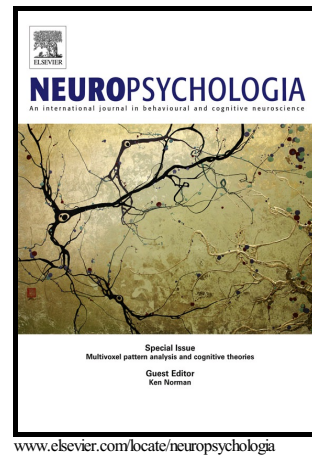# Author's Accepted Manuscript

Sensitivity to structure in action sequences: An infant event-related potential study

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Sensitivity to structure in action sequences: An infant event-related potential study

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Abstract

Infants are sensitive to structure and patterns within continuous streams of sensory input. This sensitivity relies on statistical learning, the ability to detect predictable regularities in spatial and temporal sequences. Recent evidence has shown that infants can detect statistical regularities in action sequences they observe, but little is known about the neural process that give rise to this ability. In the current experiment, we combined electroencephalography (EEG) with eye-tracking to identify electrophysiological markers that indicate whether 8-11-month-old infants detect violations to learned regularities in action sequences, and to relate these markers to behavioral measures of anticipation during learning. In a learning phase, infants observed an actor performing a sequence featuring two deterministic pairs embedded within an otherwise random sequence. Thus, the first action of each pair was predictive of what would occur next. One of the pairs caused an action-effect, whereas the second did not. In a subsequent test phase, infants observed another sequence that included deviant pairs, violating the previously observed action pairs. Event-related potential

(ERP) responses were analyzed and compared between the deviant and the original action pairs. Findings reveal that infants demonstrated a greater Negative central (Nc) ERP response to the deviant actions for the pair that caused the action-effect, which was consistent with their visual anticipations during the learning phase. Findings are discussed in terms of the neural and behavioral processes underlying perception and learning of structured action sequences.

Keywords: statistical learning, infant event-related potentials, action sequences, eye-tracking, social-cognitive development

1.0 Introduction

Infants face the constant challenge of perceiving meaningful events within the complex action sequences they observe. Human actions contain inherent statistical regularities, characterized by predictable patterns that result in specific goals or outcomes. For instance, the everyday action of 'drinking tea' always consists of the same sequence: grasping a kettle, heating water, adding milk (if you are British), and so forth. Sensitivity to sequential regularities forms the basis for the ability to predict action goals, their outcomes, and to adaptively respond during social interactions. In fact, infant's growing abilities to understand the social world may arise initially from their statistical learning skills (Ruffman et al., 2012).

Recent studies have investigated infants' sensitivity to different kinds of statistical information in actions they observe. Paulus and colleagues (2011) showed that 9-month-olds used frequency information from prior observations to predict where an agent would reappear along a path after disappearing (Paulus et al., 2011). In another experiment (Stahl et al., 2014), 18-month-olds viewed action sequences comprised of three-step deterministic action 'units' (example: A-B-C and D-E-F). Afterwards, they were tested on their ability to

discriminate intact units (A-B-C) and 'part-units', which featured lower transitional probabilities (example: C-D-E). Their results showed that 18-month-olds successfully discriminated between units and part-units, indicating that they successfully segmented the action sequence according to its transitional probabilities.

Further behavioral studies show that infants can detect regularities in visual events and actions from the statistical information alone, independently from physical or movement cues (Baldwin et al., 2001; Hespos et al., 2009; Kirkham et al., 2002; Saylor et al., 2007). One hypothesis arising from this evidence is that infants initially rely on statistical learning skills to predict upcoming events based on sequential regularities, and that these skills precede the ability to form conceptual expectations about goal-directed actions (Hunnius and Bekkering, 2014). In other words, infants first learn that someone grasping a mug typically pours tea before drinking, which in turn enables them to predict that the mug will be brought to the mouth, and ultimately leads to a meaningful concept of the act of 'drinking tea'.

The sensory consequences of an action—action-effects—are a central feature of goal-directed action. As in the tea example, each step is associated with a change in the sensory environment such as the sound of the pouring tea. The development of infants' understanding of goal-directed actions may primarily emerge through repeated observation of actions and their perceptual effects (Hunnius & Bekkering, 2014). Prior behavioral studies illustrate that action-effects are critical in guiding how infants perceive and learn about action events (Jovanovic et al., 2007; Klein et al., 2006; Verschoor et al., 2010). However, though they may enhance learning or induce changes in behavior, action-effects may not be necessary for infants to initially learn the regularities in observed action sequences. Some research has shown that infants and adults demonstrate neural responses to sequential events based only on their statistical likelihood (Abla & Okanoya, 2009; Teinonen et al., 2009). Given these findings there is no reason to expect infants could not do so for action sequences as well,

though they might acquire a stronger association between sequential actions that cause action-effects for several reasons. First, infants are drawn to contingency, and action-effects are salient sensory events that are also contingent upon the action causing them (Gergely & Watson, 1999, 1996). Second, action-effects may be perceived as goals and draw attention to the actions that precede them, as action goals have a powerful influence on how infants subsequently process observed actions (Henderson & Woodward, 2011). In the current study, we compared event-related potential (ERP) responses, as described below, to sequential actions that either did or did not cause a salient visual effect.

The ERP technique has made it possible to explore the neural mechanisms that support action processing in infants. ERPs are voltage oscillations in the electroencephalography (EEG) signal that are time-locked to the onset of perceived events (Luck, 2014). Components can be identified in the ERP waveforms that mark specific stages of perceptual and cognitive processes in infants (for a review, see de Haan, 2007). Two ERP components are particularly relevant for research on infant action processing: the Negative central (Nc) and the N400, which reflect visual attention and semantic processing, respectively (Kaduk et al., 2016; Pace et al., 2013; Reid et al., 2009).

The Nc component has been interpreted as a marker of attention orientation towards salient stimuli and is often larger in response to novel or unexpected stimuli (e.g., Courchesne, 1977; Karrer & Monti, 1995; for a review, see Reynolds, 2015). The Nc emerges shortly after birth (Karrer & Monti, 1995), and between 3 to 6 months infants begin to show a stable Nc response that is larger for novel compared to familiar stimuli (except in certain cases, such as a mother's face or emotionally salient stimuli; de Haan & Nelson, 1997). Increased negative amplitude is thought to reflect increased allocation of attention towards the stimulus (Courchesne et al., 1981; Richards, 2003). The Nc manifests as a negative deflection in the ERP waveform at central and midline electrodes, peaking between 250 and 750ms

following stimulus onset (de Haan, 2007). The neural generators of the Nc are presumed to be prefrontal and frontal regions related to attention and memory systems, reflecting cortical allocation of attention resources (Reynolds et al., 2010).

The N400 component is observed in both adults and infants during processing of 'meaningful' stimuli; that is, stimuli that grant access to semantic, or conceptual, knowledge (e.g., Reid & Striano, 2008; van Elk et al., 2014, 2009). The N400 is characterized by a negative peak that is largest over a central-parietal scalp distribution and is sensitive to semantic incongruence (for a review, see Kutas & Federmeier, 2011). N400 effects have been reported in infants as young as 9 months of age, with a peak latency that is delayed relative to the adult component (Kaduk et al., 2016; Parise & Csibra, 2012; Reid et al., 2009). By 14 months of age, N400 effects become more robust and are elicited in a broader range of modalities and conventional paradigms (Friedrich & Friederici, 2005, 2004). Infants display an N400 response following an action outcome that is strange within the semantic context, such as bringing a spoonful of food to one's forehead and is thus thought to be functionally similar to the adult N400. N400 effects during action observation indicate a violation of an expected action outcome (Kaduk et al., 2016; Reid et al., 2009).

The current experiment used ERPs to investigate learning during observation of action sequences containing statistical regularities. Infants of 8-11 months of age experienced a learning and test phase. The learning phase consisted of a continuous video of an action sequence, featuring two deterministic pairs embedded within an otherwise random sequence. At test, infants observed another sequence that included two novel 'deviant' pairs, which should violate their predictions if they had successfully learned the pairs. If infants perceive these deviants as violations of the expected sequential order, this should result in an enhanced Nc response to the deviant, relative to the original pairs, due to increased attention following the violation. We further hypothesized that these responses would be stronger for the pair

associated with the action-effect. Finally, sequence violations might also elicit an N400 response, which would indicate that statistical regularities could provide the contextual information needed for storing semantic knowledge about the expected action sequence.

The current study implemented eye-tracking in addition to EEG measurements to assess whether infants also made predictive eye movements towards upcoming actions prior to their onset as the action sequence unfolded. Specifically, we examined whether infants looked toward the second action of a pair—or the action effect, for the Effect pair—during the first action of the pair. This measure provided a behavioral indicator of learning and extended results from prior research with 18-month-old infants (Monroy et al., 2017). As an exploratory measure, we related the eye-tracking to the EEG measures to further clarify the neural correlates of learning.

In sum, our primary aim in the current study was to identify novel electrophysiological evidence for statistical learning during observation of action sequences and identify whether they relate to behavioral indicators of learning. Our second goal was to identify the presence of ERP components associated with specific attention and/or semantic processes during action observation.

2.0 Method

2.1 Participants

Fourteen infants were included in the final sample for the ERP analysis ($M = 10.9$ months, *range*: 8.9-11.9 months, 9 males). Of these, seven infants were included in the final sample for the eye-tracking analysis ($M = 10.4$ months, *range*: 9.1-11.9 months, 3 males). An additional 8 infants contributed complete datasets from eye-tracking but not EEG measurements ($N = 15$, $M = 10.3$ months, *range*: 9.0-11.9 months, 6 males). All infants were recruited from a database of families interested in participating in developmental research. Although no demographic information was collected, the families were representative of the

population of the small European city in which the data was collected (i.e., largely Caucasian and middle-class). Written informed consent was acquired from all parents, and families received a thank-you gift of 10£ for participation. Fourteen additional infants were excluded from the ERP analysis due to insufficient artifact-free trials (given a minimum criterion of three trials per condition, $N = 9$) or excessive fussiness ($N = 5$). This attrition rate (50%) is typical for EEG experiments with young infants (cf. Hoehl & Wahl, 2012; Meyer et al., 2015). An additional eighteen infants visited the lab but were unable to participate in the experiment due to equipment failure. Our final sample size was therefore smaller than the number we had aimed for *a priori*, though it is nevertheless consistent with prior infant EEG experiments reporting an Nc effect (e.g., Courchesne, Ganz, & Norcia, 1981; Parise, Handl, Palumbo, & Friederici, 2011; van Hoogmoed, van den Brink, & Janzen, 2013).

2.2 Stimuli

2.2.1 Learning Phase

Infants were first shown a video of an adult agent performing an action sequence with a novel toy, in which only the actor's hand was visible on screen (Figure 1). The toy featured six unique objects and a central star-shaped light. An action was defined as the manipulation of one object. Stimulus movies were filmed with a Sony HandyCam video camera and edited using Adobe Premiere Pro Cs5 software. All stimuli were presented on a screen with a resolution of 600 x 800 pixels, and a visual angle of 35 x 20 degrees.
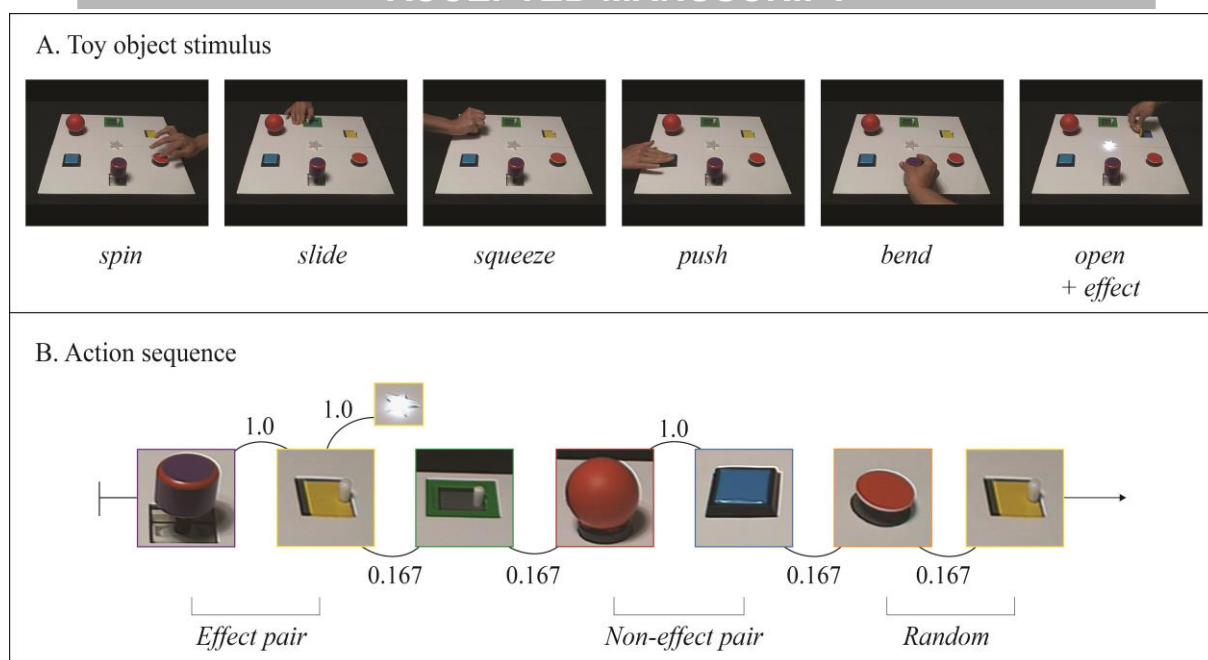
Figure 1. A: Example frames depicting each action. B: Sequence structure and action pairs. Numbers represent the transitional probabilities between actions. In (B) images are enlarged for clarity; infants actually observed the stimuli as in (A).

The sequence structure was defined according to the transitional probabilities between action steps. Two action pairs featured deterministic transitions (i.e. action 'A' followed action 'B' with 100% predictability), whereas transitions between unpaired actions had a 0.167 (1/6) probability. One of the deterministic pairs caused a light to turn on during the second action; the second pair did not cause any effect. We refer to these, respectively, as the 'Effect' and 'No-effect' pairs. For both pairs, the second actions were defined as *target actions*, as these were the events that became predictable during the unfolding of the sequence. We constrained the sequence such that no action or pair occurred more than three times consecutively, and such that all events occurred with equal frequency for a total of 12 repetitions of every action and pair. Importantly, target actions also occurred elsewhere in the sequence outside of their pairs, to ensure that infants would need to learn the two-step pair structure rather than only associating the effect with the target action. The actions that defined

the Effect and No-effect pairs were counterbalanced in two sets of videos, and infants were randomly assigned to one stimuli set.

For each action, the actor's hand entered the screen near the object, performed the action, and exited the screen in the same place. A brief pause occurred between actions, during which the object was viewed with no hand present. The onset of the light (effect) occurred at a natural mid-point of the target action during the Effect pair and ended when the action was completed. For example, during the target action 'open', the light went on the moment the small yellow door was fully open, and went off again as the hand closed the door.

Each video was divided into four blocks of 24 actions (with approximately 3 trials of each pair in each block) with the viewing angle oriented from a different side of the toy box in each block to ensure that the object location on the screen did not become a predictable cue. At the beginning of a block, one still frame of the object was presented with no hand visible to help the infant reorient to the new perspective. In total, the entire learning phase lasted approximately six minutes. Engaging, upbeat music was played throughout the entire sequence that did not correspond in any way to the unfolding action sequence.

2.2.2 Test Phase

Still frames were selected from the videos that were representative of the mid-point of each action for the test phase. The test phase consisted of one block of 144 images, in which the target action of each pair was replaced on half of the trials by a different action. For example, if the Effect pair during the learning phase was *bend-open*, infants saw *bend-open* and *bend-slide*, with both target images *open* and *slide* featuring the effect (Figure 2).
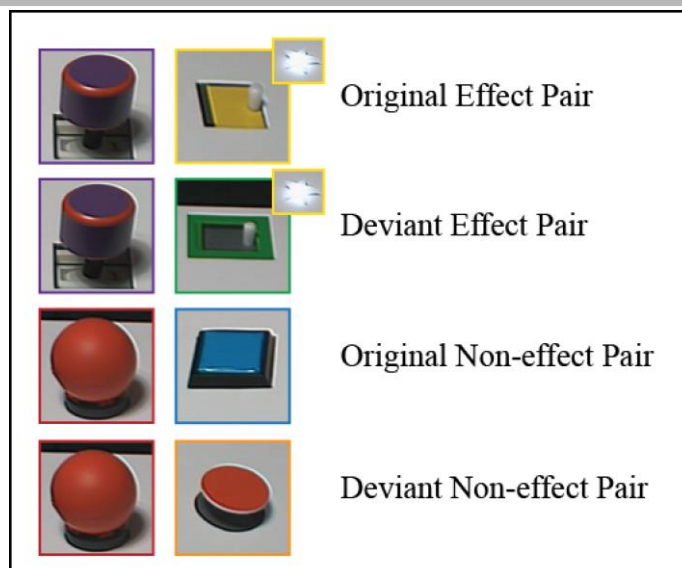
Figure 2: Test conditions: examples of the original and deviant action pairs (images enlarged for clarity; infants observed the display as they had seen it during the learning phase).

2.3 Procedure

Parents and infants were invited into the lab and first given the opportunity to become comfortable with the new surroundings. After the procedure was explained, parents provided written informed consent. Infants sat on their parent's lap throughout all phases of the study. After preparing the EEG net, parents were instructed to refrain from influencing their child during the experiment. The entire session was videotaped with the camera positioned behind and to the right of the presentation screen, with full view of the child and parent. Although we only analyzed the eye-tracking data from the learning phase, both EEG and eye-tracking data were recorded throughout both phases of the experiment. This allowed us to perform calibration and prepare the EEG cap at the beginning of data collection and avoid disrupting the flow of the experiment and potentially causing infants to become fussy.

2.3.1 EEG Acquisition and Processing

EEG was recorded continuously with the Electrical Geodesics Incorporated (Eugene, Oregon, USA) 128-channel recording system (Net Station 4.1.1). The EEG signal was

referenced to the vertex and recorded with a 0.1-100 Hz band-pass filter and a sampling rate of 500Hz. Data was preprocessed using Net Station 4.3 Waveform Tools. Recordings were digitally filtered with a 0.3-Hz high-pass filter and a 30-Hz low-pass filter, and were segmented from 200ms before to 1000ms after the stimulus onset (the test image) for each trial. Consistent with standard practices in the field, segments were visually inspected to exclude EEG artifacts such as noisy channels (e.g., channels with consistent high-frequency noise or a flat line indicating loss of signal) or artifacts caused by eye and body movements (Hoehl & Wahl, 2012). Any segments in which infants were not attending to the screen based on video recordings of the session were rejected. Participants were required to have at least three artifact-free trials per experimental condition (Figure 2) to be included in further analyses. This trial inclusion criterion was selected based on previous evidence that reliable Nc and N400 effects with infants are found with as few as three to seven trials per condition (Kaduk et al., 2013, 2016; Missana et al., 2014; Stets and Reid, 2011). The mean number of artifact-free EEG trials contributed by infants across conditions was 6.27 (range = 3–11). For each condition, the mean number of trials contributed was as follows: Deviant$_{Effectpair}$ = 5.57 (SD = 1.55), Original$_{Effectpair}$ = 6.07 (SD = 2.53), Deviant$_{Noneffectpair}$ = 6.43 (SD = 2.1), Original$_{Noneffectpair}$ = 7.07 (SD = 2.1). The mean number of trials did not differ significantly between the compared conditions.

2.3.2 Eye-Tracking

Eye movements were recorded using a Tobii TX300 eye-tracker (Tobii, Stockholm, Sweden) at 120Hz with a spatial filter of 40 pixels and a temporal filter of 100ms. First, a 5-point calibration sequence was repeated until valid calibration data was acquired for at least four points or a maximum of three attempts. Following calibration, infants watched the learning video and then were immediately shown the test phase following a brief (<1s) pause during which they observed a blank screen. During the test phase, the experimenter could

initiate attention-grabbers when the infant looked away from the stimuli, or a pause if the infant became distressed. Attention-grabbers were only implemented during the test phase— thus, the learning phase was never interrupted by them—and they could only be initiated during a fixation image so as not to further disrupt the sequence. Following attention-grabbers, the sequence resumed from where it had left off. Video stimuli were presented using Psychtoolbox for Matlab and a custom-made application written using Python. Sounds were played through external speakers.

During the test trials, infants were assigned to either a gaze-contingent or automatic presentation group. This was due to the sample also being used for a separate, unrelated methodological study (in the final ERP sample, there were 8 infants in the gaze-contingent condition and 6 infants in the automatic condition). In both groups, each test trial began with a fixation image presented at a size of 3º x 3.7º in the location of the upcoming action (Figure 3). We chose to present the fixation image in the target location in order to avoid eye movements towards the target because eye movements could distort the EEG signal and interfere with ERP components (Hoehl and Wahl, 2012). In the gaze-contingent condition, the test image was immediately presented only if the infant was looking at the fixation image. If the child was looking away, the fixation image would wiggle and play a jingling sound until the infant looked at the target location, or for a maximum of 4*s*. Trial duration thus ranged from 2*s* to a maximum of 6*s*. In the automatic condition, the fixation image remained for 1*s* before the next image automatically appeared. Each trial thus lasted for a total fixed duration of 2*s*. In both conditions, the test image was presented for an identical duration (1*s*); only the duration of the fixation image varied.
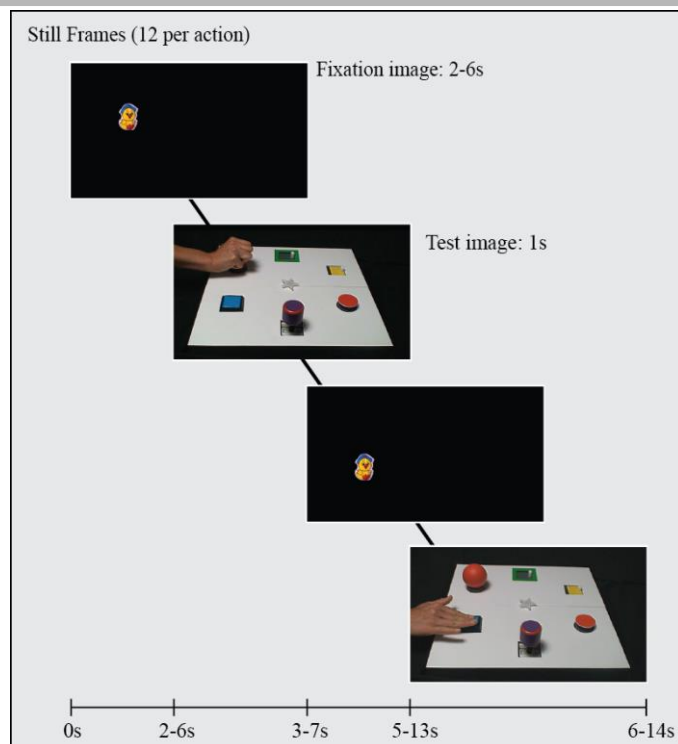
Figure 3: Two example trials from the test phase.

3.0 Data Analysis

3.1 ERP Analysis: Test Phase

To identify the presence of an Nc component during the test trials, mean minimum amplitude of the ERP was calculated in selected channel groups (Figure 4) from 250-750ms post-stimulus, consistent with prior work on this component (Reid et al., 2009; Richards, 2003). There is a lack of consistency among the infant studies that report an Nc effect; thus, we attempted to select a time window *a priori* that was consistent with most studies featuring a paradigm closest to our own. As the prefrontal cortex and anterior cingulate cortex have been suggested as the cortical source of the Nc, we expected to find a widespread frontal and central topography in our participant group (Reynolds & Richards, 2005). We confirmed our time window and channel group selection by visual inspection of the grand average waveforms. Mean amplitude was analyzed via a 2 (Pair: Effect, No-effect) x 2 (Condition: Deviant, Original) x 4 (Channel Location: Central, Frontal Midline, Frontal Left, Frontal

Right) ANOVA. Interactions were followed up with pairwise comparisons of estimated marginal means.
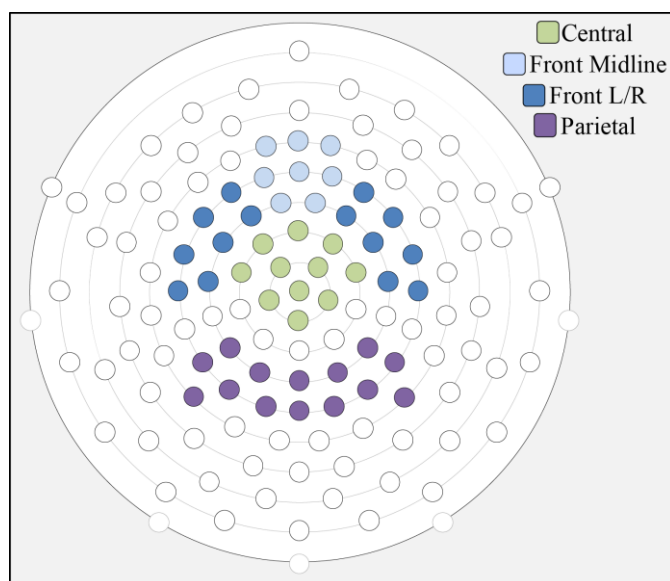

Figure 4: An illustration of the EGI 128-channel groups selected for the ERP analysis. Central and frontal channel groups (blue and green) were selected for the Nc analysis; parietal channels (purple) were selected for the N400 analysis.

For identification of the N400 component, we selected *a priori* the procedure outlined by Reid and colleagues (2009) that suggests a time-window analysis as a more appropriate statistical method when there is a defined peak in one condition but not the other. This method analyzes the variation in ERP amplitude across time-window samples between conditions and reveals the ERP effect of interest as an interaction between condition and time (for full details, see Hoormann et al., 1998). Though the N400 has a broader topography in adults, in infants it has been only observed in parietal regions most likely due to masking by the Nc component (Reid et al., 2009). For our analysis, we selected a time window from 500-700 after stimulus onset in parietal channels, as suggested in Reid et al. (2009). After normalizing the data as suggested in Hoorman et al. (1998), variance of the ERP amplitude was analyzed

using a 2 (Pair: Effect, No-effect) x 2 (Condition: Deviant, Original) x 17 (Time: one sample per 12ms) ANOVA.

3.2 Eye Tracking Data: Learning Phase

Eye movement data from the learning phase were analyzed to assess anticipatory gaze fixations to upcoming target actions during predictive time windows. These were defined as the frame when the agent's hand appeared in order to perform the first action of a deterministic pair until immediately before it reappeared for the target action (Figure 5). This corresponds to the time in which the observer has enough information about what the next action will be to make a prediction about the upcoming location before the subsequent action occurs (Monroy et al., 2017). For both action pairs, we excluded the first trial for each pair, as infants should not be able to make a prediction based on prior information during the first trial. Thus, 11 trials were included in the final analysis for each deterministic pair. Infants observed an average of 6.5 (*SEM* = 0.63) repetitions of the Effect pair and 6.08 (*SEM* = 0.64) repetitions of the No-effect pair during the learning phase. Thus, we did not apply an inclusion criterion based on looking time from the learning phase, given that previous research has shown that infants can learn these types of regularities within very few trials (Monroy et al., 2017).
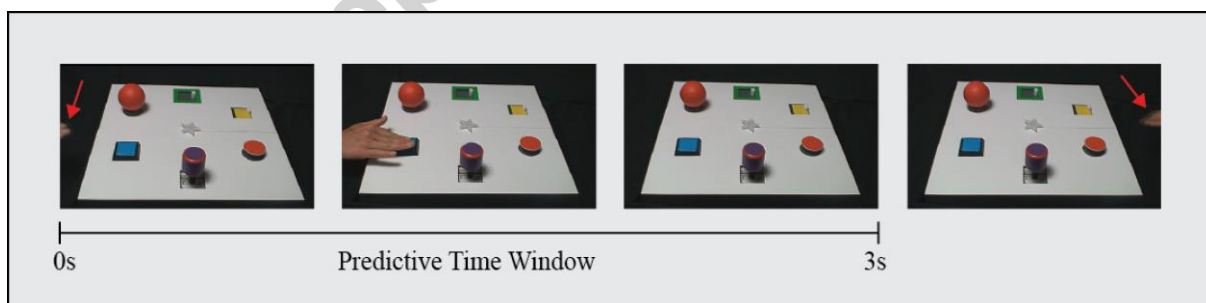

Figure 5: Example frames illustrating the predictive time window during the learning videos. Red arrows indicate the first frame in which the agent's hand appears.

Regions of interest (ROI) of equal size were defined around each stimulus object. Fixations to the ROI of the target action during the predictive time window were counted as correct, and fixations to any other ROI were incorrect. Fixations to the object currently being manipulated were excluded from calculations. For the Effect pair, fixations to the star were counted as correct; for the No-effect pair, they were excluded (Eqs. 1-4).

If infants learned the pair associations, they should look more to the target object of each pair than to all other objects during the first action. For each pair, we calculated the proportion of correct or incorrect fixations, out of the sum of all fixations within predictive time windows. For incorrect fixations, we summed the total fixations to the four alternative locations and divided by four to yield the average number of fixations to an incorrect region.

Effect Pair:

$$Correct = \frac{\# \, fixations \, to \, target \, \& \, effect}{total \, \# \, fixations \, to \, all \, objects \, \& \, effect} \qquad (1)$$

$$Incorrect = \frac{\# \, fixations \, to \, other \, 4 \, objects/4}{total \, \# \, fixations \, to \, all \, objects \, \& \, effect} \qquad (2)$$

No-effect Pair:

$$Correct = \frac{\# \, fixations \, to \, target}{total \, \# \, fixations \, to \, all \, objects} \qquad (3)$$

$$Incorrect = \frac{\# \, fixations \, to \, other \, 4 \, objects/4}{total \, \# \, fixations \, to \, all \, objects} \qquad (4)$$

Equations 1-4. Calculations of the proportion measures. For the effect pair, the effect ROI was included for the number of correct looks and the total number of looks ('all ROIs') while for the No-effect pair it was not included in the total number ('all objects').

4.0 Results

4.1 Event-related potentials

4.1.1 Negative central

The Nc component was found as a clear negative peak located in frontal and central electrodes, peaking at approximately 400ms following stimulus onset (Figure 6). Latency and amplitude of the peak were analyzed separately. No significant effects were found for Nc latency, indicating that the ERP peak amplitude featured a similar time course across conditions and pairs. For peak amplitude, the ANOVA analysis revealed a significant interaction between Pair and Condition, $F(1, 13) = 7.09$, $p = .02$, $\eta_p^2 = .35$. For the Effect pair, Nc amplitude was significantly greater following the deviant compared to the original targets (*mean difference* = 4.23μV, *SE* = 1.26, $p = .005$). For the No-effect pair, no differences were found between deviant and original targets (*mean difference* = -0.47μV, *SE* = 1.57). As can be seen in Figure 6 (top), the response elicited by deviants of the Effect pair featured a clear peak that was more negative in amplitude relative to original actions; this pattern does not vary across frontal and central electrodes.
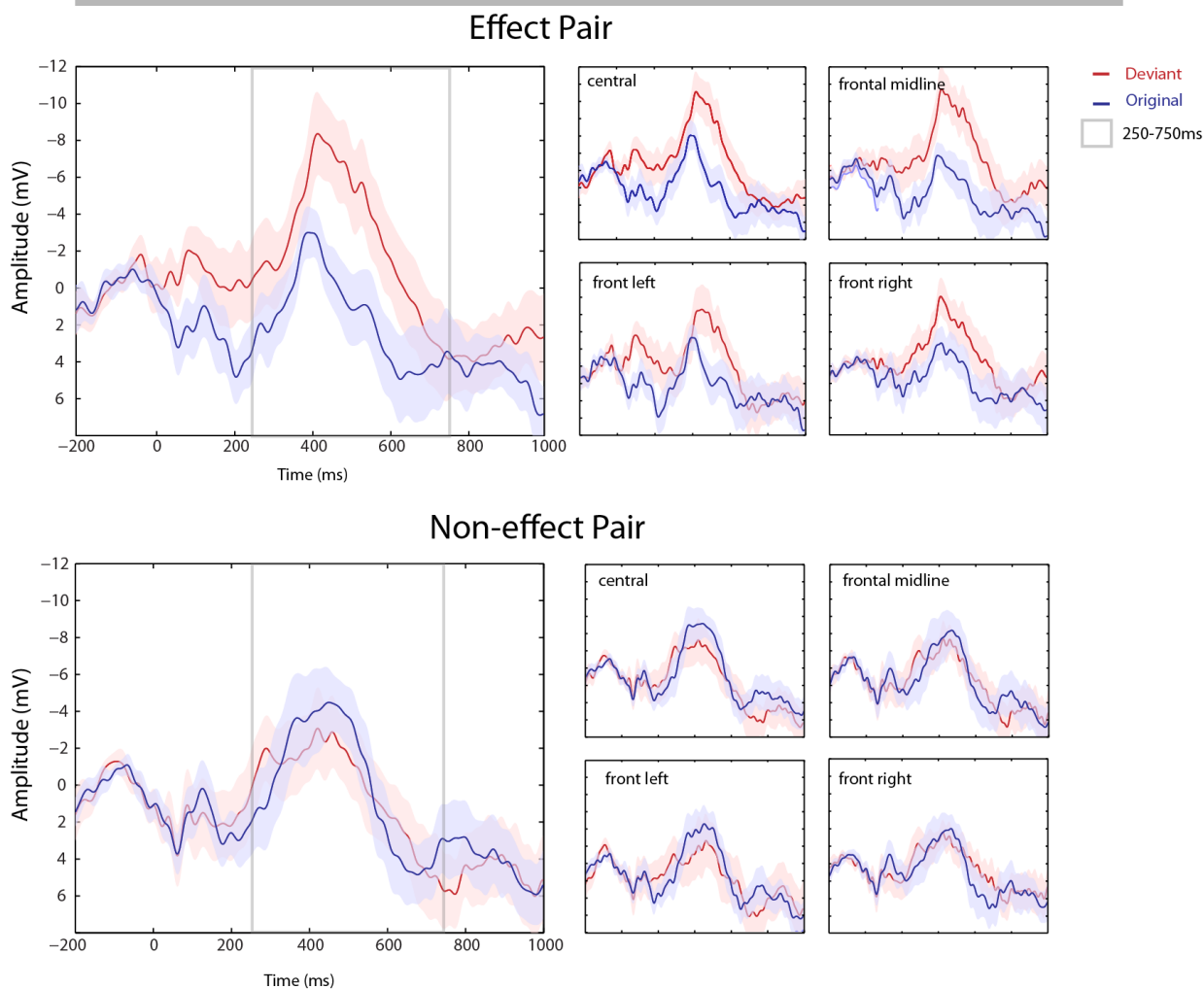
Figure 6: The grand average event-related potential (ERP) waveforms over frontal and central channels. The larger plots (left) display the average across all channel groups selected for analysis. Gray rectangles indicate the time window of analysis for the Nc component (250-750ms). The smaller plots (right) display the waveforms for each of the four channel groups (see Figure 4). Shaded regions indicate standard errors. Negative is plotted up.

Data were collapsed across the automatic and gaze-contingent groups. To verify there were no differences in the Nc amplitude because of stimulus presentation during the test phase, the ANOVA was repeated with Presentation (Gaze-contingent vs. Automatic) as a between-subjects factor. There were no significant main effects or interactions with

Presentation (*ps* > .24) confirming that the Nc amplitude during experimental trials of interest were not different between infants who observed gaze-contingent and automatic conditions.

4.1.2 N400

We found no clear evidence for an N400 effect in the grand averaged waveforms based on either statistical analyses or visual inspection of the expected channel region (Figure 7). During the time window of interest, there was no interaction effect between Pair, Condition, and Time (*p* = .37), confirming that the variation in ERP amplitude across time window samples did not differ between conditions and this was consistent across pairs. There were no other interaction effects with time or condition (*ps* > 0.27). To confirm this null finding, we also repeated this analysis using the standard technique commonly reported in the adult literature. We extracted the mean amplitude during the time window of interest (500-700ms) over the same channel groups and performed a 2 (Condition: Deviant, Original) x 3 (Channel: Pz, P3, P4) ANOVA, that also indicated no main effects or interactions with Condition (*ps* > .25).
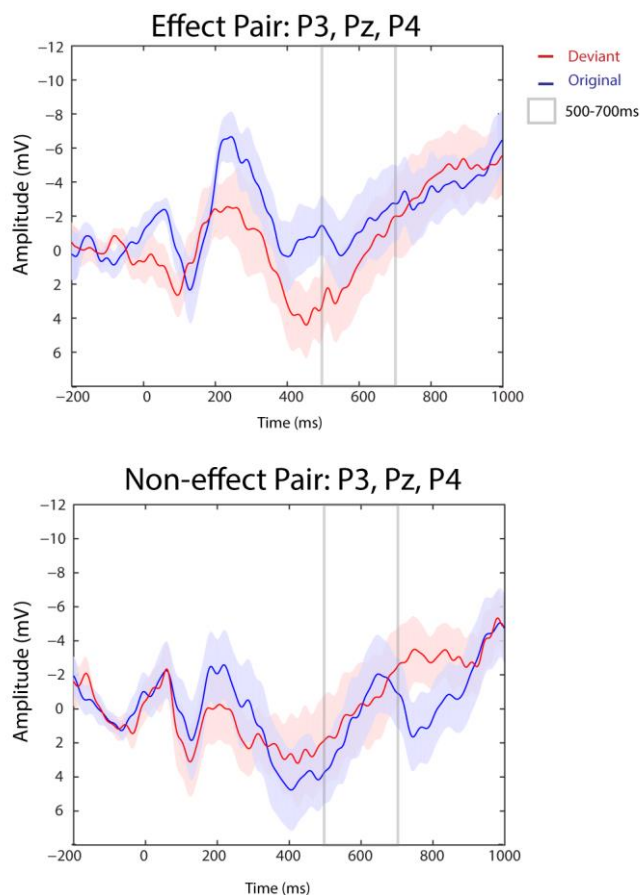
Figure 7. The grand average event-related potential (ERP) waveforms over parietal channels. The larger plots (left) display the average across all electrodes selected for analysis. Gray rectangles indicate the time window of analysis for the N400 component (500-700ms). Shaded regions indicate standard errors. Negative is plotted up.

4.2 Eye Tracking Results: Learning Phase

Data were collapsed across the automatic and gaze-contingent groups, as there were no differences in the stimulus presentation between these groups during the learning phase. Across pairs, predictive fixations accounted for 60.22% of all gaze fixations and the remaining 39.78% were fixations to the action currently occurring on screen. There were no significant differences between the mean percentage of predictive looks for the Effect and No-effect pairs ($p = .88$). A 2 (Pair: Effect, No-effect) x 2 (Location: Correct, Incorrect) ANOVA

yielded a marginal interaction effect between Location and Pair, $F(1, 14) = 3.34$, $p = .09$, η_p^2 $= .19$. As can be seen in Figure 8A, this effect was due to a greater proportion of correct relative to incorrect fixations for the Effect pair (*mean difference = .18, SE = .08; p = .05*), and no difference for the No-effect pair (*mean difference = -.02, SE = .03, p = .51*). A *t*-test comparing fixations to the effect alone during Effect and No-effect pairs revealed a marginally significant difference between pairs ($t(14) = 1.75$, $p = .10$), suggesting that gaze fixations to the effect itself were more frequent during the first action of the Effect pair compared with the No-effect pair (Figure 8B).
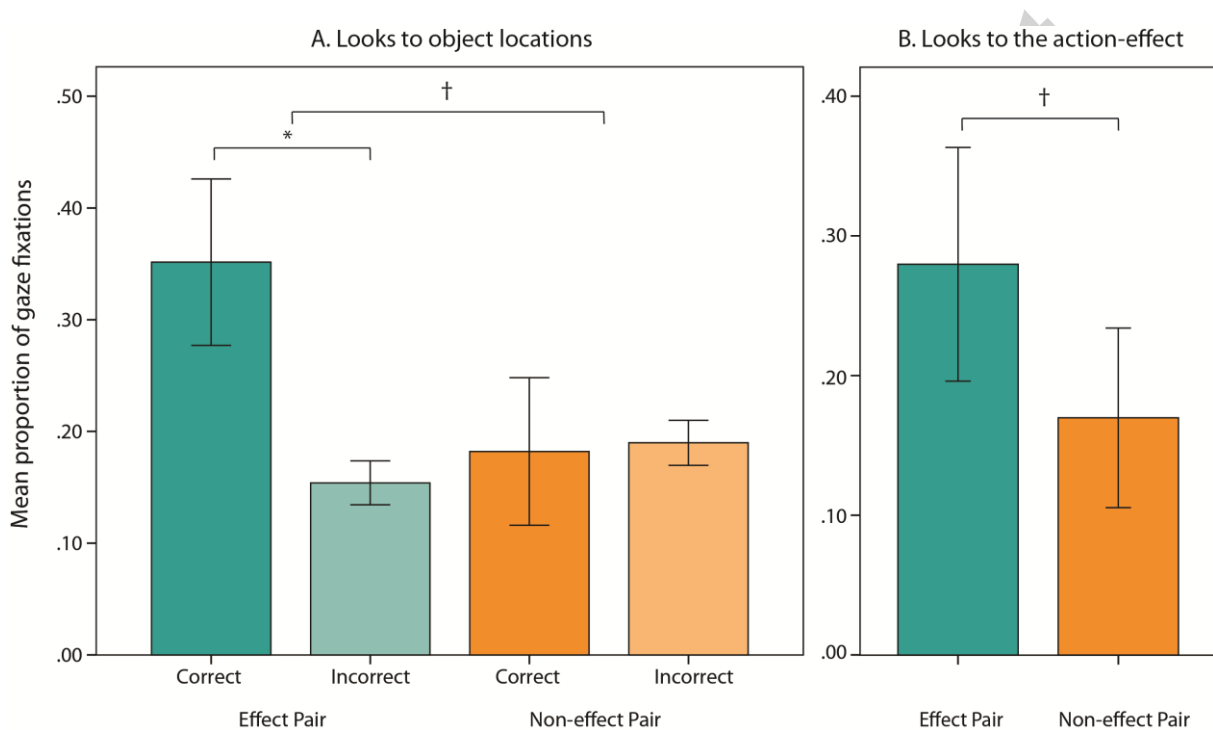

Figure 8. A: Proportions of fixations as a function of ROI and pair. B: Proportion of fixations to the action-effect location during the first action of each pair. Bars represent standard errors. †p < .10; * p < .05.

4.3 Relating Behavioral and Neural measures

In order to test for consistency between behavioral and ERP measures, we explored whether infants who demonstrated higher rates of correct predictions during the learning

phase were also those who demonstrated a robust Nc effect at test. Using a method similar to Reynolds et al. (2010), infants who contributed both eye-tracking and EEG data measurements ($N = 7$) were divided into two groups based on the mean amplitude difference between conditions across all electrodes. Infants with an Nc difference greater than the group mean (-4.23mV; $N = 5$) received a score of 1 and infants below the mean ($N = 2$) were assigned a 0. We then conducted an ANOVA analysis of gaze fixations as before, with Nc Difference (above or below mean) as an additional between-subjects factor. This revealed a main effect of Nc Difference, $F(1, 5) = 9.53$, $p = .03$, $\eta_p^2 = .66$. Infants who had a larger Nc effect also made a greater proportion of correct relative to incorrect fixations (*mean difference* = .27, *SE* = .07, *p* = .01) than those infants with a weaker Nc effect (*mean difference* = .01, *SE* = .11, *p* = .93).

5.0 Discussion

The central aim of this study was to investigate the ERP components associated with violations of prediction based on the statistical structure in action sequences. Specifically, we asked whether deviant action events, which violated a previously learned association, altered infants' ERP responses. We tested for the presence of two potential components, the Nc and N400, which are known to index perceptual and semantic cognitive responses, respectively. Second, during the learning phase of the experiment, we investigated whether infants made predictive eye movements to upcoming actions.

5.1 Nc Findings and Interpretation

To investigate the response to a violation of predictions built up on the basis of statistical learning, we examined the ERP responses following deviant actions that were inconsistent with previously learned sequential regularities. Our results illustrate an enhanced Nc component in response to deviant action pairs, relative to original action pairs, when they were associated with a salient effect. Prior studies have found an Nc effect for repeated

observations of single action events, such as bringing a spoon to the mouth (Kaduk et al., 2016; Reid et al., 2009). Our study extends these prior findings, by showing that an Nc effect can occur for individual action steps within longer sequences, and is modulated by their congruency within the learned sequential structure. However, the direction of the Nc effect differed between the current study and Reid et al. (2009) and Kaduk et al. (2016). Our findings revealed an Nc amplitude that was greater in response to the *unanticipated* action step, whereas in Reid et al. (2009) and Kaduk et al. (2016), the Nc amplitude was greater in response to the *anticipated* action outcome. This discrepancy is likely explained by the level of attentional engagement (Reynolds, 2015) for the current study when contrasted with these earlier studies. Even though the Nc is commonly reported to be larger in response to novel, or unfamiliar stimuli (which 'grab' infants' attention), the Nc has also been found to be larger for stimuli which are highly familiar and highly salient such as the maternal face of each infant (de Haan & Nelson, 1997) or eating actions (Reid et al., 2009). In addition, in the current study the compared actions were both unfamiliar, but one drew more attention due to its relative novelty within the experimental setting.

The topographical distribution of the Nc component we observed is consistent with previous findings (Reynolds & Richards, 2009, 2005). Reynolds and colleagues (2005) showed that the Nc is greater during periods of sustained attention and is likely to reflect activity from distinct brain areas involved in information processing that are independently influenced by attentional state. Likely cortical sources of the infant Nc include the inferior and superior prefrontal cortex and the anterior cingulate cortex, which are neural regions that modulate sustained attention and recognition memory (for a review, see Duncan & Owen, 2000). This suggest that the deviant targets in our paradigm triggered additional visual processing, indicating that this attention system was modulated by changes in the rules governing the sequential structure. There are two interpretations for explaining the presence

of the Nc component in our study. The first interpretation, supported by our eye-tracking results, is that infants encoded the predictive relation between the actions of the effect pair during the learning phase and perceived the deviant pair as surprising or unexpected. In other words, the Nc effect that we observed may reflect the recognition of a violation of perceptual predictions for how the following events should unfold.

A second interpretation of our findings for the Nc component is that infants recognized the association between the deviant second action and the effect, rather than surprise at observing this event contingent upon the first action of the pair. In our study, deviant items were both statistically unlikely and visual novelties. Future research aimed at dissociating the separate contributions of stimulus novelty and probability could clarify whether the Nc response reflects the buildup of stored information about stimulus probability or whether it is limited to the detection of familiar versus novel items. However, infants seemed to make correct visual predictions only for the Effect pair, an indication that learning may have only occurred when there was an upcoming salient effect. This finding, coupled with its relation to the strength of the observed Nc effect, suggests that visual novelty alone is not sufficient to explain our pattern of findings.

Though both deviant Effect and No-effect events violated the action sequence, only the deviant event co-occurring with the effect elicited the enhanced Nc peak. Previous research has shown that action-effects influence infants' learning and imitation as measured in their behavioral responses (Hauf & Aschersleben, 2008; Verschoor et al., 2010). One explanation provided in the literature is that bidirectional action-effect associations can be established through observation, which results in motor representations of the effects themselves. From this perspective, the effect may have resulted in a corresponding representation of the action 'unit' (i.e., the two-step pair) preceding it, which infants did not acquire for the No-effect pair. A second explanation is that action-effects are salient

perceptual cues that make the structure easier for infants to attend to and maintain in working memory. Accordingly, several prior studies have provided evidence that the influence of action-effects on infant behavior is due to a bias towards perceiving actions in terms of their goal structure (Buresh & Woodward, 2007; Cannon & Woodward, 2012; Klein et al., 2006). In line with this notion, it is possible that the effect was perceived as a goal or intentional outcome of the activity stream, and thus biased attention toward that particular action pair because of its temporal relation with the effect. A third possible explanation, drawn from the literature on reinforcement learning, is that the action-effect was perceived as a rewarding sensory change in the environment. Evidence from adult studies suggests that external rewards are crucial for observers to update their internal representations of the environment (Gläscher et al., 2010). Infants might have selectively updated their model of the action sequence only when observing a perceptible external reward, provided by the light turning on. Whether observing the light was rewarding to the infants or perceived as a potential reward or goal of the actor is a novel question that could be empirically tested in future research.

Our findings are consistent with a large body of literature examining the development of causal learning, which explains how children achieve increasingly sophisticated theories about the social and physical world from noisy and limited data (see for a review, Gopnik & Wellman, 2012). This work has shown that Bayesian concepts of inference can also apply to children's learning of the causal structure of the world. Bayesian inference refers to the process of combining prior evidence with current incoming data and forming a prediction about what will occur next, resulting in a probabilistic model of the world. Of relevance for the current study, probabilistic models also provide one of the most elegant explanations for how the motor system can predict the actions of other people (Kilner, 2011). Our data show that, at 10 months of age, infants can use statistical information from observation alone to generate expectations about the actions and their effects. This step may reflect the initial

building of prior knowledge about the most likely outcome of an action, a necessary prerequisite for constructing causal models of other people's actions and their social intentions.

5.2 The N400 Component

Prior studies have shown that unexpected final outcomes of familiar action sequences, such as bringing a pretzel to one's ear or a spoon with food to one's forehead, elicits an N400 effect in both infants and adults (Reid et al., 2009, Kaduk et al., 2016). Across studies, N400 effects become smaller as stimulus probability increases. The explanation proposed in the literature is that processing incoming information is facilitated when it 'fits' with the current context, if accumulated experience from previous contexts has built up meaning (Kutas & Federmeier, 2011). From this perspective, an N400 response to action stimuli is interpreted as a violation of predictions that are based on current semantic information and prior experiences.

In the current experiment, we found no evidence for an N400 response to deviant action steps. Unlike prior studies, which have shown N400 effects for action events that occur within a familiar context ('day-to-day' actions such as eating), our study featured novel action sequences which were also abstract, in the sense that they did not reach an overarching goal or take place in a familiar setting. The statistical structure was therefore the only information infants could use to build expectations about the sequence, requiring them to remember six different objects and the transitional probabilities between them. One simple explanation is that the brief learning phase was not sufficient for young infants to generate a semantic context for the observed action events. Perhaps infants need to sample extensive amounts of data to build up a context in which to compare new incoming information. Another possibility is that actions and their context need to become associated with a goal that the observer has experience with, before they engage cognitive systems associated with semantics and

conceptual knowledge. The factors that cause a shift from perceptual to semantic processing in action sequences during development are an intriguing question for further research.

5.3 Predictive gaze fixations

Infants made more predictive gaze fixations to the correct upcoming events than to other object locations during the learning phase of the experiment. This finding provides evidence they detected the pair structure of the unfolding action sequence, and used this information to guide their looking behavior. Critically, this behavior was modulated by whether or not a predictable action event was associated with a salient effect. Correct anticipations were more frequent for the Effect pair than the No-effect pair, and anticipations to the effect itself during predictive time windows were also marginally higher for Effect pairs than the No-effect pair. This finding is partially consistent with a prior experiment in which 18-month-old infants only demonstrated spontaneous, uninstructed imitation of actions that resulted in action-effects, and not of actions without a corresponding effect (Monroy et al., 2017). In that study, the older infants also only demonstrated a relation between their visual anticipations during observation and their ability to imitate upcoming actions for actions that caused effects. These findings, taken together with the current study, suggest that action-effects provide a learning cue that guides infant behaviors during both action perception and action performance. Further, Monroy et al. (2017) also found that the 18-month-olds were able learn both pair types, even in the absence of an action-effect, which suggest interesting developmental changes in sensitivity to effect-related cues occurring between the first and second year of life.

The eye-tracking data yielded marginally significant differences between experimental conditions, which may have been due to the small number of infants who yielded enough data for analysis. Alternatively, the task demands of our experiment were relatively high: infants needed to continuously attend to the screen, remember and encode the pair structure in the

unfolding sequence, and make predictive eye movements towards one of many possible locations on the screen within a brief time period. Prior research has shown that under conditions of uncertainty, even adults make fewer predictive movements—which require effort and are therefore costly—and prefer to assume a neutral position (Dale et al., 2012). It is possible that our learning effects are small because infants at this age are just beginning to acquire the ability to encode the statistical relations in more complex stimuli, or that they do not always make visual predictions during ongoing observation. Future research could aim to differentiate these two possibilities. Despite this, the consistency between our eye-tracking and ERP results provides converging evidence that infants learned to predict the outcome of the sequence structure for the Effect pair.

5.4 Relation between behavioral and ERP measures

Our method for assessing the relation between behavioral and neural measures of learning was to examine infants' predictive gaze fixations during the learning phase in relation to the magnitude of their Nc response during test trials. In a study aimed at identifying the relation between infant visual preferences and ERP responses, Reynolds and colleagues (Reynolds & Richards, 2005; 2009) provided evidence that infants aged 4.5-7.5 months who demonstrated a visual preference for novel events were those that showed an Nc effect with greater amplitude. Consistent with these findings, in our study, the infants who demonstrated a greater Nc amplitude in response to a deviant target action in the action-effect condition also made a greater proportion of correct, relative to incorrect, predictive gaze fixations in this condition. This result suggests that the Nc response may reflect predictive processes based on the perception statistical regularities, which adds to the current understanding of the functional significance of the Nc in young infants.

The sample size in the current study was limited due to difficulties in combining EEG and eye-tracking data collection methodologies with young infants, which is typical for

developmental research and is consistent with similar studies (for a meta-analysis see Stets et al., 2012). Due to the combination of a small sample size and limited number of trials in our experimental conditions, findings from the current study should be interpreted cautiously and validated in future work. However, we also note that our main finding of an Nc effect is consistent with a large body of prior studies (reviewed in de Haan, 2007). Specifically, the Nc component in the current study matches previously reported findings both in terms of the experimental context in which it was elicited—that is, a response to a perceptually unexpected event—and its characteristics, such as latency and morphology of the waveform.

5.5 Conclusion

Human action naturally contains statistical regularities that define the overall predictability of upcoming action events. The ability to recruit perceptual processes for detecting these regularities is critical for making accurate predictions during action observation. The results of this experiment suggest that, by ten months of age, infants are sensitive to the sequential structure between action steps when they result in salient effects. Our study further supports a consistency between neural and behavioral measures of statistical learning in infancy. In sum, statistical regularities provide a learning cue that guides visual expectations and attention during ongoing processing of novel action sequences. The findings reported here have direct implications for our understanding of the development of social cognition in infancy. We suggest that infants initially have the capacity to rely on their powerful statistical learning skills to detect regularities among the actions of other people, enabling them to anticipate upcoming action goals and to eventually attain understanding of the mental states of other people.

Acknowledgements

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Highlights

- Infants show neural responses to action structure based on statistical learning in the first year of life

- EEG and eye-tracking were recorded while 8-11-month-old infants observed action sequences containing statistical regularities

- Violations of statistical regularities that were paired with action-effects elicited a Negative central component, a marker of infant visual attention

- Infants' depend on the presence of action-effects to detect the statistical regularities in other people's action sequences