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## Beyond initial encoding: Measures of the post-encoding status of memory traces predict long-term recall during infancy

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#### ABSTRACT

The first years of life are witness to rapid changes in long-term recall ability. In the current research we contributed to an explanation of the changes by testing the absolute and relative contributions to long-term recall of encoding and post-encoding processes. Using elicited imitation, we sampled the status of 16-, 20-, and 24-month-old infants' memory representations at various time points after experience of events. In Experiment 1, infants were tested immediately, 1 week after encoding, and again after 1 month. The measure of 1-week trace status was a unique predictor of 1-month delayed recall. In Experiment 2, infants were tested immediately, 15 min, 48 h, and 2 weeks after encoding and again 1 month later. The measures of 15-min and 48-h trace strength contributed unique variance in 1-month delayed recall. The findings highlight the need to consider post-encoding processes in explanations of variability in long-term memory during infancy.

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#### Introduction

The ability to recall past events is a basic human capacity on which we depend. It allows us to remember the names and faces of people we have met and places we have gone, and in essence it is a central part of what makes us who we are. Memory for events from the past begins to develop early in life and undergoes pronounced changes throughout infancy and beyond (for reviews, see Bauer, 2007; Hayne, 2004; Howe & Courage, 1993; Rose, Feldman, & Jankowski, 2004). For example,

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there are well-documented developmental changes in the amount and how long children can remember (for reviews, see Bauer, 2007, in press). However, the memory processes that contribute to these patterns of remembering and forgetting are less well explicated, especially during infancy. The mnemonic processes themselves are known—encoding, consolidation, and retrieval. Less well understood are the absolute and relative contributions that each of these processes makes to the robustness of a memory representation over a delay. The objective of the current investigation was to examine the variance in long-term recall during the second year of life explained by measures of the encoding and post-encoding status of memory traces with the goal of informing the determinants of remembering and forgetting during infancy.

For a memory to be available for retrieval, it first must be encoded (initial registration of information) and then consolidated (stabilized and integrated into long-term stores). Substantial research has made clear that there are age-related and individual differences in encoding. For example, in infant preferential looking paradigms, the number of seconds of familiarization required for a stimulus to be encoded (as evidenced by a novelty response) changes with age, with younger infants requiring more encoding time to produce a novelty response relative to older infants (Rose, Gottfried, Melloy-Carminar, & Bridger, 1982). In addition, younger infants require more trials to learn multistep event sequences to a criterion (learning to a criterion indicates that the material was fully encoded) compared with older infants (Howe & Courage, 1997). Indeed, across development, older children show evidence of more rapid encoding relative to younger children (Howe & Brainerd, 1989).

The second phase in the life of a memory, consolidation, has been relatively neglected in the infant memory literature. Originally hypothesized by Müller and Pilzecker (1900), consolidation is a postencoding process by which initially labile memory traces are stabilized and integrated into long-term storage (for reviews, see McGaugh, 2000; Wixted, 2004). It is thought to be subserved by medial-temporal structures (the hippocampus) in concert with the cortex (e.g., Zola & Squire, 2000). Experimental evidence that memory traces undergo changes post-encoding come from studies with animal models in which consolidation processes have been deliberately disrupted (for reviews, see Eichenbaum & Cohen, 2001; Squire & Alvarez, 1995). For example, animals are trained to encode a new association, such as between a tone and an electrical shock, after which they experience a lesion of the hippocampus. When animals are lesioned shortly after learning (e.g., 7 days), their memory for the association is severely impaired, suggesting that the recently formed memory trace was still undergoing hippocampally dependent post-encoding processing. In contrast, when animals are lesioned after longer intervals post-encoding (e.g., 28 days), memory is unimpaired, suggesting that post-encoding processes were complete (e.g., Kim & Fanselow, 1992; Takehara, Kawahara, & Kirino, 2003). These and other similar observations imply that for new memories to be stored effectively, they must undergo additional processing after encoding.

Although there is strong evidence that memory traces undergo additional processing post-encoding, there are few studies in which the implications of the processing for long-term recall have been investigated in humans (see Wixted, 2004, for a review). In a study with adults, Bosshardt and colleagues (2005) measured retrieval-related brain activity (with functional magnetic resonance imaging) 10 min and 24 h after encoding of word pairs. They found differences in hippocampal activity 24 h post-encoding relative to 10 min post-encoding. As noted by the authors, the finding is consistent with animal models that suggest changes in hippocampal synaptic connections within 24 h after encoding (e.g., Dudai & Morris, 2000). Moreover, the change in memory trace status had implications for recall, as indicated by correlations between hippocampal activation and retrieval success; the correlation was stronger after 24 h than after 10 min. Thus, Bosshardt and colleagues (2005) provided evidence of post-encoding changes in memory that have implications for long-term recall. Their study also suggests a potentially productive means of examining the contributions of post-encoding processing to long-term recall in infants, namely, probing the status of the memory trace at different points in time post-encoding and determining the variance in long-term recall explained by each test.

In the infant literature, there are relatively few studies that allow examination of post-encoding processes as a potential source of age-related or individual variability in long-term recall. A test of the question requires a measure of the newly encoded trace and a measure of the strength of the memory trace thereafter during the period in which consolidation processes are thought to occur. Many studies of infant memory lack both of these features (e.g., Barr, Dowden, & Hayne, 1996). The

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