PAPER

Associations between infant brain activity and recall memory

Leslie J. Carver, Patricia J. Bauer and Charles A. Nelson

Institute of Child Development, University of Minnesota, USA

Abstract

Long-term explicit memory is thought to involve a complex neural circuit including the medial temporal lobe, the medial diencephalon, the prefrontal cortex, and association cortices. When this memory system and associated neural circuitry develops is of great interest to developmental psychologists and developmental cognitive neuroscience researchers. In the present report, we provide evidence of a relation between behavioral and neurophysiological measures of long-term explicit memory in 9-month-old infants. These measures provide converging evidence of the development of long-term explicit memory at least by the end of the first year of life.

Children emerge from the infancy period with the ability to form and retain explicit\(^1\) or declarative memories of past events. Whereas adults do not recall events that occurred while they were infants (Kihlstrom & Harackiewicz, 1982; Sheingold & Tenney, 1982; Winograd & Killinger, 1983), recent research has made clear that even very young infants have the capacity to retain information over long delays (e.g., Meltzoff, 1988; Rovee-Collier, 1990; Carver & Bauer, 1999). Precisely when infants begin to show signs of long-term explicit memory, i.e. the ability to recognize or recall familiar information after very long delays, is not known. Moreover, the neural events that underlie the development of this ability are largely uncharted. In this research we provide the first demonstration that brain activity recorded at one age (9 months) is related to long-term recall memory at a later age (1 month later). The current research thus provides converging evidence of the development of long-term explicit memory at least by the end of the first year of life.

Long-term explicit memory is proposed to involve a complex neural circuit, the components of which include the medial temporal lobe (Squire & Zola-Morgan, 1991; Squire, 1992), the midline diencephalon (Calabrese, Haupts, Markowitsch & Gehlen, 1993; Hodges & McCarthy, 1993; Markowitsch, von Cramon & Schuri, 1993), cortical association areas such as those in the temporal cortex that are involved in higher-order visual processes (Squire, 1986; Bachevalier, 1992; Bachevalier & Mishkin, 1994) and the prefrontal cortex (Markowitsch et al., 1994; Buckner et al., 1995; Markowitsch, 1995). Development of this circuit is essential for adult-like explicit memory. Recently, it has been hypothesized that although, in the human, the development of the explicit memory circuit proceeds over a period of years, its development begins to coalesce near the end of the first year of life (Schacter & Moscovitch, 1984; Nelson, 1995, 1997).

Because infants do not speak, the acid test of explicit memory (i.e. verbal report) is unavailable as a tool with which to examine the developmental status of this important mnemonic function. Accordingly, to evaluate the hypothesis that long-term explicit memory first appears near the end of the first year of life, we employed two separate nonverbal measures of memory: one of recognition and one of recall.

Recognition and recall memory are considered to be two different but related expressions of explicit memory (Haist, Shimamura & Squire, 1992). Recognition memory involves judgments as to whether or not perceptually available material is familiar; and by definition it requires that a cue be present (i.e. that which is being

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1 Although explicit and declarative are related terms, they are not absolutely identical in definition. For ease of communication, we will use the term explicit throughout this report.

Address for correspondence: Leslie J. Carver, CHDD, Box 357920, University of Washington, Seattle, WA 98195, USA.

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recognized). There is evidence that although infants begin to recognize material at very young ages, their recognition ability continues to develop such that, around 8 months of age, important changes occur in the types of tasks in which they evidence recognition. In research using event-related potentials (ERPs: electrical activity related to the presentation of a stimulus and recorded at the scalp), however, investigators have established that infants appear to recognize familiar stimuli early in the first year of life. For events with which the infant is familiar (e.g. a face to which they have been habituated), infants as young as 3 months show evidence of recognition memory after short (e.g. within minutes of habituation) delays (e.g. Pascalis, de Haan, Nelson & de Schonen, 1998). In studies measuring recognition memory for stimuli to which the infant is very familiar (e.g. the mother’s face), infants as young as 6 months of age show ERP evidence of recognition memory (de Haan & Nelson, 1997). Critically, in tests in which stimuli are presented to infants either frequently or infrequently, prior to about 8 months of age, infants’ ERPs differentiate frequently presented stimuli from infrequently presented stimuli, but do not differentiate infrequently occurring familiar stimuli from infrequently occurring novel stimuli (Nelson & Collins, 1991, 1992). After about 8 months, infants differentiate these two categories of infrequently seen stimuli, suggesting that not only are they capable of responding to the frequency of presentation, but they are also able to identify familiar stimuli as such even when they are presented infrequently. By about the same age, infants show ERP evidence of visual recognition memory for objects previously encountered in a different (i.e. tactile) modality\(^2\) (Nelson, Henschel & Collins, 1993).

A commonality among ERP studies with infants younger than 1 year of age has been that recognition memory has been measured either for stimuli to which the infant was familiarized very recently, within minutes, or for stimuli that are very familiar and have been seen very recently (i.e. the mother’s face). Although there is some evidence that infants’ looking behavior differentiates familiar from unfamiliar stimuli after delays of up to 2 weeks (Fagan, 1992), very little is known about the neurophysiological correlates of infants’ recognition memory for material after very long delays.

\(^2\)Cross-modal memory differs from simple cross-modal transfer (perception of object characteristics across modality) in that it involves forming associations based upon cross-modal characteristics of the recognized objects. Cross-modal transfer has been shown to involve the amygdala; cross-modal memory has been hypothesized to involve additional aspects of the medial temporal lobe including the hippocampus (Nelson, 1995).

The ability to recall differs from the ability to recognize in that recall involves retrieving a representation of an event without requiring that perceptual support be available, although it may be (e.g. Mandler, 1990; Haist et al., 1992; Bauer, 1996). One nonverbal technique that taps recall processes in infants is deferred imitation (Mandler, 1990; Bauer, Hertsgaard & Dow, 1994; Bauer, 1995, 1996; Meltzoff, 1995). In deferred imitation, infants view, but are not allowed to imitate, single actions or sequences of actions enacted with props. After the imposition of a delay, they are permitted to imitate. If they produce the target actions, memory for them is inferred. Appropriate controls are used to ensure that production of target actions is due to memory for them. In some research programs, infants’ production of actions they have seen previously is compared with production of new actions with props they have not seen previously (e.g. Bauer, Kroupina, Schwade, Droopik & Wewerka, 1998; Carver & Bauer, 1999). In other versions of the paradigm, production of target actions is compared between infants who have seen them modeled and infants who have experience viewing the props but have never seen the target actions modeled (Meltzoff, 1995; Heimann & Meltzoff, 1996). In both cases, memory for the events can be separated from other factors that might influence infants’ later behavior (e.g. experience with the test situation or experimenter).

As argued elsewhere (e.g. Mandler, 1990; Bauer, 1995; Meltzoff, 1995), infants’ memory for modeled events in deferred imitation testing can, with confidence, be attributed to explicit memory. A number of characteristics associated with explicit memory, such as acquisition in a very small number of trials and flexibility across changes in context (Squire, Knowlton & Musen, 1993), have been demonstrated in experiments using elicited imitation. Infants can imitate events after as little as one exposure to them (Meltzoff, 1988, 1995; Bauer & Hertsgaard, 1993; Bauer & Dow, 1994; Bauer, Hertsgaard & Wewerka, 1995). In contrast, performance on implicit tasks such as serial reaction time tasks requires 200–400 trials (e.g. Knopman & Nissen, 1987). Moreover, imitation is not suppressed by changes in context between training and test. For example, infants imitate in locations different from those in which they first saw the events (Klein & Meltzoff, 1999), in rooms the appearance of which are dramatically altered between exposure and test (Barnat, Klein & Meltzoff, 1996; Klein & Meltzoff, 1999), and in the absence of an expert peer who first demonstrated the events for the infants in both the same and different contexts from the test (Hanna & Meltzoff, 1993). Infants also will imitate with props functionally equivalent but perceptually
different from those with which they first encountered the event (Bauer & Dow, 1994). These demonstrations of rapid, flexible acquisition of novel behaviors indicate that explicit or declarative processes are at work. Consistent with this suggestion is the recent finding that adults with amnesia are unable to perform an age-appropriate analog of the elicited imitation task (McDonough, Mandler, McKee & Squire, 1995). Moreover, particularly when infants are required to imitate multi-step sequences of actions, recall memory, as compared to recognition memory, can be inferred. Although at the time of recall the props used to produce the to-be-remembered actions are available (indeed infants use them to ‘report’ their memory for the actions), and they provide a cue to recall, information about the order in which the sequence of actions occurs is not perceptually available. To reproduce an ordered sequence, then, the infant must encode information about temporal order at the time the sequence of actions is modeled and later must retrieve that information from a representation of the event, in the absence of ongoing perceptual support (Bauer, 1995). In this the task seems clearly to require recall processes.

There is some suggestion from the literature that infants become competent at deferred imitation near the end of the first year of life. At 6 months of age, infants can imitate simple actions immediately after seeing them modeled (Barr, Dowden & Hayne, 1996). However, with the same exposure they do not recall them 24 hours later, suggesting rapid forgetting at this young age. In contrast, at 9 months of age, some infants imitate events after delays of 24 hours (Meltzoff, 1995; Heimann & Meltzoff, 1996) to 1 month (Carver & Bauer, 1999). Whereas pronounced individual differences are not observed among infants only a few months older (e.g. 13 months, Bauer & Hertsgaard, 1993), at 9 months, approximately 50% of infants show evidence of recall after a delay (Meltzoff, 1988; Heimann & Meltzoff, 1996; Carver & Bauer, 1999). One possible explanation for these data is that some infants are simply less able to produce the motor actions required to imitate the events. This hypothesis is contraindicated, however, by evidence that, following brief re-exposure to events (in the form of re-modeling by the experimenter), infants who initially did not imitate after a delay were able to produce the target event sequences (Carver & Bauer, 1999). Rather than motor immaturity, we suggest that observed individual differences at 9 months are indicative of a watershed period in development, during which some infants have achieved the ability to recall test material whereas others have not yet done so. Consistent with this suggestion is evidence that, by 10 months, infants show robust imitation of events after both short and long delays (i.e. up to 3 months) (Carver, 1998).

The time frame laid out above for the emergence of long-term explicit memory is consistent with recent speculation that the neural circuit for explicit memory begins to develop near the end of the first year of life (e.g. Nelson, 1995, 1997). Additional support for this time-line comes from developmental neurobiology and cognitive neuroscience. Research with non-human primates suggests that the connections between cortical and subcortical components of the explicit memory system begin to conjoin at an age that roughly corresponds to the end of the first year of life in the human (Webster, Ungerleider & Bachevalier, 1991a, 1991b; Webster, Bachevalier & Ungerleider, 1993, 1994).

In the present report, we show that the capacity for long-term recall that emerges near the end of the first year of life is mirrored in the ability, as measured by ERPs, for long-term recognition of objects used in the recall memory test. We provide converging evidence from neural and behavioral measures of long-term explicit memory that this mnemonic function is emergent in infants at the end of the first year of life. These converging measures also provide important information about the development of the neural substrate of long-term explicit memory. Although explicit memory can be inferred or hypothesized based on the infant’s behavior, neurophysiological measures such as ERP add to this evidence by showing a direct relation between behavior and brain activity.

Method

Participants

The participants were 20 9-month-old infants drawn from a larger sample of 47 (Carver & Bauer, 1999). This subset of infants was selected because they provided interpretable ERP data. The mean age of these infants was 273 days (range 265–280 days). Thirteen of the infants were girls. Informed consent was obtained from parents before the beginning of the study. Data from the remaining 27 infants were excluded from further ERP analysis (a) because EEG or EOG signals exceeded limits ($n = 20$ infants), (b) because of equipment failure and/or experimenter error ($n = 3$ infants) and (c) because the infants were too fussy to complete the required number of trials ($n = 4$ infants). No infants were excluded on the basis of their performance in the deferred imitation task.
Stimuli

Infants were each shown three two-step, novel events. An event consisted of two actions and an end state, each of which could be depicted using still photography. In every event, the target actions had to be completed in the modeled order for the end state to occur. For example, in one event, ‘find Bubbles’, the infant put a red cylinder into a wooden block. The infant then pushed the block into a base, making a green dinosaur puppet ‘pop up’. Events were randomized by block such that each infant saw one of two sets of three events. The remaining set of three events served as a within-subjects control. Events were counterbalanced across infants so that each block was used for an equal number of infants. The events within each block were presented randomly, so that each event occurred in a different serial position during each of the exposure sessions. The events used are described in the Appendix.

For ERP testing, stimuli consisted of still slides of a woman’s hand completing each step of one old event (an event the infant had seen previously) and one new event (an event the infant had not seen previously). In addition, slides of the result of the completion of the actions in the correct order (the ‘end state’) were shown for the old and new event. Stimuli were counterbalanced, so that each event served as old and new equally often across infants. Slides were presented in random order for ten trials each for each step and end state of the old event and each step and end state of the new event, for a total of 60 randomly ordered trials.

Procedure

Although not necessary for recall in imitation tasks (Meltzoff, 1988, 1995), increased exposure to events to be remembered is likely to facilitate infants’ memory for them. To maximize the likelihood that infants would imitate, infants were given three brief exposures to the events. Exposure to the to-be-remembered events occurred over three sessions; recognition memory was tested via ERP one week after the last exposure session; recall memory was tested via deferred imitation one month after recognition memory testing (see Table 1).

Exposure sessions

At the beginning of the first session, infants were allowed to manipulate the props used for the imitation procedure prior to modeling of the events. In this way, baseline measures of the infants’ behavior toward the events could be measured. After the infant-controlled baseline period ended (i.e. when the infant engaged in repetitive behaviors such as banging or throwing the props), the experimenter modeled the event two times in succession and then began the baseline interval for the next event. This procedure was followed for all three of the test events. During the second and third visits, which occurred within 3 days of the initial visit and were separated from one another by no more than 3 days (mean number of days between visits 1.97; range 1–3), the events were again modeled for the infants in random order. Infants did not touch or manipulate the props after the baseline period in the first exposure session.

<table>
<thead>
<tr>
<th>Session</th>
<th>Time</th>
<th>Activity</th>
</tr>
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<tbody>
<tr>
<td>1–3</td>
<td>0</td>
<td>Initial exposure to events during each of three sessions separated by 1 to 3 days</td>
</tr>
<tr>
<td>4</td>
<td>Session 3 plus 1 week</td>
<td>Recognition memory (ERP) testing</td>
</tr>
<tr>
<td>5</td>
<td>Session 4 plus 1 month</td>
<td>Recall memory (deferred imitation) testing</td>
</tr>
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Recognition memory testing

One week following the third session (mean 7.0; range 4–10 days), infants’ recognition memory was tested using ERPs. ERPs were recorded at seven scalp locations (Pz, Cz, Fz, T3, T4, T5, T6), according to the international 10–20 system of electrode placement. Electrodes were affixed with foam pads, grass EC2 cream and cloth headbands. Impedances were kept at less than 10 kΩ, and were generally less than 5 kΩ. Scalp activity was referenced to linked ears, and a ground electrode was placed on the infant’s forehead. Electroocular activity was recorded from bipolar miniature electrodes placed in a transverse position above and below one eye. These electrodes were held in place with small adhesive collars. All electrical signals were recorded using a Grass Neurodata Acquisition System with Model 12A5 amplifiers. EEG gain was set to 20 000 and EOG gain was set to 5000. The bandpass filters were set at 0.1 and 30 Hz. A 60 Hz notch filter was in place.

Each infant was tested individually while seated on the parent’s lap facing a rear projection screen approximately 75 cm away. The screen was embedded in a black wall that blocked the infant’s view of the remainder of the room. There were small holes in the wall through which observers recorded and, when necessary, redirected the infant’s attention to the screen. The session began when the infant fixated the screen. Each trial consisted of a 100 ms baseline followed by presentation of the stimulus for 500 ms. The stimuli

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consisted of still slides depicting Step 1, Step 2, and the end state of one event to which the child had been exposed previously (‘old’ event) and the same images for an event to which the child had not been exposed previously (‘new’ event). A total of 60 trials were presented (30 trials of images from the old event and 30 trials of images from the new event).

ERP recording continued for 1200 ms after the end of stimulus presentation. The EEG was sampled every 10 ms (100 Hz) throughout each trial. The inter-trial interval varied between 500 and 1200 ms. If the observer noted that the infant looked away from the screen, she signaled the computer via a button push to repeat the trial. If needed, the observer redirected the infant’s attention to the screen by tapping the back of the wall or shaking a rattle. Brain activity was not recorded from trials during which the infant was not looking at the screen, during which the experimenter or parent spoke, or during which the observer attempted to redirect the infant’s attention to the screen. Data were digitized on line and stored on a removable hard disk cartridge. Data were edited for blink artifact by a computer algorithm. After editing, each infant’s data were corrected for the influence of eye movement on the EEG (Gratton, Coles & Donchin, 1983). The eyeblink correction algorithm calculated the effect of EOG deflections on the EEG. It then computed a model estimating the influence of eye movement on the EEG and subtracted the artifact estimated to be due to EOG influence from the EEG. Data were excluded if the EOG signal exceeded analog to digital values in any 50 ms window. Individual averages and grand means were created for infants with a minimum of five artifact-free trials. The average included an equal number of trials for each condition for each participant. For the group of infants who later produced at least one pair of target actions in the correct order (see below), the mean number of trials in the average was 11 (range 5–20). For the group of infants who did not later produce at least one pair of target actions in the correct order, the mean number of trials was 15 (range 7–24).

Recall memory testing

One month after the ERP test (mean 29.47; range 22–39 days), infants’ recall memory for the events was tested. This delay interval was chosen because it was substantially longer than delays that had been previously used in studies with children this age (e.g. Meltzoff, 1988) and thus would provide a test of long-term recall. Infants were tested in the same room by the same experimenter as in the exposure sessions. For each event in turn, infants were given the props used for the events and their behavior was observed. In a procedure identical to the baseline procedure in the initial exposure session, infants were allowed to manipulate the props for an infant-controlled period. Infants were given the props for each event they had been shown during the initial exposure sessions. As a within-subjects control, they were also tested on three events that they had not seen before. Infants’ actions on the events were video recorded, and production of target actions and correctly ordered pairs of target actions was noted by a trained observer who was unaware of the hypotheses being tested and the specific events that were old and new for each infant. These scores were averaged across events. In addition, 20% of the tapes were coded by a second coder for reliability. Inter-rater reliability was 91%. Memory for the events was inferred by comparing performance on events the infants had seen before (‘old’ events) with performance on events they had never seen before (‘new’ events). A second test of memory could be performed by comparing production of target actions and correctly ordered pairs of target actions during the baseline in the first exposure session with performance during the delay test. However, because the infant matured by one month between these intervals, the comparison of old and new events provides a more rigorous test of recall memory unconfounded with maturation. Information about performance on the delay test compared with baseline is reported by Carver and Bauer (1999).

Data reduction and analysis

Behavioral data

The elicited imitation procedure yielded two dependent variables. First, the number of target actions produced for old compared to new events was measured. Second, the number of pairs of target actions produced in order was compared between the two conditions.

Group assignment

Fifty percent of the infants produced no correctly ordered pairs of target actions. Infants who produced at least one pair of target actions in the correct order formed one recall status group (n = 10; seven girls and three boys), and infants who did not produce at least one pair of target actions in the correct order formed the second group (n = 10; six girls and four boys). Recall of pairs of actions in the correct order, and thus group assignment, was not related to the length of delay between the exposure and test sessions (see Carver & Bauer, 1999, for details). ERP data were analyzed using recall status as a grouping variable.
ERP data

Three components of the ERP that are relevant to our data have been described in infants less than 1 year of age. First, a middle latency component, referred to as the Nc component and shown in Figure 1, has been related to attentional processes (Courchesne, Ganz & Norcia, 1981; Nelson & Collins, 1991, 1992; Nelson et al., 1993; Nelson, 1994; de Haan & Nelson, 1997). When infants are tested using visual stimuli that vary on a number of dimensions (e.g. familiarity or probability of occurrence), the Nc component is largest in response to whichever stimulus infants devote most attention (e.g. a novel object; Nelson & Collins, 1991, 1992; Nelson et al., 1993). In addition, the Nc may reflect aspects of long-term recognition memory for very familiar stimuli (de Haan & Nelson, 1997). By about 1 year of age, the latency of the Nc component is approximately 500 ms (Nelson, 1994). To compare the Nc component between conditions and groups, the maximum negative amplitude in the time interval including the component was calculated and used as the dependent measure.

The second and third components occur within the same time window immediately following the Nc component. The second component, a negative slow wave (NSW), is thought to reflect detection of novel events (Nelson, 1994). The positive slow wave (PSW) typically is invoked by stimuli the infant has seen previously and that have been partially encoded (i.e. stimuli that are being updated in memory; see Figure 1; Nelson, 1994). To compare the slow wave components between groups and conditions, the area beneath the curve during the time frame that included the positive and negative slow waves was calculated and used as the dependent measure.

Results

Recall memory

A 2 (condition) × 2 (group) repeated measures analysis of variance (ANOVA) was conducted for each dependent measure (number of target actions produced and number of correctly ordered pairs of target actions produced). For the number of target actions produced, a main effect of condition was observed: $F(1, 18) = 10.67, p < 0.005$. Infants produced more target actions for old than for new events. In addition, a group × condition interaction was observed: $F(1, 18) = 24.47, p < 0.0001$. As can be seen in Figure 2(a), the main effect was carried by infants who imitated at least one correctly ordered event: post hoc testing revealed that these infants produced a larger number of individual target actions on old than on new events. For pairs of actions in the target order there was a group × condition interaction: $F(1, 18) = 19.1, p < 0.0001$. Analysis of the interaction showed that infants who did imitate an event in the correct order did so more for old than for new events. In addition, these infants produced more pairs of target

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3The specific event sequences that the infants recalled were not necessarily those to which they had been re-exposed via the ERP session. As reported in Carver and Bauer (1999), later recall was not affected by re- (old events) or pre- (new events) exposure to the event sequences in the ERP session.
actions in the correct order than would be expected by chance: $t(9) = 23.0$, $p < 0.01$ (see Carver & Bauer, 1999, for details). Because the groups were constructed on the basis of whether or not the infants produced a correctly ordered pair of target actions, by definition only one group produced any correctly ordered pairs. Therefore, only the data for those infants are shown in Figure 2(b).

**Recognition memory**

ERP waveforms for infants who later did and did not imitate at least one event in the correct order are shown for all leads in Figures 3 and 4, respectively. Analysis of the data at the lateral leads showed no effects of group or condition. Therefore, the data discussed here are limited to the midline leads. ERP data were analyzed in two time frames, or windows. Window 1 consisted of the data collected between 260 and 870 ms after stimulus onset. This window was intended to capture the mid-latency component thought to be associated with attentional processes and recognition memory (de Haan & Nelson, 1997). A $2 \times 3$ (midline leads: Pz, Cz, Fz) x 2 (condition: old events, new events) repeated measures ANOVA was conducted. A mid-latency negative peak (the Nc component) was observed at about 520 ms. Analysis of the amplitude of this waveform revealed a main effect of condition: $F(1, 18) = 7.18$, $p < 0.02$. The amplitude of the component was larger in response to new than to old events. Further, a condition x group interaction that approached significance, $F(1, 18) = 3.02$, $p = 0.09$, was also observed. Inspection of this interaction (Figure 5) suggests that the main effect was carried exclusively by the group of infants who recalled at least one complete event sequence in the recall portion of the test. The planned simple effects test indicated that the response to old events differed from that to new events for the infants who recalled at least one complete sequence in order, $F(1, 18) = 4.69$, $p < 0.05$, but not for infants who did not, $F(1, 18) = 0.16$, $p = 0.69$. No main effects or interactions with lead were observed.

The second time window contained the interval from 870 ms after stimulus presentation to the end of the recording interval. This window was intended to capture both the positive and negative slow waves that have been associated with memory updating and novelty detection (Nelson, 1994). A $2 \times$ (group: infants who completed at least one event sequence in order, infants who did not complete an event sequence in order) x 3 (midline leads: Pz, Cz, Fz) x 2 (condition: old events, new events) ANOVA was conducted. The dependent measure was obtained by integrating the area above and below baseline for the second window, deriving the area under the curve for positive and negative slow wave activity. A condition x group interaction was observed, $F(1, 18) = 4.1$, $p < 0.05$. As suggested by Figure 6, simple effects tests revealed that the area under the curve in window 2 was marginally greater for old than for new events only for those infants who completed at least one correctly ordered event in the recall portion of the test: $F(1, 18) = 3.57$, $p = 0.07$. There was no difference between the area under the curve in response to old and new events for the infants who did not recall at least one complete event sequence: $F(1, 18) = 0.02$, $p = 0.82$. There was no main effect or interaction with lead.

In summary, for the component of the ERP thought to be associated with attention to salient stimuli and recognition memory (i.e. the Nc component), the amplitude of the response differed only for those infants who later imitated at least one complete event. This suggests that only this group of infants treated the two

![Figure 2](image-url)  
*Figure 2* Production of (a) target actions and (b) correctly ordered pairs of target actions in the recall task.

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Figure 3  ERP's for infants who imitated at least one complete event in the correct order during the recall test.

Figure 4  ERP's for infants who did not imitate at least one complete event in the correct order during the recall test.

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Figure 5  Amplitude of the Nc component for infants who did and did not recall complete event sequences. The amplitude of this component differed only for those infants who imitated at least one entire sequence in the correct order.

Figure 6  Area under the curve for the interval including the positive and negative slow waves for infants who did and did not recall complete event sequences. Area under the curve differentiated old from new events only for those infants who imitated at least one entire sequence in the correct order.

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sets of stimuli differentially. For the components thought to be associated with memory for familiar events and detection of novelty (i.e. the positive and negative slow wave activity), the area under the curve differentiated old from new events only for those infants who later recalled the events. This result suggests that only this group of infants recognized the images of the familiar events and detected that the novel events were unfamiliar.

Discussion

The long-term recall performance of the 9-month-olds in this research was indicative of individual differences in this ability. As a group, infants produced more individual target actions for old than for new events. However, they did not reliably produce more correctly ordered pairs of target actions for old than for new events. Production of correctly ordered pairs of target actions provides particularly compelling evidence of long-term explicit memory: Although it could be argued that production of individual target actions may be triggered or ‘afforded’ by the props, information about the order in which those actions should be produced is not perceptually available (Bauer, 1995, 1996). Production of correctly ordered pairs of target actions therefore requires the infants to encode, maintain, and retrieve a representation of the temporal order of the event, in the absence of ongoing perceptual support. Because of this, production of correctly ordered pairs of target actions is the dependent measure most likely to tap explicit memory processes (Bauer, 1995, 1996). Inspection of individual performance patterns indicated that, consistent with previous research (Meltzoff, 1995; Heimann & Meltzoff, 1996) as well as the larger sample from which these infants were drawn (Carver & Bauer, 1999), 50% of infants imitated at least one pair of target actions in the previously modeled order. This dichotomy was used to group the infants (in effect, a median split based on production of pairs of target actions). Analyses by group revealed that infants who recalled at least one complete event were the only ones to produce more individual target actions and pairs of correctly ordered target actions on events they had seen previously than on new events.

The long-term recognition memory performance of the infants was also indicative of individual differences in mnemonic performance. Analysis of the Nc component at the midline leads revealed that, for infants who later recalled a complete sequence, brain activity differentiated images of old and new events at all scalp leads. Although an Nc component was observed both for infants who later recalled the events and infants who did not, the amplitude of this component in response to pictures of props used in old and new events differed only for the group of infants who later recalled the events (see Figure 5). In this group of infants, the amplitude of the Nc component in response to new stimuli was greater than that to old stimuli. Thus, although all the infants attended to the visual stimuli, as evidenced by the presence of the Nc component in both groups, only those infants who later imitated the events attended differentially to the pictures of the new and old stimuli. These data may also be indicative of recognition memory for the stimuli, as the Nc component has been attributed to aspects of recognition memory as well as attention (de Haan & Nelson, 1997).

Consistent with previous research using ERPs to measure recognition memory in infancy, a positive slow wave was observed in response to the old stimuli, suggesting memory updating in response to those stimuli. In addition, a negative slow wave was seen in response to the novel stimulus, suggesting detection of novelty. These late slow wave components were only seen in those infants who later recalled the event (see Figure 6). For those infants only, the area under the positive slow wave (i.e. the memory updating response to pictures of old events) was significantly different from that under the negative slow wave (i.e. the novelty detection response to new events). Infants who only produced isolated target actions showed a return to baseline for both old and new events, and a lack of differentiation between the responses to old and new events in this window. Thus, only infants who later imitated the events showed brain activity patterns consistent with recognition memory and detection of novelty in response to the images of the old and new events.

In contrast to previous research, no effect of lead or condition × lead interaction was observed for either component. Visual inspection of the waveforms showed that the distribution of the Nc component was more posterior than has been reported in previous research (Nelson & Collins, 1992; de Haan & Nelson, 1997), and the distribution of the slow wave activity was also more posterior than was expected. In previous reports, the Nc and slow wave components were focused over central and frontal midline leads (Courchesne, Ganz & Norcia, 1982; Nelson & Collins, 1992; de Haan & Nelson, 1997). In contrast, the components observed here were distributed evenly across frontal and posterior scalp leads, such that no effects of lead were seen. It is unclear why the activity was distributed differently than has been observed.
previously. One possible explanation is that the distribution was changed because, in the present research, the delay between exposure to the events and testing was longer than in previous research. Often, infants are familiarized with stimuli, and recognition memory is tested virtually immediately thereafter (e.g. Nelson & Collins, 1992; Nelson et al., 1993). Future research should address this possibility by measuring recognition memory for demonstrated events both soon after exposure and following a longer delay to determine the effect of delay interval on scalp topography.

An issue raised by the current results is whether the infants who did not remember at least one of the events failed to recall because they failed to encode the events, because they failed to store representations of them in long-term memory, or because they were unable to retrieve representations of the events from long-term memory. Research measuring recognition at a time closer to encoding, in addition to addressing questions about the topographic distribution of the ERP, will be able to address this issue. If infants failed to encode representation of the event, they should also fail to recognize stimuli taken from the event even shortly after exposure.

The results of the present research suggest that infants who show recognition (based on their brain activity) of pictures of familiar events are also able to recall events over long delays. They are consistent with the suggestion that the memory system that is involved in recognition and recall memory undergoes significant developmental change near the end of the first year of life. The observed relation between the different indices of memory is important evidence that the neural systems that underlie long-term explicit memory, as studied by elicited imitation and ERP, develop concomitantly. Those infants who recognized the props used in the events one week after they last saw them were the same infants who, one month later, were able to recall the events. These data mark the first instance in which converging measures of long-term recall and recognition memory have been used together with the same group of participants to describe the emergence of long-term memory function in infancy.

### Appendix: Descriptions of events used in recall testing

<table>
<thead>
<tr>
<th>Event title</th>
<th>Step 1</th>
<th>Step 2</th>
<th>End state</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bubbles</td>
<td>Put round cylinder into block</td>
<td>Push block into base</td>
<td>Dinosaur puppet pops up</td>
</tr>
<tr>
<td>Big bird</td>
<td>Put toy car (with big bird) into chute</td>
<td>Push wooden rod</td>
<td>Light at end of chute illuminates</td>
</tr>
<tr>
<td>Glow ball</td>
<td>Put clear ball containing tissue paper onto base</td>
<td>Pull out drawer</td>
<td>Ball illuminates</td>
</tr>
<tr>
<td>Pop-up book</td>
<td>Open book</td>
<td>Pull handle</td>
<td>Picture of duck pops up</td>
</tr>
<tr>
<td>Happy face</td>
<td>Put block with bottom half of face on base</td>
<td>Push block under base</td>
<td>Top of face drops, makes a whole face</td>
</tr>
<tr>
<td>Balloon</td>
<td>Put balloon into hole on base</td>
<td>Push lever</td>
<td>Balloon inflates</td>
</tr>
</tbody>
</table>

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### References


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