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Patterns of brain-electrical activity during declarative memory performance in 10-month-old infants

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ABSTRACT

This study of infant declarative memory concurrently examined brain-electrical activity and deferred imitation performance in 10-month-old infants. Continuous electroencephalogram (EEG) measures were collected throughout the activity-matched baseline, encoding (modeling) and retrieval (delayed test) phases of a within-subjects deferred imitation task. Infants were divided into two memory performance groups based on the exhibition of ordered-recall after a 24-h delay. Whereas no group differences were found in EEG collected during encoding, performance-group differences in EEG were present during retrieval. Infants who successfully displayed ordered-recall showed a pattern of increasing EEG from baseline to task at anterior temporal scalp locations, whereas infants showing no ordered-recall displayed no changes in EEG from baseline to task. These findings are discussed with respect to the biobehavioral developments underlying declarative memory abilities.

1. Introduction

One of the most intriguing and enduring issues in contemporary developmental cognitive neuroscience concerns the development of the ability to remember past experiences and the neural systems which support this capacity. Whereas we know much about age-related trends and the parameters governing remembering and forgetting of declarative memories in infancy (Bauer, 2004, 2008; Bauer, DeBoer, & Lukowski, 2007; Hayne, 2004, 2007; Mandler & McDonough, 1995), the functional development of the neurological components supporting the emergence and expression of this ability in infancy are not as clearly understood (Bauer, 2008). In a recent review examining the development of declarative memory from a cognitive neuroscience perspective, Richmond and Nelson (2007) call for future work to further examine memory development during infancy and early childhood by incorporating both behavior and brain measures. The purpose of this study was to examine infant declarative memory by concurrently recording continuous brain-electrical activity as infants encoded and retrieved new event memories during a deferred imitation task.

Over the last several decades, deferred imitation has become the standard for assessing infants' declarative memory abilities. This observational learning paradigm is used to examine infants' ability to create, store, and consciously retrieve new event memories and was classically described by Piaget as the hallmark test for representational abilities (Piaget, 1952). Indeed, the deferred imitation paradigm is especially powerful in infancy because it is a non-verbal analog of verbal recall, the standard measure of adult declarative processing. As proficiency at exercising declarative memory increases across the second half of the first year of life, so do the efficiency and flexibility of this ability.

Our understanding of the neurological components supporting declarative memory function has made tremendous progress over the past 30 years. The majority of evidence for the neural basis of declarative memory, however, has relied on data collected from imaging studies of intact human adults, clinical studies of patients with neurological disorders or surgical ablations, and lesions studies from the animal literature (Eichenbaum, 1997), rather than human infants. This work implicates two major neurological systems as supporting declarative memory expression: the medial temporal lobe (MTL), the prefrontal cortex (PFC) (Eichenbaum & Cohen, 2001).

The MTL consists of the hippocampus, amygdala, and the surrounding cortical areas (e.g. parahippocampal structures such as the entorhinal cortex and dentate gyrus), and is thought to be involved in the process of encoding and consolidating declarative memories. Studies of adult patients with temporal lobe lesions have shown that the MTL is essential for acquisition of new declarative memories (McDonough, Mandler, McKee, & Squire, 1995). Indeed, temporal lobe amnesiacs tend to perform poorly on tasks designed to assess declarative memory processes, such as deferred imitation (Zola & Squire, 2000).

Developmentally, the hippocampus and surrounding cortical areas begin to be functional relatively early within the first year

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of life (Nelson, 1995). In contrast with those in the cortex which mature later, the distribution of cholinergic receptors in the monkey hippocampus is adult-like at birth (O'Neil, Friedman, Bachevalier, & Ungerleider, 1986). Additionally, metabolic activity in the temporal lobes increases significantly by the third month of life and precedes that of the prefrontal cortex (PFC) by several months (Chugani, 1994). However, the dentate gyrus, a region within the hippocampual formation, does undergo protracted postnatal development (Eckenhoff & Rakic, 1991; Seress & Abraham, 2008) and has been shown play a central role in supporting new declarative memories (Pauli, Hildebrandt, Romstöck, Stefan, & Blümcke, 2006). Developmentally, this region has been linked to successful long-term retention and mnemonic flexibility during childhood (Richmond & Nelson, 2007). Therefore, temporal lobe structure and function are likely to be psychophysiologically related to the range of performance reported on deferred imitation tasks in infancy.

Whereas the development and function of MTL are clearly necessary for the expression of declarative memories, some have suggested that the PFC also plays a critical role in declarative processing. Specifically, it is speculated that the PFC is responsible for the active retrieval of information from long-term storage (Nyberg et al., 1996; Wheeler, Struss, & Tulving, 1997), as well as temporal sequencing of stored information (Fuster, 2002; Luria, 1966). Damage to the frontal lobes has been shown to impact the expression of delayed recall in adults, specifically, sequential recall on deferred imitation tasks. Frontal lobe patients often fail tasks of imitating actions in a displayed sequential order; even when target behaviors are reproduced correctly, the temporal sequence connecting these actions is disrupted (Zanini, Rumiati, & Shallice, 2002). Thus, the integrity of the PFC is central to the conscious retrieval of ordered-recall.

The development of the PFC is unique from other cortical areas in that it is both delayed (typically not functionally mature until the second half of the first year of life as indicated by associations with task performance; Bell & Fox, 1994; Chugani, 1994; Diamond, 2001, 2002; Goldman-Rakic & Leung, 2002), and protracted (it continues to structurally develop from infancy and into early adulthood; Luna, Carver, Urban, Lazar, & Sweeney, 2004). Performance on other infant tasks of delayed recall, such as object retrieval (Diamond, 2001) and a looking version of the A-not-B task (Bell, 2001) have been linked to the development of the PFC, and reflect a pattern of better performance on increasingly challenging tasks with age, similar to developmental trends in declarative memory. In addition, superior performance on an infant working memory task has been associated with baseline-to-task increases in 6–9 Hz brain-electrical activity at frontal sites during the stages of short-term encoding, storage, and retrieval (Bell, 2001).

To date, few studies have examined performance-related differences in physiology during the course of infant recall processing. Carver, Bauer, and Nelson (2000) were the first to demonstrate that brain activity at one age (event-related potentials at 9 months) was predictive of long-term declarative memory at a later age (ordered-recall at 10 months). These findings were extended by Bauer, Wiebe, Carver, Waters, and Nelson (2003), who sampled recognition memory twice in the retention interval and found that delayed, not immediate recognition, was predictive of later recall performance. Although these studies are the first to investigate both behavioral and electrophysiological indices of infant declarative memory, to date, no work has simultaneously explored changes in brain activity examined *during* the actual encoding or retrieval stages of recall processing.

Electroencephalography (EEG) is a psychophysiological tool used to record and measure electrical activity from the scalp which is related to underlying cortical activity (Stern, Ray, & Quigley, 2001). EEG collection is advantageous for use with infants in that it is a non-invasive technique and robust to gross motor movements, making it more suitable for use with developmental populations (Casey & de Haan, 2002). Although EEG does not offer the spatial resolution afforded by MRI and fMRI, correlational work exploring infant measures of glucose metabolism (Chugani & Phelps, 1986) and high-density EEG during cognitive tasks (Reynolds & Richards, 2005) bolster arguments for regional cortical activity. EEG does, however, offer optimal temporal resolution (Casey & de Haan, 2002) and the continuous collection of EEG permits real-time psychophysiological collection *during* cognitive processing (Stern et al., 2001). Recordings can be collected during both non-active (baseline) periods, as well as throughout cognitive tasks to identify patterns of cortical activation during processing.

For imitation-based tasks, simultaneously recording continuous EEG and behavior does not require any adjustment of the imitation protocol. The physical demands on the infant for encoding, storing, and retrieving declarative memories (i.e. imitating an event sequence) involve a varying level of gross motor movement and require infants to observe demonstrations lasting several seconds. Continuous EEG can be collected during infant behavior despite these constraints. Studies using evoked potentials to index declarative memory, however, require adjustment to the standard imitation protocol. Indeed, these studies examine the quality of the memory trace using recognition tests (ERP measures) immediately after encoding and/or during the retention interval and thus, are forced to rely on intermediate neurological responses to pictorial representations of the events. Researchers then infer where the trace degrades based on these responses. An investigation employing continuous EEG during the imitation task would allow direct physiological data collection during real-time memory processing.

By measuring continuous brain-electrical activity as infants participated in a deferred imitation task, we were able to explore performance-related changes in EEG from baseline-to-task during encoding and retrieval. To this end, we utilized a within-subjects deferred imitation protocol and tested 10-month-old infants, the age group (at test) used in several previously cited psychophysiological explorations of infant recall (Bauer et al., 2003; Carver et al., 2000). Towards the end of the first year, the frontal lobes undergo a period of rapid development, and yet individual differences in functional maturity are still high. Therefore, selecting 10-month-olds for our sample ensured both physiological and behavioral variability, allowing us to explore patterns of individual and group differences in this emergent skill.

We hypothesized that infants who showed ordered-recall for events after 24 h would demonstrate increases in EEG power (relative to baseline) during encoding and retrieval. Additionally, we hypothesized that infants who did not show ordered-recall would show no changes in EEG power from baseline to task phases. Regionally, we hypothesized that these effects would be found at frontal and temporal sites, as these areas have been implicated in supporting declarative memory function and development.

2. Methods

2.1. Participants

Forty-eight healthy 10-month-old infants (32 boys, 16 girls; 43 Caucasian, 2 American Indian/Alaska Native, 1 Asian, and 2 Hispanic) were participants in this study and were recruited using a commercial mailing list of new parent names and addresses. Infants were seen when they were between 10 months and 10.75-month-old (mean age was 10 months, 6 days), so that only 3 weeks separated the oldest and youngest infants in the study. All parents completed a high school education, with 85% of parents having a college degree. Average maternal age was 30 years (range 23–42)