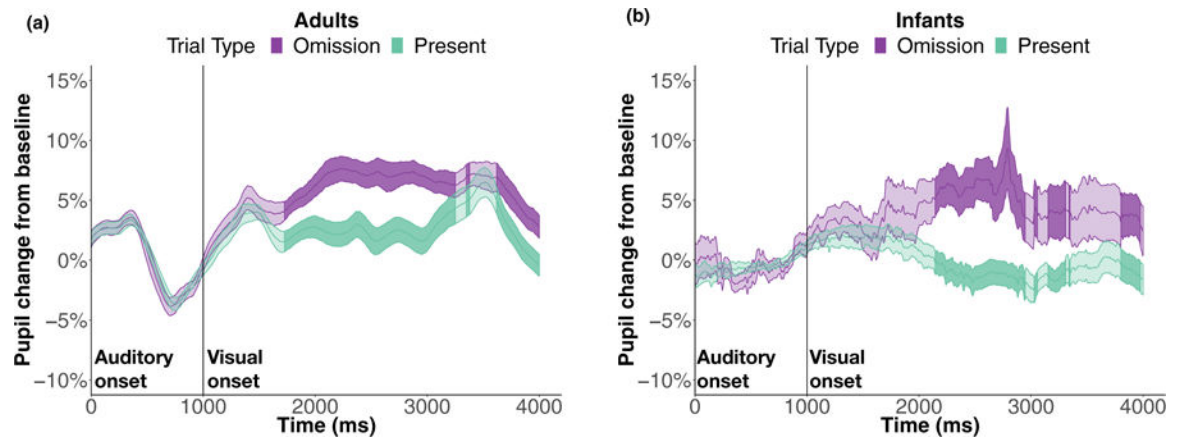
FIGURE 2.

PDR plotted against time for the two trial types. Significant results, darkened, are identified after FDR correction, pFDR <0.05. Data depicted as Mean ± SEM. The first line indicates on average when the predicting auditory cue plays. The second line indicates on average when the predicted visual stimulus appears/suppose to appear. (a) Significant differences in adults were found in three periods: 1726–3250ms, 3350–3378ms and 3620–4000ms. (b) Significant differences in infants were found in five periods: 2144–2948ms, 3028–3056ms, 3152–3308ms, 3340–3348ms, and 3804–3976ms
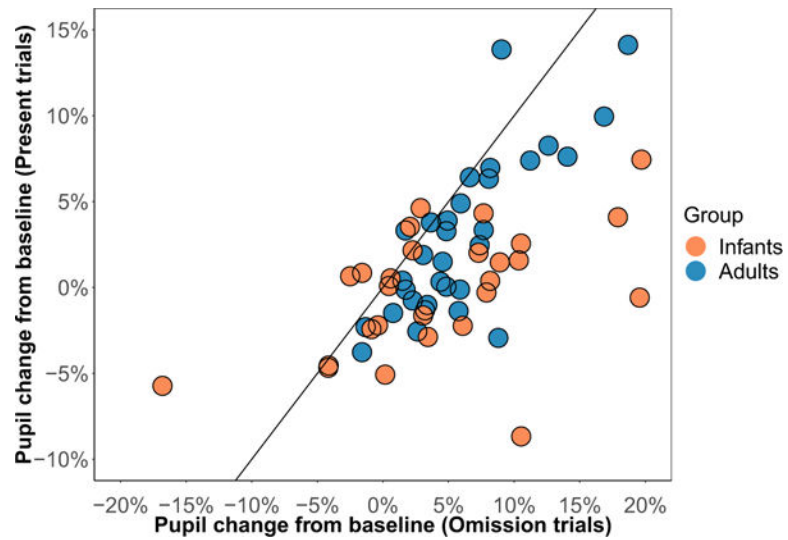
FIGURE 3.

Scatterplot of average PDR (average calculated from immediately after the visual stimulus appears/supposed to appear to 4000ms) to present trial versus omission trial, for both age groups. The diagonal line represents equal average PDR to both trials. Participants below the diagonal line show greater PDR to omission trials than present trials. Participants above the diagonal line show greater PDR to present trials than omission trials
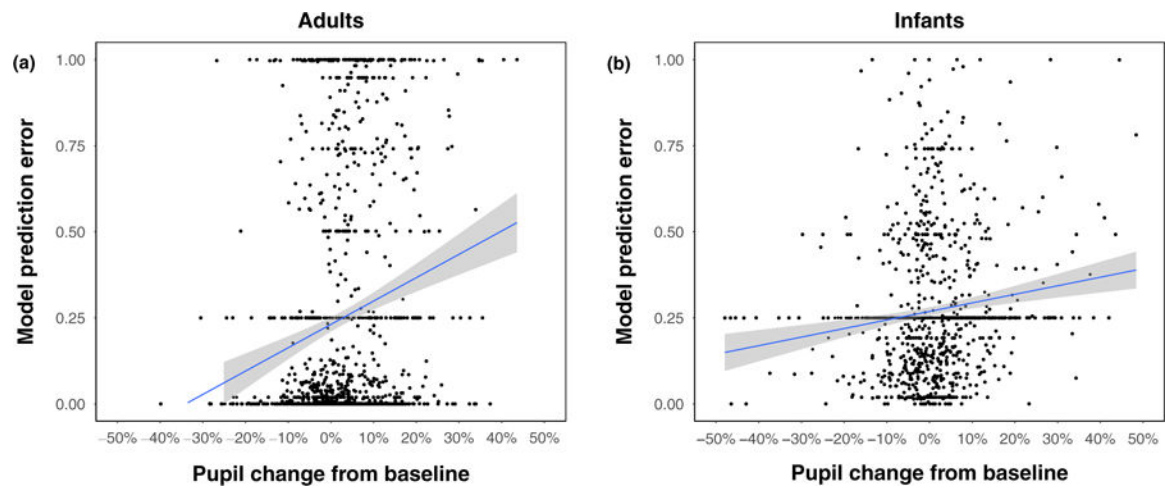
FIGURE 4.
Correlation of PDR and prediction error magnitude (R^2) from the model for every trial of every subject to determine model fit. (a) Results revealed significantly positive correlation for adults. (b) Results revealed significantly positive correlation for infants
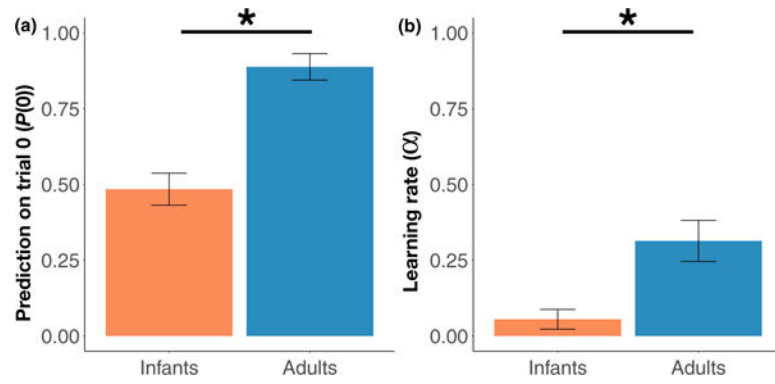
FIGURE 5.
Comparing parameters from the learning model for infants and adults. (a) Comparing initial prediction, $P(0)$, between infants and adults. Adults had significantly higher initial predictions than infants. (b) Comparing the learning rate, α, between infants and adults. Adults had significantly higher learning rate than infants
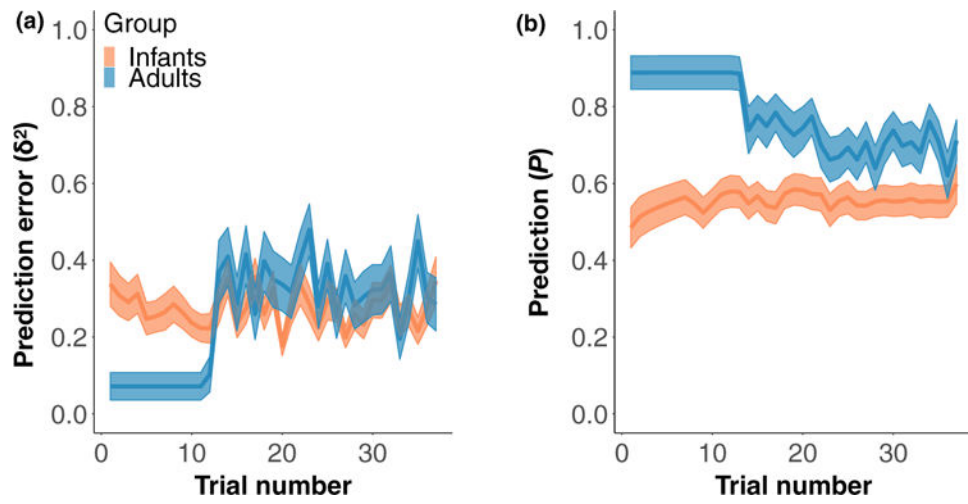
FIGURE 6.

Comparing simulated parameters generated from the infant and adult learning model on a trial-by-trial basis. (a) Prediction error. (b) Prediction