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Infants' ERP Responses to Novel and Familiar Stimuli Change Over Time: Implications for Novelty Detection and Memory

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Detection of novelty is an important cognitive ability early in development, when infants must learn a great deal about their world. Work with adults has identified networks of brain areas involved in novelty detection; this study investigated electrophysiological correlates of detection of novelty and recognition of familiarity in 9-month-old infants, using event-related potentials (ERPs). Infants were familiarized with an event in the laboratory, then ERPs were recorded as they viewed repeated presentations of pictures of this familiar event and a novel event, along with single presentations of 30 trial-unique events. A middle-latency negative component was sensitive to degree of novelty, differing in amplitude and latency by stimulus condition and across repeated presentations. Long-latency slow-wave activity also related to stimulus condition. Findings have implications for our understanding of infants' detection of novel information and the processes that render the novel familiar.

Recognition memory and the detection of novelty are related but distinct processes. To recognize something as familiar is to identify it as previously experienced; to detect novelty is to identify a mismatch between a stimulus and existing memory representations. Both of these abilities are important for day-to-day function: Memory allows experience to influence current and future behavior, whereas detection of novelty allows the allocation of resources to learning about novel

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stimuli or situations (Daffner et al., 2003). Identifying a stimulus as novel could therefore be thought of as the first step in the process of rendering it familiar. The purpose of this research was to trace the process of familiarization with novel stimuli in 9-month-old infants by recording electrophysiological indexes.

The neural bases of memory have been of long-standing interest to cognitive neuroscientists. The famous case of H. M. illustrated that bilateral damage to the medial temporal lobes results in an inability to form new explicit memories, and retrograde amnesia for as long as a decade prior to injury (Corkin, Amaral, Gonzalez, Johnson, & Hyman, 1997; Penfield & Milner, 1958). Further studies of patients with selective brain lesions, animal models of lesions and disease, and neuroimaging studies of healthy adults have confirmed the importance of medial temporal lobe structures for memory formation, consolidation, and retrieval (Eichenbaum & Cohen, 2001). Similarly, brain imaging studies of processing of novel stimuli have revealed that medial temporal lobe structures, most prominently the hippocampus, are also strongly activated by the presentation of novel stimuli and novel arrangements of stimuli (Stern et al., 1996; Strange & Dolan, 2001). Indeed, Habib, McIntosh, Wheeler, and Tulving (2003) found that the same regions within the hippocampus were involved in separate brain networks subserving processing of familiar and novel information.

Structures outside of the medial temporal lobe are also implicated in the detection of novelty. Dias and Honey (2002) found evidence that midline prefrontal structures (e.g., anterior cingulate) may play a role in detection of novelty, in that dishabituation to a novel stimulus was impaired when medial prefrontal cortex was damaged in rats. Prefrontal activation was seen in an event-related functional magnetic resonance imaging (erfMRI) study of novelty processing (Kiehl, Laurens, Duty, Forster, & Liddle, 2001). Daffner and colleagues (2003) found that patients with damage to the frontal lobes showed impaired responses to novelty, as did patients with posterior parietal lesions, although to a lesser extent. Thus, response to novelty appears to recruit wide-ranging networks within cerebral cortex.

Processing of novelty and familiarity are of particular interest in the study of infant cognitive development. Infants prefer a novel stimulus to one that is well encoded (Fantz, 1964), although early in the encoding process they show a preference for the familiar (Hunter & Ames, 1988; Roder, Bushnell, & Sasseville, 2000). This general preference for novelty serves infants' need to learn about their world, as they are more likely to attend to novel contexts and stimuli, setting up opportunities to learn (Hunter & Ames, 1988). For example, in the process of learning language, infants and young children tend to assign novel words to novel objects, a bias that helps facilitate vocabulary building (Woodward & Markman, 1998). Logically, responses to novelty and familiarity are equally diagnostic of memory, although underlying processes may be different. This has allowed infant memory researchers to use novelty preference to study mnemonic capacity early in life when infants' repertoire of behavioral responses is limited (e.g., Bahrick &

Pickens, 1995). Using this tool, researchers have found substantial increases in recognition memory capacity across the first year of life.

Development of recognition memory and, presumably, novelty detection abilities, are thought to reflect in large part developments in the brain networks that support these processes. The primary tool available for assessing infant brain activity during the process of cognition is the recording of event-related potentials (ERPs; for a review see Nelson & Monk, 2001). In this methodology, the scalp EEG is recorded while infants are exposed to stimuli such as pictures. The EEG is then averaged to extract the signal related to processing the stimuli. Even if there is no behavioral difference between infants' responses to familiar and novel stimuli, differences in scalp electrical activity (reflecting differences in neural processing) may be observed. ERP differences related to novelty or memory have been seen in middle- and long-latency components, including the middle-latency negative component (Nc), a negative deflection approximately 500 msec following stimulus onset, observed most prominently at anterior midline leads; the positive slow wave (PSW), a late positivity beginning approximately 1,000 msec after stimulus onset; and the negative slow wave (NSW), a late negativity occurring over the same time period (e.g., de Haan & Nelson, 1997). The Nc is thought to reflect allocation of attentional resources, the PSW has been posited to reflect working memory updating for partially encoded stimuli, and the NSW appears to be elicited by novel stimuli (de Haan & Nelson, 1997; Nelson & Monk, 2001; Richards, 2003).

Many studies of novelty processing have utilized the oddball paradigm, in which two stimuli are presented with differing probabilities. Both stimuli are initially novel, but the more frequent stimulus becomes familiar at a faster rate than does the rare stimulus. Studies using the oddball paradigm have shown that 6-month-old infants respond differentially to stimuli on the basis of stimulus probability (e.g., Ackles & Cook, 1998). Generally, a larger Nc is seen to the less frequent and thus more novel stimulus.

Infants also show differential ERPs to stimuli on the basis of experience outside the laboratory. Infants produce different ERPs to pictures of their mothers' faces relative to strangers' faces (de Haan & Nelson, 1997); there are also differences between ERPs to a favorite toy relative to a novel toy (de Haan & Nelson, 1999). At 9 months, infants show different ERPs to pictures of events they have experienced only a few times in the laboratory setting, relative to pictures of similar events that they have never experienced (Bauer et al., in press; Bauer, Wiebe, Carver, Waters, & Nelson, 2003; Carver, Bauer, & Nelson, 2000; Lukowski et al., 2005). This group of studies shared the same general methodology: 9.5-month-old infants were familiarized with a two-step event on 2 or 3 separate days. Then, either immediately or after a 1-week delay, infants watched still photographs of this familiar event and a novel event while ERPs were recorded. Immediately after familiarization, all infants showed differential ERPs to familiar and novel pictures (Bauer et al., in press; Bauer et al., 2003). After a 1-week delay, differentiation of photo-

graphs of familiar and novel events was related to later behavioral evidence of memory (Bauer et al., 2003; Carver et al., 2000).

Previous studies have typically compared only two classes of stimuli: familiar and novel. However, interpretation of differences between familiar and novel stimuli is complicated by the observation that novel stimuli are only truly novel at the beginning of testing. That is, although infants have not seen the novel faces, toys, or events prior to ERP testing, over the course of testing they see multiple brief pictorial representations, and thus they have some opportunity to become familiar with the novel stimulus. In interpreting these differences in terms of memory, this if anything works against researchers (i.e., it makes it more difficult to detect differences between responses to familiar and novel stimuli); but if one wants to talk about novelty, this may be more problematic.

Is there reason to suspect that processing of novel stimuli changes after a relatively small amount of experience? Strange and Dolan (2001) studied the dynamic characteristics of hippocampal activity in adults in a variant of the oddball task using erfMRI. All stimuli were unique words, and different sets of oddball stimuli varied from the standard on unique dimensions such as color, font, or emotional valence. Strange and Dolan found that anterior hippocampal activity was initially strong to each class of oddball stimuli, but with repeated presentations of further stimuli in a given class, hippocampal activity underwent adaptation and thus, if averaged over multiple trials, was no longer detectable. There is also evidence that infants show changes in ERPs across repeated stimulus presentations. In a study of 6-month-olds, Nikkel and Karrer (1994) saw reductions in the amplitude of the Nc across repeated presentations of the more frequent stimulus in an oddball task, presumably reflecting reductions in the allocation of attention across trials. Also at 6 months, Snyder, Webb, and Nelson (2002) observed a decrease in slow-wave activity, but failed to find changes at the Nc, between early and late blocks of trials to pictures of mothers' and strangers' faces. Because slow-wave changes were seen for both types of faces, these changes were interpreted as repetition effects rather than mnemonic processes. These results also indicate that ERPs can be a useful index of changes in processing over time, but inconsistencies in findings indicate that further work is necessary.

Nelson and Collins (1991) used ERPs to explicitly study 6-month-olds' processing of novelty by including a condition in which novel faces were presented once and only once. ERPs to this trial-unique condition reflect processing of a completely novel stimulus, contrasted in this study with responses to frequently and infrequently presented familiar faces. A different pattern was observed to the novel stimulus relative to the two familiar stimuli: Between 750 and 1,450 msec, a large NSW was observed at the lead Cz. Thus, the inclusion of trial-unique stimuli appears to be a useful approach to studying neural responses to novelty.

In this study, we used elicited imitation procedures combined with ERPs as in previous work by Bauer and colleagues (Bauer et al., in press; Bauer et al., 2003;

Carver et al., 2000; Lukowski et al., 2005). Pictures of one familiar and one novel event were tested, as in previous work. In addition, following the lead of Nelson and Collins (1991), a third condition was included: a set of nonrepeating pictures from different novel events. With this design we were able to make three comparisons: (a) between the familiar and novel events, to test for replication of previous findings and to examine effects of familiarization with the event in the laboratory setting; (b) between the familiar condition and the trial-unique condition, testing the summed effect of familiarization prior to and during the ERP test; and (c) between the two novel conditions, the condition including repeated pictures of a single novel event (novel-repeated) and the condition including multiple nonrepeating novel pictures (novel-trial-unique). The latter comparison allowed us to examine processing of stimuli that are completely novel in comparison with stimuli that are novel at the beginning of the ERP test but become familiar across the course of the session.

Finally, we assessed changes in responses across the ERP test by comparing early and late trials across all three conditions. Based on previous research, we expected to see changes across the session (Nikkel & Karrer, 1994; Snyder et al., 2002). However, if these changes were due to infants' increasing familiarity with the repeated pictures, these changes would be confined to the familiar and novel-repeated trials, and novel-trial-unique ERPs would not change. On the other hand, if changes across the session were due to general changes in infant state, such as fatigue or habituation to the ERP procedure, parallel changes would be seen across all three conditions.

In combination, these approaches allow us to draw conclusions about 9-month-olds' detection of novelty, as well as their processing of stimuli that are familiar to various degrees. This research thus informs our understanding of the cognitive and neural processes that allow infants to understand their world.

METHOD

Participants

Forty-two infants (23 girls and 19 boys) participated. The average age of the infants at their first visit was 9 months, 13 days (range = 9;7–9;24). All infants were full-term and experiencing an apparently normal course of development. Infants were recruited from a database of families who had expressed interest in participating in research. The database is primarily composed of middle- and upper-middle-class families. The sample included 38 White children (including 1 child of Hispanic descent), and 4 children of mixed race, including 1 child of African American and White descent, 2 children of Asian American and White descent, and 1 child of Native American and White descent. Five other infants were

enrolled, but were not included in the final sample: 3 were unable to complete the ERP test, 1 had a medical history of seizures, and 1 did not return for the second session because of illness. All parents gave informed consent for their infants' participation before the start of the study. On completion of the study, each infant received a small toy or book, and parents received either a pair of movie tickets or a $10 gift certificate to a local merchant.

Materials

Stimuli included two novel two-step events, depicted in the first two rows of Figure 1. Both events have been used in prior research with this age group (Bauer et al., in press; Bauer, Wiebe, Waters, & Bangston, 2001). For each infant, one event served as the familiar event and the other served as the novel-repeated event during the ERP recognition memory test; this was counterbalanced across infants. For one

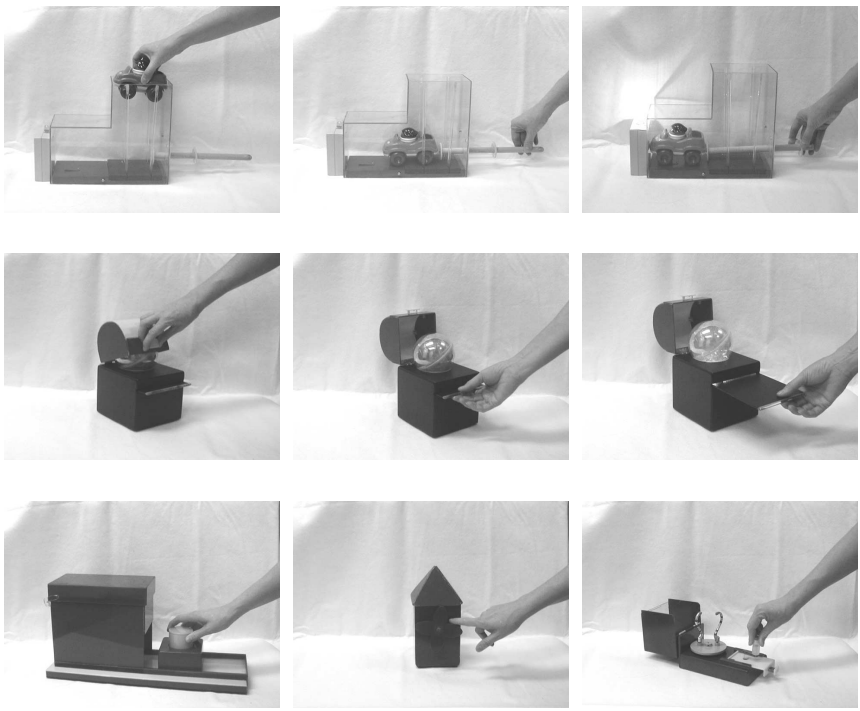

FIGURE 1 Sample slides used in ERP testing. The first row includes the three slides depicting the event "turn on the light." The second row includes the three slides depicting the event "make a glowball." The third row includes 3 of the 30 slides used in the novel trial-unique condition, each of which depicted one action utilizing unfamiliar props.

event—"Turn on the light"— the experimenter first placed a car into a clear covered track; then she pushed a wooden plunger, moving the car to the end of the track, where it triggered a switch on the base of the track, turning on a light (Figure 1, top row). For the other event—"Make a glowball"—the experimenter lifted a cover, revealing a translucent orange ball; this released a catch, enabling a drawer to be pulled out, causing the ball to be illuminated (Figure 1, middle row). These events were chosen to be physically dissimilar but identical in causal structure, such that the two actions could be attempted in any order, but had to be performed in a particular order to successfully reach the goal (see Bauer, 2002, for discussion of the importance of causal structure in memory in infancy and beyond).

At the ERP recognition memory test, infants saw digitized still photographs of the familiar event (which infants had seen demonstrated), the novel-repeated event (which infants had not seen), and 30 novel-trial-unique events similar to the familiar and novel-repeated events (which infants had not seen; see examples in Figure 1, bottom row). There were three photographs of each of the familiar and novel-repeated events that included a woman's hand performing each step, and demonstrating the goal or end state of the event. Each of the 30 novel-trial-unique events was represented by one picture, including a woman's hand performing an action with the props. All pictures used in the ERP test shared the following features: (a) a white background, (b) props varying in shape and color but occupying a similar area on screen, and (c) a woman's hand performing an action using these props.

In addition, parents completed the MacArthur Communicative Development Inventory: Words and Gestures (Fenson et al., 1993) and the Infant Behavior Questionnaire (IBQ), a measure of temperament (Rothbart, 1981). These instruments were used to determine whether the subset of infants whose data were used in the analyses differed from the subset whose data could not be used (see "Data Reduction").

Procedure

Familiarization. Infants sat on their parents' laps or on the testing table. Each session began with a brief warm-up period during which the experimenter and infant played with a commercially available toy (musical shape sorter). At the first session, infants were then given the props used to produce one event and were allowed to explore them for a baseline period lasting 1.5 to 2 min. The experimenter then modeled the event twice, labeling the event ("This is how I turn on the light") and narrating the steps as they were performed ("Put in the girl." "Push the stick."); immediate imitation was not permitted. The second session took place within 3 days of the first (M = 1.24 days, range = 1–3 days), and began with two more demonstrations of the familiar event. Infants in this age range have been shown to re-

quire more than one exposure to events of this type to reliably demonstrate delayed recall (Bauer et al., 2001).

Recognition memory testing. At the second session, infants' recognition memory was tested using ERPs. Because of the time necessary to apply electrodes, there was a delay between demonstration of the event and the beginning of the ERP test ($M = 27.3$ min, range 17–43 min). ERPs were recorded at 29 scalp locations illustrated in Figure 2, placed according to the international 10–20 system (Jasper, 1958). Electrodes were sewn into a nylon cap fastened under the infant's chin with a Velcro chin-strap. Electrodes were filled with a conductive gel and a mildly abrasive cream. Impedances were kept below 10 kΩ, and were generally less than 5 kΩ. Scalp activity was referenced to Cz during data collection, and rereferenced to digitally linked mastoids offline. Electroocular activity was recorded from bipolar miniature electrodes placed in a transverse position above and below the infant's right eye. All electrical signals were recorded using a Grass Neurodata Acquisition System with Model 15 amplifiers. EEG gain was set to 20,000 and EOG gain was set to 5,000. Bandpass filters were set at 0.1 and 30 Hz. A 60-Hz notch filter was in place.

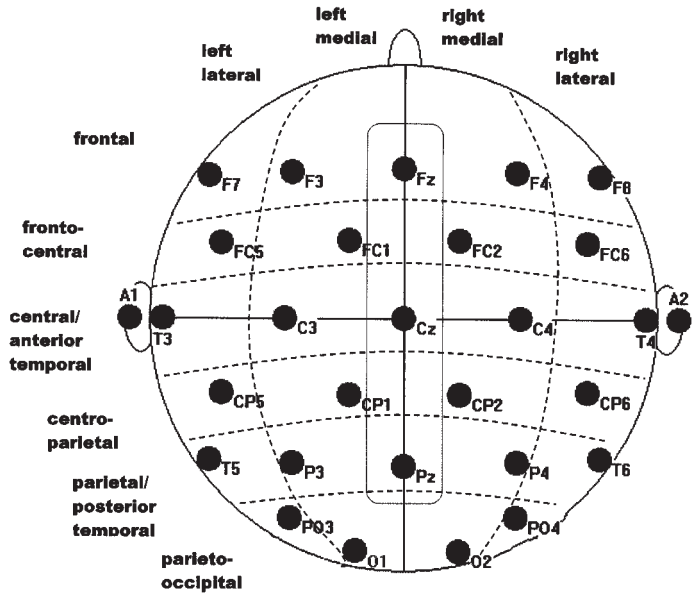

FIGURE 2 Schematic of leads. The midline leads (Fz, Cz, and Pz) are outlined in the solid gray box. The black dotted lines represent the boundaries between the different anterior–posterior and lateral coefficients used in analyses of the lateral leads.

Each infant was tested individually while seated on a parent's lap or in a high chair facing a computer monitor approximately 75 cm away. The monitor was embedded in a black screen that blocked the infant's view of the rest of the room. The screen contained small holes through which an observer could watch the infant, and, when necessary, redirect the infant's attention to the screen. Each trial consisted of a 100-msec baseline followed by presentation of the stimulus for 500 msec. EEG recording continued for an additional 1,200 msec. EEG was sampled every 10 msec (100 Hz) throughout each trial. This was followed by an intertrial interval that varied randomly between 500 and 1,200 msec. The observer controlled presentation of stimuli with a button box, and pressed a button while the infant was looking away, thereby signaling the computer to repeat the trial. Brain activity was not recorded when the infant was not looking at the screen. Up to 90 trials were presented, including repeated presentation of three pictures of one event to which the infant had been exposed (familiar condition), repeated presentation of three pictures of one event to which the infant had not been exposed (novel-repeated condition), and 30 pictures of 30 additional events to which the infant had not been exposed (novel-trial-unique condition). Stimuli were block-randomized such that each block of nine trials included the 3 familiar pictures, the 3 novel-repeated pictures, and 3 of the 30 novel-trial-unique pictures; thus, the probability for each condition was equal (one third or 33.3%). Pictures were presented in a random order, so that pictures of the same event did not follow each other in sequence. However, all pictures of the same event included the same props in different configurations, and previous work using randomized presentation has demonstrated that ERPs to pictures of familiar events are related to subsequent recall of those events (Bauer et al., 2001). If the infant became upset during testing, the ERP test was terminated. As a result, some infants completed fewer than 90 trials (M = 69.7 trials, range = 24–90 trials).

Recall memory testing. To verify that infants had encoded the familiar event, recall of the familiar event was tested behaviorally. This took place after the ERP test and another intervening task unrelated to this research. The experimenter placed the props on the table in front of the infant and provided a general verbal prompt ("What can you do with this stuff?"). The infant was then allowed to manipulate the props for approximately 1.5 to 2 min. Infants' behavior during this phase provided a measure of delayed recall.

Data Reduction

Electrophysiological data. In constructing the ERP waveforms, data were excluded if the EEG signal exceeded analog to digital values in any 50-msec window, or if the EOG signal exceeded 250 microvolts in any 100-msec window. For infants who completed at least 70 trials, individual averages were obtained sepa-

rately by condition (familiar, novel-repeated, novel-trial-unique) and trial block (Trials 1–45, Trials 46–90), with the constraint that an equal number of trials was included in each average. Each trial block included up to 15 trials in each condition, enough to construct a stable cross-average. Infants without a minimum of eight trials in each average were excluded; for the remaining infants, the average waveforms were then visually inspected, and if they were judged to be contaminated by motion artifact or high-frequency noise, the data were excluded.

Data from 13 infants met our criteria for inclusion. Data from the other 29 infants were excluded from further analysis because of (a) equipment failure ($n = 1$ infant), (b) an insufficient number of trials ($n = 10$ infants), (c) blink or movement artifact ($n = 4$ infants), or (d) procedural error ($n = 14$ infants). Of the infants excluded due to procedural error, 4 were excluded because the amplifier was configured incorrectly, so no data were collected, and 10 were excluded because of a programming error. For infants included in the analyses, the average number of trials completed was 86.5 (range 74–90 trials).[1]

Cross-averages were constructed by averaging infants' ERP waveforms for each condition and trial block. To ensure that signal-to-noise ratio was equivalent across all conditions, an equal number of trials were included in each cross-average for a given infant, randomly selected from available trials. On average, 12.4 trials were included (range = 8–14 trials). We identified two windows of interest: (a) a middle-latency window from 350 to 750 msec after stimulus onset, and (b) a long-latency window from 900 to 1,700 msec. Windows were determined by first viewing the grand mean waveforms averaged across all infants, and then checking individual infants' cross-averaged waveforms to ascertain that the windows captured the components of interest. For middle-latency components, we an-

[1]A common concern in infant ERP studies is whether there are systematic differences between infants who contribute valid ERP data and infants who do not. To address this question, we compared infants who were and were not included in the ERP analysis on a variety of characteristics, using group t tests, corrected for unequal variances when necessary. No differences were observed for performance of actions or correctly ordered pairs at baseline or recall during behavioral testing (ps > .15). Infants did differ in the number of trials they viewed, $t(38.3) = 7.04$, $p < .05$ (Ms = 86.5 and 62.2, SDs = 5.6 and 16.5, for infants included and excluded, respectively). This was expected, because viewing the majority of the trials was a condition for inclusion. Infants did not differ in the time required to apply the electrodes ($p > .80$). There were no differences in parent report of language comprehension or production (ps > .30). When infants' scores on the IBQ were compared, differences in smiling and laughter were found between infants included ($M = 5.61$, $SD = 0.50$) and infants excluded ($M = 4.87$, $SD = 0.73$), $t(39) = 3.33$, $p < .05$. This may have been because the length of the ERP testing protocol in this study was such that infants with more easy-going temperaments were more likely to complete it. However, perhaps more important, in a study of response to novelty, infants did not differ on the dimension of temperament distress to novelty ($p > .45$). Additionally, no significant differences were observed for activity level, soothability, distress to limits, or duration of orientation (ps > .25). Differences in temperament must, however, be considered in interpreting the findings of this study and other infant ERP work.

alyzed the minimum amplitude and the latency to peak. In the long-latency window, there are no identifiable peaks; hence, the dependent measure was an area score integrating the area under and over the curve relative to baseline. Previous studies of memory and ERPs have used the same dependent variables, facilitating comparisons across studies (e.g., Bauer et al., 2003; Carver et al., 2000; Lukowski et al., 2005).

Behavioral data. Due to recording equipment malfunction, the behavioral data of 2 infants were unavailable for coding. A trained behavioral coder who was naive to the hypotheses of the study viewed videotapes of the remaining 40 infants and noted the production of the actions that made up each event and the order in which they were produced. To determine the reliability of coding, data from 12 of the infants (30% of the sample) were independently recoded by a different trained coder. Average reliability of coding was 92.3% (range = 80–100%).

As in previous research (e.g., Bauer et al., 2001), we derived two dependent variables. For the baseline and recall phases separately, the number of actions of the event produced was tallied for each infant (maximum = 2.0). In addition, the production of correctly ordered pairs of actions was noted based on the first occurrence of each action (maximum = 1.0).

RESULTS

Recall of the Familiar Event

To confirm that infants had in fact learned the familiar event, behavior at baseline and at test was compared using Wilcoxon signed-rank tests. As a group, infants demonstrated that they learned the actions comprising the event, producing more actions at recall ($M = 0.97$, $SD = 0.73$) than at baseline ($M = 0.53$, $SD = 0.68$): $S = 72.5$, $n = 37$, $p < .005$. However, infants did not show evidence of recall of order information, in that the number of pairs produced at the recall test ($M = 0.11$, $SD = 0.31$) did not increase significantly relative to baseline ($M = 0.05$, $SD = 0.22$), $S = 4.5$, $n = 37$, $p > .30$. Nevertheless, recall of individual actions indicates that infants learned from the experimenter's demonstration during the exposure phases.

Analyses of ERP Components

Infants' ERP responses reveal whether they processed pictures differently on the basis of trial condition, and can be used to make inferences about infants' processing of familiar and novel stimuli and whether it changes over time. In previous research, memory-related differences have often been reported at midline leads (e.g.,

Bauer et al., 2003); thus, midline leads were analyzed separately from the remaining leads. Analyses were conducted using a linear mixed models approach, with SAS's proc mixed (Littell, Stroup, & Freund, 2002).[2] Follow-up analyses for main effects were conducted by comparing least-squares means with the Tukey–Kramer adjustment; interactions were interpreted using simple effects.

Midline leads. Analyses of midline ERP responses were conducted for peak amplitude and latency to peak during the middle-latency window (350–750 msec), and area score for the long-latency window (900–1,700 msec). For each dependent variable, we initially tested a full factorial model, a 3 (condition: familiar, novel-repeated, novel-trial-unique) × 2 (phase: early trials, late trials) × 3 (lead: Fz, Cz, Pz) repeated measures ANOVA. Because we did not have specific predictions relating to higher order interactions, and there was no hint of a three-way interaction between the factors ($p > .45$), we adopted a reduced model including only main effects and two-way interactions between the factors.[3] Results of the reduced model are presented.

Amplitude of the Nc differed by lead, $F(2, 24) = 14.34$, $p < .0001$. The amplitude of the Nc was largest (or most negative) at Fz ($M = –24.0$ μV, $SD = 13.12$) and Cz ($M = –25.4$ μV, $SD = 16.24$), which did not differ, and was smaller in amplitude at Pz ($M = –17.9$ μV, $SD = 14.68$); this is consistent with the known fronto-central distribution of this component. There was also a marginal effect of phase, $F(1, 12) = 4.30$, $p = .06$. For early trials, the amplitude of the Nc was larger ($M = –25.8$ μV, $SD = 14.66$) than for trials late in the session ($M = –19.4$ μV, $SD = 14.80$).

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[2]An advantage of a mixed models approach to repeated measures analyses, relative to the traditional analysis of variance (ANOVA) approach, is that it is possible to select a covariance structure appropriate to the data. This is especially useful in the case of psychophysiological data, which often violate normality assumptions (Vasey & Thayer, 1987).

Following model selection procedures outlined by Littell et al. (2002), we compared several alternate covariance structures, including compound symmetry, autoregressive, and Toeplitz models. Model comparison was conducted separately for each dependent variable, and yielded comparable results. The autoregressive and Toeplitz models were comparable in fit, and better than the compound symmetry model, based on Akaike's (1974) and Schwarz's (1978) information criteria. Because the autoregressive model required estimation of fewer parameters and was therefore more parsimonious, we used this model for analyses of ERP. In the autogressive model, observations that are closer in time (or in this case, in space) are more highly correlated than observations with greater separation. Neural activity results in changes in voltage on the scalp as a result of volume conduction of electrical current, so that the activity of the same neural source will be evident in multiple electrodes across the scalp, varying to some degree with distance from the source; thus, the autoregressive model is intuitively appealing as useful in application to ERP data.

[3]We followed Kirk's (1995) recommendations regarding preliminary tests on the model and pooling sources of variance. Kirk indicated that to avoid Type II error, a higher level of α should be adopted before eliminating higher order interactions from the model (e.g., $\alpha = 0.25$). In these analyses, in no instances were higher order interactions eliminated when they were close to statistical significance (all $ps \geq .50$).

Latency of the Nc differed by lead as well, $F(2, 24) = 15.85$, $p < .0001$. A longer latency to peak was seen at Fz (M = 545 msec, SD = 72.1) than at Pz (M = 478 msec, SD = 103.5) or Cz (M = 502 msec, SD = 101.0), which did not differ.

Contrary to our expectations, there was no effect of condition on amplitude or latency at the midline leads, Fs(2, 24) = 0.27 and 0.24, ps > .70. Some possible reasons for this are explored in the Discussion. In addition, no significant effects were observed for slow-wave activity during the long-latency window.

Lateral leads. We used the same general approach to analyze the lateral leads as that taken at the midlines. However, because the position of the lateral leads on the scalp could not be represented in one dimension, two variables were created that roughly specified each lead's relative position on the scalp in the lateral and anterior–posterior dimensions. This is illustrated in Figure 2. Analyses of middle-latency activity included the frontal, fronto-central, central, and centro-parietal leads, along with anterior temporal leads T3 and T4. These leads were grouped because they all evidenced a negative deflection in this window (the Nc) that is not observed at more posterior locations. Analyses of long-latency slow-wave activity were conducted across all lateral leads.

For middle-latency analyses, minimum peak amplitude and latency to peak were analyzed using a 3 (condition) × 2 (phase) × 4 (lateral lead position: left lateral, left medial, right medial, right lateral) × 4 (anterior–posterior lead position: frontal, fronto-central, central/anterior temporal, centro-parietal) repeated measures ANOVA. In the absence of significant three- or four-way interactions (all ps > .50), we adopted a reduced model including only main effects and two-way interactions between the factors.

Analyses of the amplitude of the middle-latency negativity revealed differences by condition, $F(2, 24) = 3.74$, $p < .05$. The amplitude of the Nc was significantly larger to the novel-trial-unique condition (M = –23.6 μV, SD = 13.78) than it was to pictures of familiar events (M = –19.6 μV, SD = 12.60). The novel-repeated condition was intermediate (M = –22.2 μV, SD = 12.85), and did not differ from the other two conditions. This effect is consistent with recognition memory for the familiar event, relative to the trial-unique condition. Furthermore, the direction of the effect is the same as that seen in previous work with 9-month-old infants (Bauer et al., in press; Bauer et al., 2003; Carver et al., 2000).

Consistent with the trend seen at the midline leads, amplitude also differed by phase, with a larger amplitude seen at early trials (M = –24.8 μV, SD = 12.93) relative to late trials (M = –18.8 μV, SD = 12.74), $F(1, 12) = 21.31$, $p < .001$. There were also topographic differences, including an effect of lateral lead location, $F(3, 36) = 6.33$, $p < .005$. This effect was qualified by an interaction with phase, $F(3, 36) = 4.98$, $p < .01$. For early trials there was a large lateral lead position effect, $F(3, 36) = 7.72$, $p < .0005$. Follow-up tests indicated that amplitude was largest, and equivalent, for the left and right medial lead groups (Ms = –26.4 μV and –26.8 μV,

*SD*s = 14.27 and 14.08); amplitude was smaller, and equivalent, for the left and right lateral lead groups (*M*s = –22.9 μV and –23.0 μV, *SD*s = 11.61 and 11.06). In contrast, for late trials, there was a smaller but significant effect of lateral lead location, $F(3, 36) = 3.06$, $p < .05$; however, no lead positions differed significantly from each other. These findings indicate that initially the middle-latency negative deflection was large and most evident nearer the midline, but over time Nc amplitude waned and became more diffuse.

A primary goal of this study was to understand how processing of the three stimulus types changed over time. There was a marginal Condition × Phase interaction, $F(2, 24) = 2.60$, $p < .10$. Because understanding this trend in the data was central to our research question, we pursued this interaction by examining the effect of condition separately for early and late trials. During the early trials, amplitude did not differ by condition, $F(2, 24) = 0.88$, $p > .40$. Differences by condition emerged during late trials, $F(2, 24) = 4.71$, $p < .05$. Again, the smallest amplitude was seen for familiar pictures ($M = –15.6$ μV, $SD = 10.48$), which differed significantly from the novel-trial-unique condition ($M = –22.5$ μV, $SD = 13.90$). The novel-repeated condition was intermediate and did not differ from the other two conditions ($M = –18.4$ μV, $SD = 12.7$). Examined another way, when the effect of phase was analyzed separately for each condition (see Figures 3 and 4), there were significant decreases in amplitude from early to late trials for the familiar and novel-repeated conditions, *F*s(1, 24) = 14.29 and 14.53, *p*s < .001. However, for the novel-trial-unique condition, the decrease in amplitude did not approach significance, $F(1, 24) = 0.91$, $p > .30$.

We next analyzed the latency to peak amplitude. Analyses of latency did not reveal main effects of condition, phase, or lead position. An interaction between lateral lead position and phase was seen for latency to peak, $F(3, 36) = 5.16$, $p < .005$. For early trials there were no laterality differences in latency, $F(3, 36) = 1.30$, $p > .25$. Differences only emerged during late trials, $F(3, 36) = 4.08$, $p < .05$. Latency was longest for the right lateral leads ($M = 531.3$ msec, $SD = 102.23$), differing significantly only from the left lateral leads ($M = 501.0$ msec, $SD = 88.84$). Latency also differed topographically between anterior and posterior scalp leads: $F(3, 36) = 6.59$, $p < .005$. As was observed for midline leads, the latency to peak was shorter toward the back of the head (*M*s = 535.5 msec, 528.0 msec, 504.8 msec, and 499.6 msec, *SD*s = 89.85, 83.17, 95.27, and 101.27, for frontal, fronto-central, temporal/central, and centroparietal leads, respectively). Follow-up tests revealed that latency for adjacent lead groupings did not differ, but all longer range pairings did differ.

Just as was seen for amplitude, we found a marginal Condition × Phase interaction, $F(2, 24) = 2.63$, $p < .10$; again, we examined the effects of condition separately for early and late trials. There was a marginal effect of condition on latency for early trials, $F(2, 24) = 3.21$, $p < .06$. Latency was shorter to photographs of familiar events ($M = 501.9$ msec, $SD = 85.6$) than to photographs of novel-trial-unique events ($M = 536.1$ msec, $SD = 97.4$). Latency to photographs of

FIGURE 3 Waveforms illustrating changes in the Nc across trial phase, separately for each stimulus condition. ERP waveforms are averaged across all lateral leads included in the analysis of the middle-latency component. The Nc is indicated by a dashed oval.

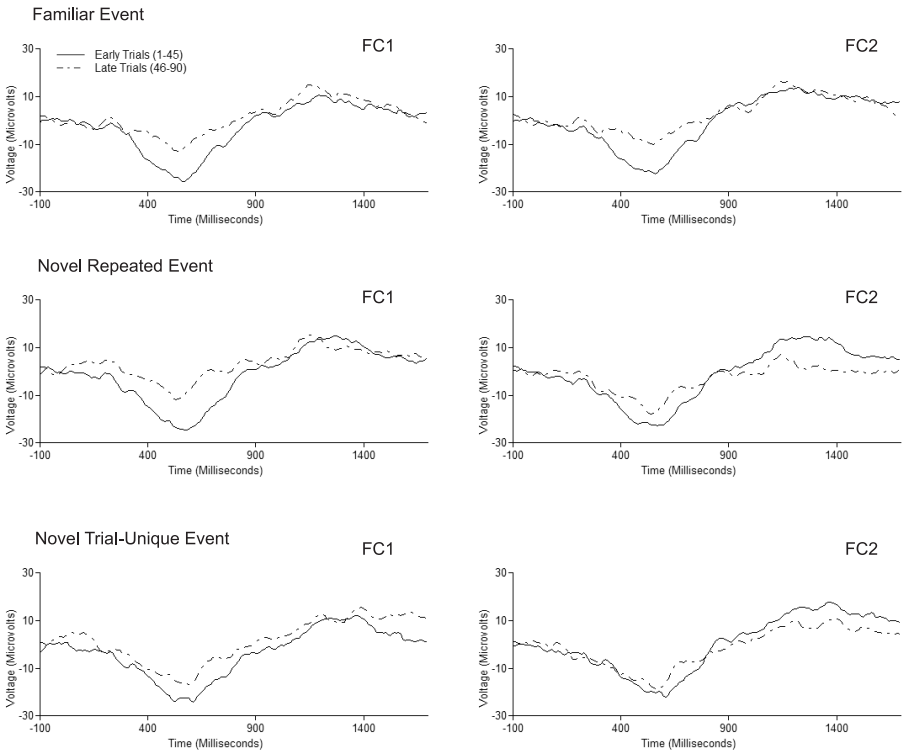

FIGURE 4 ERP waveforms at FC1 and FC2, illustrating changes in the Nc across trial phase, separately for each stimulus condition.

novel-repeated events was intermediate and did not differ from the other conditions ($M = 523.7$ msec, $SD = 86.1$). During late trials, latency did not differ by condition, $F(2, 24) = 0.72$, $p > .40$. The pattern of this interaction for latency to peak amplitude is the opposite of that observed for amplitude: In the case of latency, differences were seen early in testing, whereas differences in amplitude were only observed on the later trials. These results are consistent with dynamic change across the ERP test in infants' processing of familiar and novel stimuli. Initially, differences were not apparent in the gross morphology of the waveform, but subtle latency differences were consistent with an advantage in processing familiar stimuli. After increasing experience with the ERP paradigm and the familiar and novel-repeated conditions, differences were observed in amplitude but not latency, in that responding was minimal to the familiar condition, consistent with infants' having fully processed the stimuli or having become habituated to them.

Finally, we examined the slow-wave activity. For analyses of long-latency slow-wave activity, we initially analyzed area under the curve in a 3 (condition) × 2 (phase) × 4 (lateral position) × 6 (anterior–posterior position: frontal, fronto-central, central/anterior temporal, centro-parietal, parietal/posterior temporal, parieto-occipital) repeated measures ANOVA. In the absence of significant three- or four-way interactions (all *p*s > .80), we adopted a reduced model including only main effects and two-way interactions between the factors.

Slow-wave activity was modulated by condition, $F(2, 24) = 3.27$, $p = .05$, as illustrated in Figure 5. The novel-trial-unique condition elicited the largest positive slow wave, which differed significantly from the novel-repeated condition. Positive slow-wave activity was also seen for the familiar condition, but it did not differ from either of the novel conditions. In contrast to the middle-latency component, however, the Phase × Condition interaction did not approach significance, $F(2, 24) = 0.23$, $p > .75$.

There were also topographical differences in long-latency slow-wave activity. There was a main effect of anterior position, $F(5, 60) = 19.50$, $p < .0001$. This reflected a reversal in the polarity of slow-wave activity in the vicinity of the parietal leads. At occipital and parieto-occipital leads, there was a negative-going slow wave ($M = –1{,}936$ μV × msec, $SD = 9{,}423.0$) that differed significantly from all other lead

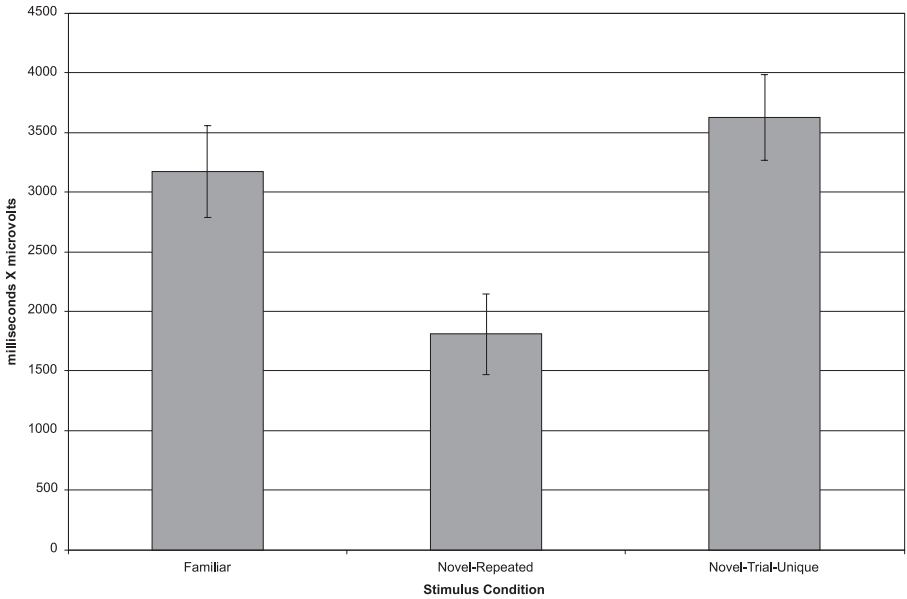

FIGURE 5 Amplitude of slow wave area scores (msec × microvolts), by condition. Error bars are standard errors.

groupings. At parietal and posterior-temporal leads, there was a return to baseline (M = 854 μV × msec, SD = 9,984.8), that differed from all other lead groupings except centroparietal leads. Positive slow-wave activity was observed at frontal (M = 5,006 μV × msec, SD = 8,281.3), fronto-central (M = 5,611 μV × msec, SD = 8,333.8), central and anterior temporal (M = 4,417 μV × msec, SD = 7,970.7), and centroparietal (M = 3,246.8 μV × msec, SD = 7,890.3) lead groupings, which did not differ from each other. There were also changes in topography between phases, as evidenced by a Lateral Position × Phase interaction, $F(3, 36) = 3.43$, $p < .05$. For early trials, the effect of lateral position was not significant, $F(3, 36) = 1.38$, $p > .25$. For late trials, there was an effect of lateral position, $F(3, 36) = 3.24$, $p < .05$. The smallest amplitude slow-wave activity was seen across left medial leads (M = 1,881 μV × msec, SD = 9,121.0), which differed significantly from left lateral leads (M = 3,701 μV × msec, SD = 12,007.4) and right medial leads (M = 3,500.9 μV × msec, SD = 8,843.0). Visual inspection of the waveforms suggested that this effect was driven by the negative slow wave at O1 that was present for all conditions. Right lateral leads did not differ from any other lead groupings (M = 2,417 μV × msec, SD = 8,577.9).

DISCUSSION

We used ERPs to gain a better understanding of 9-month-olds' processing of stimuli of varying degrees of novelty, and how processing changes over time and with repeated presentations. This study was the first to use a trial-unique condition with 9-month-old infants; it was also the first time ERPs for trial-unique stimuli were used to study processing of pictures of events infants had experienced in the laboratory. Our analyses of change in ERP components between early and late phases of the session permitted us to draw conclusions about changes in the morphology and topography of components over time; in addition, there were trends suggesting that differentiation between stimuli of different levels of familiarity also changed across repeated presentations. First, we discuss findings related to stimulus novelty and changes across trial phase more generally; then, we move on to describe patterns of findings relating to stimulus type and how this informs our understanding of infants' novelty-related and mnemonic processes.

Patterns of findings indicative of novelty detection were seen for the Nc, a middle-latency negative component, in analyses of lateral leads. Negative-going components during this time period have previously been characterized as reflective of novelty processing (Ackles & Cook, 1998); however, the use of repeated stimuli in previous studies has meant that, strictly speaking, these studies addressed relative rather than absolute novelty. Our inclusion of a trial-unique condition allowed us to examine processing of novelty with more precision. For the trial-unique condition, we did not observe adaptation of middle-latency negative components from early to late trials; that is, when infants saw brand new pictures late in the session, ampli-

tude was not significantly smaller than when they saw pictures in the same class earlier in the session. In contrast, for pictures of the test event and the control event (familiar and novel-repeated), amplitude was diminished over repeated presentations.

Interestingly, the amplitude of the middle-latency component for pictures of a familiar event decreased across testing, indicating that it was not at its minimum value from the beginning. Although infants had seen the events demonstrated several times using physical props, they had never before seen the pictorial representation used in the ERP test; thus, even for the familiar stimuli, there was an element of novelty. Furthermore, there is reason to believe that 9-month-old infants have not fully encoded a two-step event on the basis of four demonstrations distributed over 2 days (Bauer et al., 2001). Presumably, this could result in less robust recognition, even when tested immediately. Thus, although the information presented in the familiar condition was relatively familiar, it was by no means fully encoded at the start of the ERP test.

Differential patterns of response to the three stimulus conditions were also informative; there were trend-level indications that differences across condition changed as the ERP test progressed. Early in testing, there were differences in latency: The latency to Nc peak at anterior lateral leads was shortest to familiar pictures. Later in testing, Nc latency was equivalent across conditions. The direction of the difference seen early on contrasts with some previous findings: Bauer and colleagues (2003) found a longer Nc latency to familiar pictures. However, this was after a week-long delay; it could be that a lengthened Nc latency to a familiar stimulus results after the memory trace has lost integrity, resulting in increased time required to reactivate it. In this study, the ERP test took place shortly after familiarization, when infants' memory trace should be stronger and more easily accessible, so a shorter Nc latency may reflect rapid recognition of the familiar stimuli as such.

Analyses of Nc amplitude at lateral leads also differed by condition. This effect was seen across the entire ERP test, although separate analyses of early and late trials showed that differences in amplitude emerged as testing progressed. There was an orderly relationship between the amplitude and stimulus familiarity. Specifically, the more familiar the stimulus was, the smaller the amplitude of the middle-latency negative component. This is consistent with the literature relating levels of neuronal activity and the level of encoding of a stimulus. In the medial temporal lobe, familiar stimuli and contexts result in decreased responding for individual neurons (Xiang & Brown, 1998), and reduced levels of activation in general as revealed by functional imaging (Martin, 1999).

Differences between stimulus conditions were also observed for late slow-wave components, but the pattern was different, and less clearly related to stimulus familiarity. The novel-repeated condition elicited lower amplitude slow-wave activity than did the familiar and novel-trial-unique conditions. This pattern does not

immediately invite interpretation in terms of memory or recognition of novelty. Nelson and Monk (2001) related positive slow-wave activity to memory updating, drawing a parallel with the adult P300 component. In this study, the familiar condition elicited a PSW; this could reflect the access and updating of a memory representation for the familiar event. However, the novel-trial-unique condition also elicited a PSW of marginally greater amplitude, and in this condition memory access and updating was not possible, because no prior memory representation existed. It is possible that slow-wave responses to the familiar and novel-trial-unique conditions reflect different processes that result in similar changes in voltage at the scalp. Future studies using a denser electrode array may better detect differences in the distribution of electrical activity that would indicate distinct neural generators.

Previous studies have observed NSW activity to infrequent novel stimuli similar to our novel-trial-unique condition (Nelson & Collins, 1991; Richards, 2003). We were expecting to observe something similar, but instead we observed a large PSW to novel-trial-unique stimuli. This difference might be explained by one or more of the marked differences between this study and earlier work. The infants in this study were older: They were 9.5 months of age, whereas the oldest infants tested by Nelson and Collins (1991) or Richards (2003) were 7.5 months. Furthermore, Richards (2003) found pronounced changes in slow-wave morphology between 4 and 7.5 months, so it would not be surprising if further developmental changes take place by 9.5 months. The stimuli and mode of familiarization differ across studies. In this study, infants were shown color photographs of brightly colored props, some of which they had previously encountered in the laboratory. Nelson and Collins (1991) familiarized infants with color photographs of unfamiliar women's faces, then showed infants those photos along with additional, novel photos. Richards (2003) used black-and-white abstract patterns, familiarizing infants with some of these patterns but not others before the test. A final difference between this study and earlier studies relates to the relative probabilities of different conditions. Both Nelson and Collins (1991) and Richards (2003) used modified oddball paradigms. Infants were preexposed to two stimuli; one of these was presented on the majority of trials (60%), and the other was presented less frequently (20%). The rest of the trials were infrequent novel (20%). In this study, the probabilities for all three conditions were equal, with familiar, novel-repeated, and novel-trial-unique trials each comprising one third of the total (33.3%). In this study, particularly at the beginning of testing, most stimuli were new to the infant, and only rarely was a familiar image presented. In contrast, in the earlier studies, most stimuli were familiar, and a novel stimulus appeared on only one fifth of all trials. Infants' responses to novel stimuli might be expected to vary depending on whether those novel stimuli appear in a context of general novelty or general familiarity. More work is necessary to elucidate the conditions that elicit different patterns of slow-wave activity such as the NSW, and how slow-wave activity changes over the latter half of the first year.

In previous work, differentiation of familiar and novel stimuli has been observed at midline leads (Bauer et al., in press; Bauer et al., 2003; Carver et al., 2000). In contrast, in this study, differences involving stimulus condition were not observed at midline leads, although the amplitude of the Nc at the midlines did diminish from the early to late phases of testing. However, the pattern of results observed with respect to the Nc at anterior lateral leads parallels that seen at midlines in earlier studies using similar methods (e.g., Bauer et al., 2003). We know from previous infant ERP studies that the context of testing, including the broader array of stimuli used in testing, influence ERP morphology: Infant ERPs to the mother's face differ when it is contrasted with a similar or dissimilar stranger's face, for example (de Haan & Nelson, 1997). The inclusion of a trial-unique condition in this study may have had a similar effect, perhaps reducing the contrast between the two repeated conditions, such that differences were detectable in lateral lead analyses, which were aggregated across the scalp, but were not discernable at midlines.

ERPs result from activity of localized sources within the cortex, but due to volume conduction they are detectable to varying degrees at electrodes across the scalp (Nunez, 1990). As a result, it is difficult to draw conclusions as to the location of the neural circuits recruited for novelty detection or recognition memory in this paradigm. An array of 29 electrodes does not afford us sufficient coverage to conduct source localization analyses, and even denser electrode arrays suffer from the inverse problem, namely that multiple combinations of neuronal sources can produce the same patterns of electrical activity at the scalp (Nunez, 1990). Differences most clearly related to processing of novel stimuli were seen for the Nc component, which is maximal at frontal and central electrodes. Reynolds and Richards (2005) recently used independent components analysis of ERPs collected with a high-density electrode array, in conjunction with source localization techniques, to study the neural sources of infant ERPs. In this study of 6-month-old infants, they localized the Nc to the anterior cingulate and areas in prefrontal cortex including the medial and inferior frontal gyri. These findings coincide with studies implicating anterior cingulate in novelty-detection processes (Dias & Honey, 2002). It is plausible that differences in brain activity observed in this study reflect prefrontal and anterior cingulate activity, possibly in conjunction with other areas known to play a role in processing of novelty, such as the hippocampus (Strange & Dolan, 2001).

Infants are by definition neophytes in the world, encountering new circumstances and events daily. Processing of novelty is thus crucial to the learning and development that are necessary for their ultimate functioning in society as new people, objects, and speech sounds become familiar with increased experience. The inclination to orient to novelty can be conceived of as a tool available to infants to assist them in these tasks. It is thus important that we understand the neural mechanisms underlying this ability and how they develop. In the course of ERP testing, infants who participated in this study encountered the novel-repeated stim-

uli for a maximum of 30 presentations of 500 msec. With only this minimal experience, totaling 15 sec, we were able to detect changes in brain activity that were related to processing of these stimuli. This suggests that learning about novel information begins immediately and has rapidly observable effects, with important functional implications for infant cognitive processes.

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