

How Visual is Visual Prediction?

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Infants are readily able to use their recent experience to shape their future behavior. Recent work has confirmed that infants generate neural predictions based on their recent experience (Emberson, Richards, & Aslin, 2015) and that neural predictions trigger visual system activity similar to that elicited by visual stimulation. This study uses behavioral methods to ask, how *visual* is visual prediction? In Experiment 1, we confirmed that when additional trials provide additional visual experience with the experimental shape, infants exhibit a robust novelty preference. In Experiment 2, we removed the visual stimulus from some trials and presented the predictive auditory cue alone, allowing the effects of neural prediction to be assessed. We found no evidence of looking preferences at test, suggesting that visual prediction does not contribute to the computation of visual familiarity. In Experiment 3, we provided infants with a degraded visual stimulus to test whether visual prediction could bias visual perception under ambiguous conditions. Again, we found no evidence of looking preferences at test, suggesting that visual prediction is not biasing perception of an uncertain stimulus. Overall, our results suggest that visual prediction is not *visual*, in the strictest sense, despite the presence of visual system activation.

Infants are excellent at taking their recent experience and using it to shape their ongoing behavior. In fact, this ability forms the basis of many paradigms used to study early development: Habituation/dishabituation methods rely on infants quickly forming some kind of representation of their environment and applying that representation to future sensory input (i.e., identifying a change in their sensory input and exhibiting

a shift in their behavior). These processes are also central to studies of statistical learning where infants form representations about the structure of their environment in response to the statistical information in their sensory input (e.g., Kirkham, Slemmer, & Johnson, 2002; Saffran, Aslin, & Newport, 1996). Moreover, infants use the informational value of their sensory input to guide their attention (Kidd, Piantadosi, & Aslin, 2012).

While many studies have documented the important learning capacities that young infants possess, few studies have investigated what consequences learning has on the processing of new sensory input. For example, how does learning affect perceptual processing? In one of the few studies to directly test the consequences of statistical learning, Graf Estes, Evans, Alibali, and Saffran (2007) found that infants were more likely to engage in word learning with segments of speech that they had just learned compared to segments that violated their recent experience. While Graf Estes et al. (2007) provide evidence for a clear *benefit* of statistical learning, it is unclear why infants accept the learned segments as words more readily than the segments that violate their expectations.

Recent work has explored the possibility that learning allows infants to engage in top-down sensory prediction. Using functional near-infrared spectroscopy (fNIRS), Emberson, Richards, and Aslin (2015) found that the visual system of 6-month-olds is activated during visual prediction. Specifically, after learning an audiovisual association (nine exposures to two novel audiovisual associations), the visual system was activated in response to the auditory cue alone. In other words, infants exhibited signs of visual prediction (a top-down process) that could be dissociated from low-level sensory novelty responses. Kouider et al. (2015) provide convergent findings where after learning an audiovisual association, infants exhibit augmented perceptual components to predicted stimuli compared to unpredicted (i.e., those that conform to the audiovisual association compared to those that violate the association). These findings mirror work in adults showing that predictive auditory cues elicit predictive activation of the visual system (Den Ouden, Friston, Daw, McIntosh, & Stephan, 2009; Kok, Failing, & de Lange, 2014) suggesting developmental continuity in this type of visual prediction.

An important take home from Emberson et al. (2015) is that young infants' visual prediction looks *visual* in the infant brain. Specifically, the level of activation for infants' visual anticipation was indistinguishable from the level of activation when they saw the actual visual event. Moreover, these patterns were in the early regions of the visual system where activation is typically seen only during visual perception. Here, we follow up the visual prediction signatures found in 6-month-olds in Emberson et al. (2015) to ask *how visual is visual prediction?* Specifically, is predicting a visual event functionally similar to seeing a visual event?

These questions dovetail with a long-standing debate in cognitive psychology as to whether visual imagery in adults involves the visual system. Numerous neuroimaging studies have found that visual imagery does activate the adult visual system. For example, a classic study by Cui, Jeter, Yang, Montague, and Eagleman (2007) found a strong correlation between the vividness of an adult's mental imagery and activation of their visual system when participants were asked to visualize (see Lee, Kravitz, & Baker, 2012; for systematic differences in visual activation during imagery and perception despite presence of activation for both). Thus, this literature would suggest that if infants are like adults, that this visual activation during visual prediction is like imagery, and there is some visual aspect to their visual predictions. There is also a

possibility that visual prediction might offer some kind of memory benefit to infants. Recent studies in adults have linked visual activation during imagery with visual working memory (Albers, Kok, Toni, Dijkerman, & De Lange, 2013), suggesting that top-down visual activation might affect memories of the visual events being imagined or the degree of learning about current sensory input.

In the current study, we examine whether simply predicting a visual event has similar effects on visual recognition memory as actually seeing the event for infants at 6 months of age (Figure 1). Specifically, infants learn two novel audiovisual associations. One audiovisual association is presented 25 times throughout the experiment in a method that never varies (control pair). Infants' exposure to the other audiovisual association is manipulated across three experiments (experimental pair). Specifically, the experimental pair has 25 trials that match the methods of exposure for the control pair, but 23 additional trials are introduced toward the end of familiarization to manipulate infant's exposure (or predictions) to the experimental pair.

In the first experiment, these additional trials simply provide additional sensory experience with the experimental pair to confirm that infants exhibit a novelty preference for the shape of the control pair after seeing the experimental pair almost double the number of times. Our dependent measure is the proportion of looking to each of two shapes (control and experimental) in two alternative forced-choice (2AFC) trials at the beginning and the end of familiarization.

Experiment 1 provides a point of comparison to test how visual prediction is and, in Experiment 2, the additional trials only provide the infant with an opportunity to predict the shape from the additional experimental pairings. In other words, infants hear the predictive sound but do not see the shape. This is the same trial structure used in Emberson et al. (2015) that found visual activation when 6-month-olds only hear a predictive auditory cue after audiovisual association. If visual prediction is as visual as visual perception, one would predict similar results in Experiments 1 and 2. However, if visual prediction is not visual, infants should not exhibit any visual preference as each shape has been presented equally throughout the experiment. In

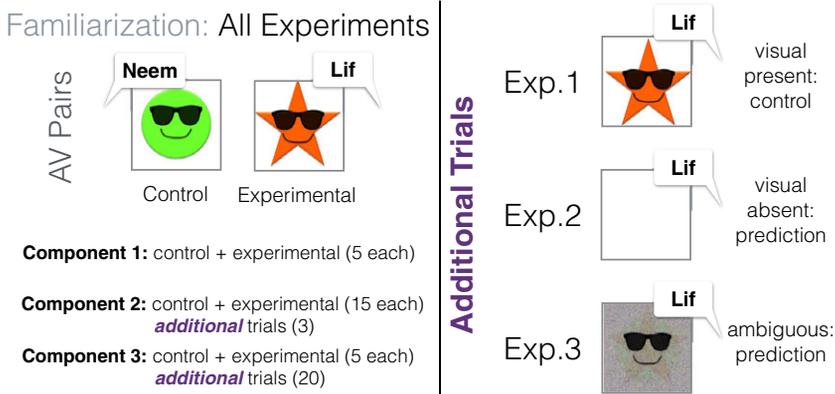


Figure 1 Infographic of the familiarization phase. Left panel presents the methods common for all three experiments. Note that only a single, central box was presented during familiarization and shapes, and auditory stimuli were presented sequentially. The only aspect of familiarization that changes across experiments is the content of the *additional* trials (right panel).

Experiment 3, we examine whether visual prediction can bias visual input. Specifically, additional trials present infants with the predictive sounds of the experimental pair but an ambiguous visual stimulus.

EXPERIMENT 1: VISUAL PRESENT CONTROL

In this first experiment, we validate our general approach by examining infants' looking preferences for two shapes when they have viewed one shape double the number of times as the other shape. Specifically, each shape was embedded in an audiovisual association (e.g., the word *lif* predicting the star, the word *neem* predicting the circle). There were three components of the familiarization phase: In the first component, the infant experienced the two audiovisual pairs equally (i.e., equal visual experience), and in the second and third components, infants gradually experienced one of the audiovisual pairs more frequently until, at the end of the familiarization phase, they have experienced one audiovisual pair nearly twice the frequency of the other. We will refer to these two pairs as the control pair and the experimental pair. With this bias in visual experience, there is a strong hypothesis that infants will exhibit a novelty preference for the control shape over the more frequent shape. To foreshadow, in subsequent experiments, we will alter visual experience between the two pairs and replace this ramping up of *additional* experience (to be called *additional* trials) with a visual-absent prediction of the manipulated shape. Thus, this initial experiment provides a clear baseline for subsequent experiments that focused on the effects of predicting a visual input vs. the actual sensory experience of that visual input.

Methods

Participants

Infants were recruited from the Rochester Baby Lab database and in line with IRB approval at the University of Rochester. All infants were born at full-term (min 36 weeks), had no major health difficulties, and normal hearing and vision. There were a total of 22 participants (12 female; age: $M = 5.32$, $SD = .48$ months). All participants reported hearing 100% English within their homes. For race and ethnicity, four infants were reported to be black, 17 white and one "other"; all infants were reported to be non-Hispanic. Five infants were excluded if the eye tracker failed to record at least 4-sec of infant looking for at least one pretest and post-test trial,¹ and one was excluded for being over two standard deviations from the mean looking time (defined by average looking during test trials).²

¹As we have a small number of trials and infants were general well-engaged with the stimuli, these trials indicated poor eye tracker data quality. Removing eye-tracking trials when the eye tracker records one-third of the trial or less has also been previously reported in the literature (e.g., Bergelson & Swingley, 2015).

²A number of previous studies have employed two standard deviations to identify outliers (Conway, Bauernschmidt, Huang, & Pisoni, 2010; De Haan & Nelson, 1997; Maye, Weiss, & Aslin, 2008). A criterion of 2.5 standard deviations would also identify these same outliers. Including this outlier does remove the significance of the final result.

Audiovisual stimuli

Infants experienced two novel audiovisual pairs. Stimuli were presented using MATLAB for Mac (R2007b) and Psychtoolbox (3.0.8 Beta, SVN revision 1245). Visual stimuli were designed to be distinct (green circle, orange star) but with an identical “face” to engage attention without allowing infants to use this aspect of the stimuli to differentiate the shapes (Figure 1). Shapes appeared on the screen by rising into a box (500 ms) then reversing course and lowering out of the box (500 ms, a total of 1,000 ms) and were presented at ~15 degrees of visual angle on a Tobii eye-tracking monitor (33.7 × 27 cm). Each shape was paired with a novel sound: either the nonsense word, “lif” or “neem” (1 sec), and these were spoken by a female native English speaker. The sounds preceded the shapes’ appearance by 500 ms, during which time the empty box was present. Thus, the sound and the shape had an overlapping presentation for 500 ms. Computer speakers were placed behind the curtain below the monitor. The pairing of the audiovisual stimuli and their assignment within the experimental design were counterbalanced throughout the experiment.

Procedure

Infants were seated on their caregiver’s lap in a darkened room. The caregiver was unaware of the purpose of the experiment and wore a visor to prevent them from seeing the screen but while allowing interaction with their child.

Familiarization

The familiarization phase had three components with gradually increasing exposure to the experimental pair through *additional* trials:

Component 1: Five presentations of each pair (10 trials).

Component 2: Fifteen presentations of each control and experimental pair and three additional experimental pairs (33 trials).

Component 3: Five presentations of each control and experimental pair and 20 additional experimental pairs (30 trials).

By the end of familiarization, infants viewed the control pair 25 times and the experimental 48 times. Importantly, 23 of these 48 trials are *additional* trials that occur later in the experiment. These details are relevant for the variation on this experimental design in subsequent experiments.

Within each component of the familiarization phase, all trials were presented in random order with the constraint that no trial type was presented more than two times in a row. Each AV pair was separated by a 500–750 ms ISI during which the empty box was present. Stimuli were presented to the infants until they looked away from the screen for two consecutive seconds, at which point a simple attention getter was played (calm music and a flashing white dot on a gray background). When infants returned their gaze, the stimulus presentation resumed with the repetition of the previous stimulus. Looking time for this portion of the study was calculated based on the button presses of a trained, nonblind online coder whose task was simply to report when infants were looking and when they were looking away, to ensure that all infants

received the same exposure (i.e., in this phase of the experiment, we were not gathering our dependent measure).

Test trials (prefamiliarization and postfamiliarization) and eye tracking

Before and after familiarization, infants were presented with both shapes in two alternative forced choice (2AFC) trials and an eye-tracker was used to record infant's eye position. In these trials, two boxes (identical to those used in familiarization) were placed on the left and right sides of the screen. The two shapes appeared in the same fashion as the familiarization phase (rising into the box for 500 ms) but two boxes were appeared (one to the left and one to the right of the screen) and both shapes were presented. Both shapes stayed on the screen for 16 sec before leaving the screen (lowering out of the box for 500 ms). Shape position was counterbalanced across the two pretrials and two post-trials with initial configuration counterbalanced across pretrials and post-trials. In between test trials, if the infant was not looking at the screen the attention getter was played until infants looked at the screen and then the next test trial was started. No auditory cues were played during test trials.

Eye tracking was recorded using a Tobii 1750 system (with a 17-inch screen). Infants first performed a five-point calibration with .5 degrees of error. Based on the x - y coordinates, all eye-tracking data points were classified as either off the screen, on the left or the right of the screen, and then mapped onto the stimulus that was being presented at that location (control vs. experimental shape). The amount of time (seconds) for looking at each stimulus was calculated for each trial and then, proportion looking (our dependent measure) was calculated for each stimulus for each trial. Then, proportion looking was averaged for each infant for all pretest trials and post-test trials. Looking time was analyzed through R-studio Version 0.98.1049. The mean proportion of looking time allocated toward the familiar and novel stimuli was calculated for each study.

Results and discussion

As expected, proportion looking did not differ across the two visual stimuli in the pretest trials (mean proportion looking to the experimental and control stimulus was both 0.50, $SDs = 0.11$, $t(15) = -0.17$, $p = .87$). Also as expected, at the post-test trials after infants viewed the experimental shape twice the number of times as the control shape, they preferred to look at the control or novel shape (mean proportion looking to control = 0.55, $SD = 0.085$; experimental = 0.45, $SD = 0.09$). This difference in looking was significant whether evaluated based on parametric tests of proportion looking time ($t(15) = -2.38$, $p = .03$, Figure 2, left column) or based on nonparametric tests of looking preferences per baby (12 control/novelty and four experimental/familiarity preferences: Wilcoxon signed-rank test, $V = 25$, $p = .03$, Figure 3, left column).

Thus, as expected, infants exhibited a strong novelty response in the post-test trials confirming that infants prefer to look at a shape that they have seen half the number of times. This result confirms our general approach and provides a baseline for comparison: Knowing the consequences of visual perception during the additional trials, Experiment 2 asks whether visual prediction (but not perception) during these trials has the same consequences.

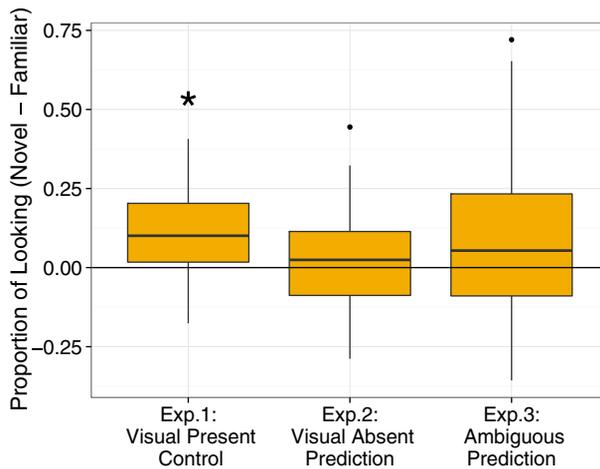


Figure 2 Proportion looking time to control – experimental shapes at post-test trials. The center-line in the box represents the population mean, and the height of the box represents the first and third quartiles of the population (the variance of the distribution). In contrast with error bars in bar plots, the vertical lines represent the maximum and minimum of the population ($* p < 0.05$). Only the looking times of the first experiment are significantly different than chance (equal looking to each post-test item).

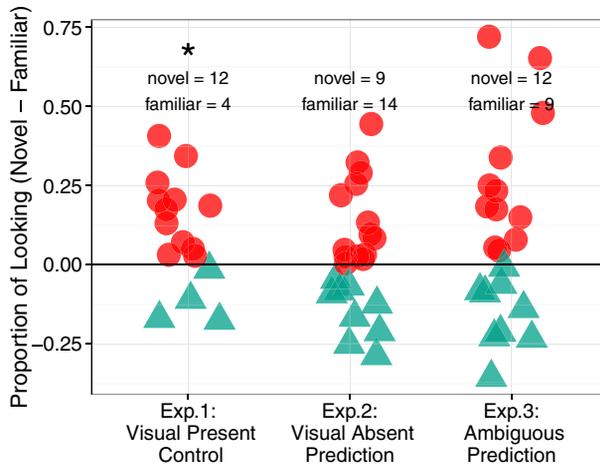


Figure 3 Representation of looking time preferences for each infant in all three experiments with points coded by their looking time preference ($* p < 0.05$; circle = longer looking to control shape or novelty preference; triangle = longer looking to experimental shape or familiarity preference).

EXPERIMENT 2: HOW VISUAL IS A VISUAL OMISSION?

Based on the results from Experiment 1, we now consider how visual activation from a predicted but absent visual stimulus (Emberson et al., 2015) affects infants’ evaluation of the relative frequency of that stimulus. To this end, we replaced the *additional* trials in Experiment 1 (where infants received additional visual experience with the experimental shape) with trials where infants hear the predictive auditory cue, but the

experimental shape was not presented. In these circumstances, previous neuroimaging work has found that the infant visual system (occipital cortex) is active when infants hear a sound that predicts a visual event after an audio-visual association (Emberson et al., 2015). Thus, the present experiment tests whether this visual system activity has an effect on perception. In other words, does visual prediction (i.e., elicited by the visual cue alone) bias visual recognition memory as visual perception of these stimuli in Experiment 1.

Methods

Participants

Twenty-five additional infants were recruited using the same methods described above (16 females; age: $M = 5.76$, $SD = .60$ months). All participants heard 100% English around their homes with the exception of one who reported hearing 95% English in their home. For race and ethnicity, 24 were reported as being “white” and one “black”; 23 participants were reported as being Non-Hispanic and two did not report their ethnicity. Two infants were excluded for failing to look 4-sec or more at the pre-test or post-test trials.

Procedure

The methods were identical to Experiment 1 with the exception that all *additional* trials presented the sound of the experimental pair only. In other words, the experimental shape was unexpectedly omitted during these trials. This design ensures that infants had equal visual experience with the two shapes (control, experimental: 25 times each), but infants experienced 23 additional trials where they heard the sound that predicted the experimental shape but not the additional visual experience of this shape. It is important to note that the majority of these additional trials occur at the end of the familiarization when infants will have formed the AV association and have strong predictions for a particular visual shape.

Results and discussion

As expected, infants did not differ in their looking to the two visual stimuli in the pre-test trials (proportion looking to experimental = 0.49, $SD = 0.10$, control = 0.51, $SD = 0.10$, $t(22) = -0.41$, $p = .68$). However, we also saw no difference in looking at the post-test trials (proportion looking to experimental = 0.49, $SD = 0.09$, control = 0.51, $SD = 0.09$). This was confirmed through both parametric ($t(22) = -0.73$, $p = .47$, Figure 2, middle column) and nonparametric tests (control/novelty preference = 9; experimental/familiarity preference = 14 infants; $V = 118$, $p = .56$, Figure 3, middle column). These results indicate that infants’ visual preference is being driven by the number of times they saw the item and is not influenced by the number of times that infants hear the predictive auditory cue for one of the shapes. In other words, visual prediction for one of the shapes does not influence infants’ visual memory for the predicted object as measured in this task.

Thus, compared to the visual presentation during the additional trials, visual prediction does not appear to have the same perceptual consequences. These results suggest

that visual prediction, despite activating the visual system of young babies (Emberson et al., 2015), is not “visual.” However, in the third experiment, we examine whether a visual prediction can bias a weak or ambiguous perceptual signal.

EXPERIMENT 3: AMBIGUOUS VISUAL INPUT

There is ample evidence that the brain, starting in infancy, generates predictions about upcoming sensory input that affect perceptual cortices. While the functions of these predictions are entirely unknown in infancy, and are the focus of the current study, there is some evidence that predictions bias the content of visual prediction but only in specific circumstances. In a review by Panichello, Cheung, and Bar (2013), the authors conclude that predictions can bias conscious perception under circumstances of uncertainty. In other words when the perceptual signal is not strong or clear, this provides an opportunity for prediction to bias what is being seen.

In this final experiment, we change our approach to be more in line with adult experiments which probe the effects of visual prediction under circumstances of perceptual uncertainty. We investigate whether an infant’s visual prediction can bias visual perception of a stimulus that is present but ambiguous and noisy (Figure 1). Specifically, we presented infants with a sound predicting a specific experimental shape, as in the previous two experiments, but, instead of omitting this stimulus, we showed them an image that combines both shapes embedded in noise. The intention of adding the noise and the ambiguity was to increase infants’ uncertainty about their sensory input and thus provide an opportunity for prediction to bias sensory processing toward the predicted visual input. These are the circumstances in which prediction or top-down processing has been found to bias visual perception in adults (see review by Panichello et al., 2013).

Methods

Participants

Twenty-eight additional infants were recruited using the same methods described above (15 females; age: $M = 5.29$, $SD = .42$ months). All participants heard 100% English around their homes. For race and ethnicity, 24 were reported as being “white,” two were Asian, and two chose not to report their race; 28 infants were reported as being Non-Hispanic. Three infants were excluded for failing to look 4-sec or more at the pretest or post-test trials, and three were excluded for being over two standard deviations from the mean looking time.

Procedure

The methods were identical to Experiment 2 with the exception that all *additional* trials presented an ambiguous visual image. This image was a merger of both the experimental and the control shapes (without their face) with visual noise added to weaken the visual signal (imnoise function in MATLAB salt and pepper at level 0.88). Then, the face was added on the surface of the ambiguous visual image. As with Experiment 2, this design ensures that infants had equal visual experience with the two

shapes (control, experimental: 25 times each), but infants experienced 23 additional trials where they heard the sound that predicted the experimental shape paired with the ambiguous visual input.

Results and discussion

As with the previous two experiments, infants had no visual preference for either stimulus during the pretest trials (proportion looking to experimental = 0.48, $SD = 0.12$, control = 0.52, $SD = 0.12$). At test, infants continued to have no preference for either of the stimuli. While the mean post-test looking times were similar to Experiment 1 when we did see a clear novelty preference (proportion looking to experimental = 0.45, control = 0.55), the standard deviation was larger in this sample ($SD = 0.14$), and correspondingly, this mean difference did not reach significance ($t(20) = -1.48$, $p = .15$, Figure 2 right panel). When examining the number of infants with novelty vs. familiarity preferences in the sample, it becomes clear that the mean difference is driven by a few infants, and broadly, the infants in this sample exhibit an equal preference for the stimuli (control/novelty preference = 12, experimental/familiarity preference = 9, $V = 83$, $p = .27$, Figure 3 right column). Indeed, when considering the data without these three infants, there is no hint of a preference (proportion looking to control = 0.50, familiar = 0.50, $t(17) = -0.11$, $p = .91$; nine infants each with control/novel and experimental/familiarity preferences). Thus, despite some suggestion in the means of the entire sample, further exploration reveals that this mean difference is driven by a minority of infants, and by and large infants are exhibiting an equal preference for both stimuli. Again, this suggests that the combination of the predictive auditory cue does not boost infants' visual memory even in the presence of a weak or ambiguous visual stimulus. Instead, infants' preference appears to be driven by the presented visual stimuli. Note that when considering the unambiguous stimuli (no noise) and the balanced nature of the ambiguous stimuli (with noise and both shapes present), the two visual stimuli were presented equally often in this experiment.

GENERAL DISCUSSION

Building from recent work that provided clear evidence of visual system activation when infants hear an auditory cue that predicts a visual stimulus (Emberson et al., 2015; Kouider et al., 2015), the current study uses behavioral methods to ask how *visual* is this visual-prediction activation? Specifically, we asked how much this neural activation of the visual system from a predicted visual stimulus contributes to visual recognition memory in infants. Experiment 1 established a baseline for comparison in which infants experience additional visual stimulation with the experimental shape (Figure 1). Infants showed a robust novelty response by looking longer to the control or less-frequent shape. Experiment 2 replaced this additional visual experience with visual prediction only (i.e., only the auditory cue was presented) and found no evidence of visual preference after familiarization, suggesting that visual prediction does not perform the same function as visual perception. Experiment 3 presented infants with the predictive auditory cue and a noisy, ambiguous sensory input to examine whether infants could use visual prediction to bias an uncertain visual signal. Again, we find no evidence that visual prediction biases uncertain visual perception by altering

looking time preferences after familiarization. Thus, overall, we find no evidence that visual prediction is *visual* in its function.

It is important to note that our experiments were designed to test the visual function of visual prediction in the strictest sense. In Experiment 2, we directly compared visual prediction based on an auditory cue to visual perception. While we found compelling evidence that prediction does not bias visual familiarity, it may have more transient effects on perception that do not propagate to the computation of stimulus frequency relevant to memory (and resultant novelty preferences). However, this fragility is not seen in the neural signals of visual prediction, which are robust across minutes of exposure (Emberson & Boldin, unpublished; Emberson et al., 2015).

In Experiment 3 the effects of visual prediction on the disambiguation of a perceptual signal were examined to assess top-down effects on perception. Indeed, recent work in adults has directly linked prediction to top-down effects on perception (Lupyan, 2015; Panichello et al., 2013). However, we found no effect of prediction that could be seen in looking preferences. While there have been many demonstrations of top-down influences on perception in adults (e.g., Lupyan & Ward, 2013), these effects are notoriously difficult to capture and require careful control of stimulus parameters (Firestone & Scholl, 2016), typically using input that is just beyond the threshold of conscious perception. In this case, it could be that the current test was too blunt to capture these subtle effects. Similarly, with infants it is difficult to perform the staircasing necessary to determine their precise threshold for perception, but ongoing work is incorporating both more rapid presentation at various levels of perceptual difficulty (Gelskov & Kouider, 2010) and staircasing methods (Jones, Kalwarowsky, Atkinson, Braddick, & Nardini, 2014) to investigate the effects of visual prediction on visual perception.

It should be noted that the current study is testing a strong case of visual prediction where we are investigating visual prediction for a specific object as opposed to visual prediction for a visual event more generally. The neural findings upon which this work is based (Emberson et al., 2015) do not differentiate between these two alternatives, and thus, it is possible that visual prediction does have a functional consequence but it is not specific enough to modulate perception and, consequently memory, for a specific shape as is being tested here. Future neuroimaging experiments could help answer this question by using multivariate analytic methods to determine whether the pattern of visual activation can be decoded for each of the two stimuli. In other words, this method would determine whether visual prediction is characterized by neural patterns that are specific to a stimulus or whether they are more general.

Another possibility is that prediction does not serve a perceptual function in infants. This would be a divergence from the many findings in adults that top-down signals can readily bias perception (e.g., Gilbert & Li, 2013). Perhaps the infant brain is not yet able to employ these signals to bias perception as it is in adults, and with better connectivity between regions later in development, the more mature brain may be able to use these signals to bias behavior. Another, not mutually exclusive, possibility is that prediction serves a function *other* than biasing perception. Recent work by Stahl and Feigenson (2015) linked violations of expectation with subsequent learning. One hypothesis consistent with their findings is that the stronger the prediction, the better infants can detect violations from this prediction and use this error signal to evaluate their internal model of the world and learn more about their environment. These prediction signals might be present in the visual system not to bias

perceptual processing but instead to help generate sophisticated error signals relevant to vision that propagate to the rest of the brain. This view of top-down signals is consistent with a predictive coding theory of the brain where each area of the brain compares the expectations relevant to that area (e.g., the visual expectations) with the incoming sensory input (e.g., the current visual stimulus, Friston, 2005; Rao & Ballard, 1999). However, while this theory is well articulated, the exact function of these signals is not clear.

How do these questions relate to the larger literature documenting that infants are quite sensitive to violations of expectation and, in general, exhibit longer looking to unexpected or novel stimuli? While changes of looking time based on violations of expectation provide evidence that infants are learning and engaging in some kind of novelty detection, they do not provide evidence about the nature of the mechanisms that support this process. Specifically, there is no in-principle reason why a violation of expectation should require feedback or predictive modulation of the visual system. For example, a violation of expectation could engage an entirely feed-forward process where a central pattern matcher beyond the visual system (e.g., in learning and memory systems) determines whether a stimulus is consistent with recent experience and, thereby, not involving modulation of the visual system in any way. Another possibility is that learning allows infants to engage in top-down predictions that directly modulate the visual system, thereby not only supporting a violation of expectation response but also facilitating changes in perception directly (e.g., Emberson et al., 2015). It is this latter possibility that has been investigated here. While we have found a suggestive null effect that visual prediction does not lead to greater visual familiarity, other perceptual functions of visual prediction will be investigated in future work (see above for a discussion).

Certainly, there are many complementary pathways by which learning can shape the developing mind and brain beyond what is being investigated here. Relevant to the multisensory associative learning that is the basis for this study, previous work has found that the auditory only cue from an audiovisual association can result in biases of eye movements in 6-month-olds (e.g., Richardson & Kirkham, 2004). This is an example where multisensory learning can affect perception through biasing eye movements in a feedforward fashion and are likely distinct from the top-down or feedback changes that are being investigated here. While distinct, there are complementary ways in which learning can shape the developing brain and allow infants to more efficiently and effectively process their sensory input as a result of experience.

In sum, we investigated the effects of visual prediction on visual perception. This work follows from recent neuroimaging results showing that 6-month-old infants activate their visual system during anticipation of an expected visual event (Emberson et al., 2015). We found that visual perception biases looking time preferences (Experiment 1) but visual prediction alone does not bias looking time (Experiment 2), nor does visual prediction in the presence of a noisy, ambiguous stimulus (Experiment 3) alter computations of stimulus frequency. Overall, we find no evidence that visual prediction is visual in function in the context of the current experimental design. This study opens the door for future investigations with other paradigms to investigate how visual prediction is as well as other potential functions of prediction (e.g., learning, error detection).

ACKNOWLEDGMENTS

First and foremost, thank you to all the infants and caregivers who volunteered their time to participate in the current study! Thank you to Holly Palmeri for your amazing help, as always. Thank you to Dan Swingley for feedback on these findings and palette introductions. This work was funded by NICHD (K99 HD076166-01A1/4R00HD076166-02) and a Canadian Institutes of Health Research (CIHR) postdoctoral fellowship to (to L.L.E.), and NIH Grant R01 HD-37082 and NSF EAGER BCS-1514351 (to R.N.A.).

REFERENCES

- Albers, A. M., Kok, P., Toni, I., Dijkerman, H. C., & De Lange, F. P. (2013). Shared representations for working memory and mental imagery in early visual cortex. *Current Biology*, *23*, 1427–1431.
- Bergelson, E., & Swingley, D. (2015). Early word comprehension in infants: Replication and extension. *Language Learning and Development*, *11*, 369–380.
- Conway, C. M., Bauernschmidt, A., Huang, S. S., & Pisoni, D. B. (2010). Implicit statistical learning in language processing: Word predictability is the key. *Cognition*, *114*, 356–371.
- Cui, X., Jeter, C. B., Yang, D., Montague, P. R., & Eagleman, D. M. (2007). Vividness of mental imagery: Individual variability can be measured objectively. *Vision Research*, *47*, 474–478.
- de Haan, M., & Nelson, C. A. (1997). Recognition of the mother's face by six-month-old infants: A neurobehavioral study. *Child Development*, *68*, 187–210.
- den Ouden, H. E. M., 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.
- 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 of the United States of America*, *112*, 9585–9590.
- Firestone, C., & Scholl, B. (2016). Cognition does not affect perception: Evaluating the evidence for “top-down” effects. *Behavioral and Brain Sciences*, *39*, e229.
- Friston, K. (2005). A theory of cortical responses. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences*, *360*, 815–836.
- Gelskov, S. V., & Kouider, S. (2010). Psychophysical thresholds of face visibility during infancy. *Cognition*, *114*, 285–292.
- Gilbert, C. D., & Li, W. (2013). Top-down influences on visual processing. *Nature Reviews Neuroscience*, *14*, 350–363.
- Graf Estes, K., Evans, J. L., Alibali, M. W., & Saffran, J. R. (2007). Can infants map meaning to newly segmented words? Statistical segmentation and word learning. *Psychological Science*, *18*, 254–260.
- Jones, P. R., Kalwarowsky, S., Atkinson, J., Braddick, O. J., & Nardini, M. (2014). Automated measurement of resolution acuity in infants using remote eye-tracking. *Investigative Ophthalmology and Visual Science*, *55*, 8102–8110.
- Kidd, C., Piantadosi, S. T., & Aslin, R. N. (2012). The Goldilocks effect: Human infants allocate attention to visual sequences that are neither too simple nor too complex. *PLoS One*, *7*, e36399.
- Kirkham, N. Z., Slemmer, J. A., & Johnson, S. P. (2002). Visual statistical learning in infancy: Evidence for a domain general learning mechanism. *Cognition*, *83*, B35–B42.
- Kok, P., Failing, M. F., & de Lange, F. P. (2014). Prior expectations evoke stimulus templates in the primary visual cortex. *Journal of Cognitive Neuroscience*, *26*, 1546–1554.
- Kouider, S., Long, B., Le Stanc, L., Charron, S., Fievet, A., Barbosa, L. S., & Gelskov, S. V. (2015). Neural dynamics of prediction and surprise in infants. *Nature Communications*, *6*, 8537.
- Lee, S. H., Kravitz, D. J., & Baker, C. I. (2012). Disentangling visual imagery and perception of real-world objects. *NeuroImage*, *59*, 4064–4073.
- Lupyan, G. (2015). Cognitive penetrability in the age of prediction: Predictive systems are penetrable systems. *Review of Philosophy and Psychology*, *6*, 547–569.

- Lupyan, G., & Ward, E. J. (2013). Language can boost otherwise unseen objects into visual awareness. *Proceedings of the National Academy of Sciences of the United States of America*, *110*, 14196–14201.
- Maye, J., Weiss, D. J., & Aslin, R. N. (2008). Statistical phonetic learning in infants: Facilitation and feature generalization. *Developmental Science*, *11*, 122–134.
- Panichello, M. F., Cheung, O. S., & Bar, M. (2013). Predictive feedback and conscious visual experience. *Frontiers in Psychology*, *3*, 620.
- Rao, R. P. N., & 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.
- Richardson, D. C., & Kirkham, N. Z. (2004). Multimodal events and moving locations: Eye movements of adults and 6-month-olds reveal dynamic spatial indexing. *Journal of Experimental Psychology. General*, *133*, 46–62.
- Saffran, J. R., Aslin, R. N., & Newport, E. L. (1996). Statistical learning by 8-month-old infants. *Science*, *274*, 1926–1928.
- Stahl, A. E., & Feigenson, L. (2015). Observing the unexpected enhances infants' learning and exploration. *Science*, *348*, 91–94.