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In the Language of Multiple Memory Systems

Defining and Describing Developments in Long-Term Declarative Memory

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Memory is a fundamental cognitive capacity. Without it, we would live only for the moment. Although we might do well to heed advice to "live for today," appreciation of today is significantly enhanced by the ability to remember yesterday and to anticipate tomorrow. Memory permits these functions by allowing us to store and reflect upon previous experience and use it to guide present as well as future behavior. The continuity afforded by memory is readily apparent as soon as children develop the capacity to use language to share mental experiences. The status of the capacity before language has been a source of active debate. The perspective that infants and preverbal children lack the capacity for storage and retrieval of accessible memory representations is well represented in the traditional (e.g., Piaget, 1952) as well as the contemporary (e.g., K. Nelson & Ross, 1980; Pillemer, 1998; Pillemer & White, 1989) literature. The perspective in this chapter is that the capacity begins to develop well before language and undergoes significant age-related change before first memories are expressed verbally. We develop this perspective by addressing each of the questions posed to contributors to this volume.

What Kind of Memory Is It?

An adequate answer to the question, What kind of memory is it? is absolutely central because, as argued by Bauer (2006b), memory is not pudding.

Pudding is a homogeneous entity. When you put a spoon into a bowl of pudding, you draw out pudding. Each new spoonful looks like the last. Comments, characterizations, and truths declared about one spoonful are equally true of the next, and the next, and the next.¹ But memory is not pudding. Rather, there are many different types of memory. One common division of memory—that used to organize this volume—is along a temporal dimension. Some memories are short term, lasting only seconds. Others are long term and may even last a lifetime. A "truth" about short-term memory is that its capacity is limited (i.e., to seven "units" of information, plus or minus two). In contrast, long-term memory is boundless in its capacity. For all practical purposes, there is no upper limit on the amount of information that can be maintained in long-term wariety: They persist for hours, days, weeks, and even months.

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If memory were pudding that came in two varieties—vanilla (short-term) and chocolate (long-term)-it would not be important to go beyond the temporal dimension to distinguish the specific "flavor" under consideration. However, at least three different lines of evidence suggest that there are dimensions other than the temporal along which memory differs. Data from patients with focal or localized lesions, from animal models of lesion and disease, and from neuroimaging studies suggest that there are different types of memory that are distinguished by content, function, rules of operation, and neural substrates (e.g., Schacter, Wagner, & Buckner, 2000; Squire, Knowlton, & Musen, 1993). Declarative or explicit memory—the subject of this chapter—involves conscious recognition or recall. It is devoted to recollection of such things as names, dates, places, facts, and events, and descriptive details about them. These are entities that we think of as being encoded symbolically and that thus can be described with language. Declarative memory is specialized for rapid, even one-trial learning that is not tied to a specific modality or context. As described in more detail in a later section, it is subserved by a multicomponent neural network that includes temporal and cortical structures.

In contrast to declarative memory, *nondeclarative* or *implicit* memory represents a variety of nonconscious abilities, including the capacity for learning skills and procedures, priming, and some forms of conditioning. The content of nondeclarative memory is not names, dates, facts, and events, but finely tuned motor patterns, procedures, and perceptual skills. It is not encoded symbolically and thus is not accessible to language. Nondeclarative memory is characterized as slow (i.e., with the exception of priming, it results from gradual or incremental learning) and inflexible. Different types of nondeclarative memory are subserved by different neural substrates, including the cerebellum and basal ganglia. In addition, the hippocampus—one of the medial temporal lobe structures involved in declarative memory—also is implicated in some nondeclarative tasks.

The distinction between different types of memory is widely accepted in the adult cognitive and cognitive neuroscience communities. In the developmental literature, it is less firmly established, in no small part because of the difficulties evaluating one of the features of declarative memory, namely, its accessibility to consciousness (e.g., C. A. Nelson, 1997; Rovee-Collier, 1997). In adults, conscious access to the contents of memory is assessed verbally. By definition, infants do not speak (in Latin, *infantia* means "inability to speak"). Critically, however, definitions of the construct do not require that it be expressed verbally. Indeed, some scholars have specifically noted that conscious awareness may be expressed nonverbally (e.g., Köhler & Moscovitch, 1997). Empirically, concern about the criterion of consciousness has been addressed by designing tasks that bear other characteristic features of tests of declarative memory—such as requiring acquisition of novel behaviors on the basis of a single trial.

For developmental scientists, the distinction between declarative and nondeclarative memory is vitally important for two major reasons. First, as discussed by Mandler (2004), if we are to make progress in understanding cognitive development, we must be clear about the capacities we are studying. In essence, Mandler's argument is that if we do not know with what kind of knowledge we are dealing, we cannot begin to answer questions regarding the mechanisms by which it was acquired. In other words, if we treat memory as pudding, we cannot hope to discover specific information regarding how it is made. Thus, from a general theoretical perspective, it is important to specify what type of memory we are studying, in order to constrain our theories of how it develops.

Second, the distinction between declarative and nondeclarative forms of memory is important developmentally because the neural structures that contribute to these different types of memory mature at different rates. Specifically, as reviewed by Bauer (2004, 2006a, 2006b), Carver and Bauer (2001), and C. A. Nelson (1995, 1997, 2000), it seems that the structures that permit some of the different forms of nondeclarative memory are functional at an earlier age, relative to those that permit declarative memory. For example, instrumental conditioning, such as is observed in the mobile conjugate reinforcement paradigm (see Rovee-Collier & Hayne, 2000, for a review) likely depends largely on early developing cerebellum and certain deep nuclei of the brain stem. In contrast, as will be seen in a later section, the temporal-cortical network that supports declarative memory has a slower, longer course of development. The differing rates of development make clear that if we are to fully understand age-related changes in memory, we will need to chart neurodevelopmental changes in the specific structures under question. Our understanding of brain development should constrain our expectations regarding performance as well as inform our interpretation of data. A goal of the balance of this chapter is to evaluate the "fit" between what we know about age-related changes in long-term declarative memory behavior and what we know about the development of the neural substrate responsible for it.

Measuring Long-Term Declarative Memory in Infancy and Early Childhood

In older, verbal children and adults, declarative memory is assessed verbally. For example, study participants are given lists of words to remember and then are asked to recall the list ("Tell me all the words on the list") or make explicit judgments of recognition ("Was the word X on the list?"). Memory for naturally occurring events is studied in much the same way, namely, by asking the participant for a verbal report of the experience.

Because infants do not benefit from the ability to speak, researchers interested in the emergence of long-term declarative memory have developed nonverbal means of assessment. The technique that has been the source of the bulk of the data in this chapter involves infants' imitation of another's actions. Typically, the actions are performed by adults using props. For example, the model may "make a gong" by placing a bar across a support to form a crosspiece, hanging a metal disk from the crosspiece, and using a mallet to hit the disk and make it ring. Although the demonstration may be accompanied by narration of the model's actions, verbal support is not necessary for successful imitation (e.g., Hayne & Herbert, 2004). Thus the task does not require verbal instructions. Nor does it require a verbal response: The measure of memory is behavioral (i.e., imitation).

As summarized in Table 10.1, there are a number of reasons to argue that imitation-based tasks measure declarative memory (see also Bauer, 2005b, 2006b, for discussion). First, when infants imitate another's actions on objects, they show that they remember content such as is encoded into declarative memory: what happened, where, when, and even why. When they "make a gong," for example, they show that they remember that a disk was suspended from a crosspiece, and that the crosspiece had to be put in place before the disk could be suspended from it (see Travis, 1997, for evidence that infants have some understanding of the why or the goal of such sequences). Second, the contents of memories formed in imitationbased tasks are accessible to language. Once children acquire the linguistic capacity to do so, they talk about multistep sequences they experienced as preverbal infants (e.g., Bauer, Kroupina, Schwade, Dropik, & Wewerka, 1998; Cheatham & Bauer, 2005; although see Simcock & Hayne, 2002, for a suggestion to the contrary, and Bauer et al., 2004, for discussion of possible reasons for the negative findings in Simcock & Hayne). Third, although performance is facilitated by multiple experiences (e.g., Bauer, Hertsgaard, & Wewerka, 1995), infants learn and remember on the basis of a single experience (e.g., Bauer & Hertsgaard, 1993). Rapid learning is characteristic of declarative memory.

Fourth and fifth, the memory traces formed in imitation-based tasks are relatively fallible yet flexible. Forgetting sets in as early as 10 minutes after experience of events (Bauer, Cheatham, Strand Cary, & Van Abbema, 2002) and is readily apparent after 48 hours (Bauer, Van Abbema, & de Haan, 1999).

Feature	Behavior			
Content	Memories are elements such as those expressed via verbal			
Verbal access	The contents of memories formed in imitation-based tasks are accessible to language			
One-trial learning	Learning occurs in a single trial (though performance is facilitated by multiple learning trials)			
Fallible traces	Forgetting sets in as early as 10 minutes and is readily apparent after 48 hours			
Flexible traces	Memories "survive" across changes in the retrieval relative to			
Amnesia test	Individuals with damage to medial temporal structures inflicted as adults or as children are impaired on the task			

Table 10.1 Imitation-Based Tasks as Measures of Explicit Memory

Memory as tested in imitation-based paradigms also is flexible. Infants show that they remember even when (a) the objects available at the time of retrieval differ in size, shape, color, and/or material composition from those used by the model at the time of encoding (e.g., Bauer & Dow, 1994; Bauer & Fivush, 1992; Lechuga, Marcos-Ruiz, & Bauer, 2001; (b) the appearance of the room at the time of retrieval is different from that at the time of encoding (e.g., Barnat, Klein, & Meltzoff, 1996; Klein & Meltzoff, 1999); (c) encoding and retrieval take place in different settings (e.g., Hanna & Meltzoff, 1993; Klein & Meltzoff, 1999); and (d) the individual who elicits recall is different from the individual who demonstrated the actions (e.g., Hanna & Meltzoff, 1993). Evidence of flexible extension of event knowledge is apparent in infants as young as 9 to 11 months of age (e.g., Baldwin, Markman, & Melartin, 1993; McDonough & Mandler, 1998).

Finally, imitation-based tasks pass the "amnesia test." McDonough, Mandler, McKee, and Squire (1995) tested adults with amnesia (in whom declarative memory processes are impaired) and control participants in an imitation-based task using multistep sequences. Whereas normal adults produced the model's actions even after a delay, patients with amnesia did poorly, performing no better than control participants who had never seen the events demonstrated. Older children and young adults who were rendered amnesic as a result of pre- or perinatal insults also show decreased performance on imitation-based tasks (Adlam, Vargha-Khadem, Mishkin, & de Haan, 2005). These findings strongly suggest that although imitationbased tasks are behavioral rather than verbal, they tap declarative memory.

Development of imitation-based tasks as means of assessing long-term declarative memory in infants and very young children represented a significant advance by allowing empirical tests of long-standing assumptions that declarative memory was a late developmental achievement (see Bauer, 2004, 2005b, 2006b, for discussions). As reviewed in the next section, in the 20 years since the tasks have been in use (Bauer & Shore, 1987; Meltzoff,

1995), we have gathered a great deal of descriptive information about developmental differences in declarative memory in infancy. As we begin to face the challenges of *explaining* the age-related changes, we hit one of the limits of the task, however: With any performance-based measure, there is a chasm between overt behavior and the memory representation presumably underlying it. In the case of the study of declarative memory in infancy, this means that it is difficult to know whether younger infants actually remember less than older infants, or whether they are simply less skilled at "showing what they know." Additionally, it is difficult to identify the locus of developmental difference: Relative to older infants, do younger infants encode less, store less, or retrieve less, or perhaps all of the above?

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In an attempt to bridge the chasm between behavior and memory representation, we have begun combining measures from imitation-based tasks with event-related potentials (ERPs). ERPs are scalp-recorded electrical oscillations associated with excitatory and inhibitory postsynaptic potentials. Because they are time locked to a stimulus, differences in the latency and amplitude of the response to different classes of stimuli-familiar and novel, for example-can be interpreted as evidence of differential neural processing. Moreover, because they are noninvasive and make no performance demands on the participant (e.g., ERPs to auditory stimuli can be recorded while the participant sleeps), they are ideal for use with human infants. As discussed in a later section, we have used ERPs to determine the locus of both individual and developmental differences in memory. Research thus far has revealed systematic variability in encoding processes and in storage processes, as measured by ERPs; the variability in ERPs is related to variability in performance on imitation-based tasks (see later section). The combination of electrophysiological and behavioral measures is thus allowing us to pave new ground in the study of declarative memory in infancy and very early childhood.

Describing Age-Related Changes in Long-Term Declarative Memory

From nearly 20 years of work on infants' and young children's performance on imitation-based tasks, a number of age-related changes in early long-term declarative memory are apparent (see Bauer, 2004, 2005b, 2006a, 2006b, for reviews). Two especially salient changes are in the temporal extent of declarative memory and the reliability with which it is observed. We discuss each in turn.

Changes in the Temporal Extent of Declarative Memory

Over the first two years of life, there are pronounced changes in how long memories seemingly last. Importantly, because like any complex behavior,

the length of time over which an event is remembered is multiply determined, there is no "growth chart" function that specifies that children of x age should remember for y long. Nonetheless, across numerous studies evidence has emerged that with increasing age, infants tolerate lengthier retention intervals. Beginning with infants only 6 months of age, Barr, Dowden, and Hayne (1996) tested recall of a three-step sequence involving (1) taking a mitten off a puppet's hand; (2) shaking the mitten, which, at the time of demonstration, held a bell that rang; and (3) replacing the mitten. The youngest infants remembered an average of one action of the three-step sequence for 24 hours. In a study by Collie and Hayne (1999), 6-month-old infants remembered an average of one out of five possible actions over the same delay. These results signal the "budding" of long-term declarative memory, at least by 6 months of age. On the other hand, observations that over 24 hours 6-month-olds apparently remember only a small proportion of what they observed have not "inspired" researchers to examine retention over longer intervals.

As schematically illustrated in Table 10.2, by 9 to 11 months of age, the length of time over which memory for laboratory events is apparent has increased substantially. Thus, 9-month-olds remember individual actions over delays of as many as 5 weeks (Carver & Bauer, 1999, 2001). By 10 to 11 months, infants remember for as long as 3 months (Carver & Bauer, 2001; Mandler & McDonough, 1995), and 13- to 14-month-olds remember over delays of 4 to 6 months (Bauer et al., 2000; Meltzoff, 1995). By 20 months of age, children show evidence of memory after as many as 12 months (Bauer et al., 2000). Clearly, between the latter half of the first year and the middle of the second year of life, the temporal extent of declarative memory increases substantially.

Changes in the Reliability of Declarative Memory

Along with changes in the temporal extent of declarative memory come changes in the reliability with which it is observed in the population. Age-related increases are especially apparent on the measure of ordered

Age at Exposure (in months)		Time Over Which Memory Is Apparent				
	24 Hours	5 Weeks	3 Months	4–6 Months	12 Months	
6						
9						
10–11						
13-14						
20						

Table 10.2 Changes in the Temporal Extension of Recall Memory Over the First Two Years of Life

recall of multistep sequences. Whereas a majority of 6-month-old infants recall the individual actions of a multistep sequence (i.e., 67%), as shown in Table 10.3, only one quarter show evidence of temporally ordered recall (Barr et al., 1996). By 9 months of age, ordered recall is more reliably observed: Almost half of 9-month-olds exhibit ordered reproduction of sequences after a 1-month delay (Bauer, Wiebe, Carver, Waters, & Nelson, 2003; Bauer, Wiebe, Waters, & Bangston, 2001; Carver & Bauer, 1999). By 13 months of age, the substantial individual variability in ordered recall has resolved: Three quarters of 13-month-olds remember the temporal order of multistep sequences after 1 month (Bauer et al., 2000).

Although by the beginning of the second year of life long-term ordered recall is reliably observed over a 1-month delay, as illustrated in Table 10.3, there are further developments over the course of the year. At delays of longer than 1 month, few 13-month-olds show ordered recall. For instance, in Bauer et al. (2000), at delays of 6 months and longer, there was less than a 40% chance that a random selection from the group of 13-month-olds tested would yield a child who remembered temporal order information. In contrast, even after 12 months, two thirds of 20-month-olds showed temporally ordered recall. These data are strongly suggestive of increases in the reliability of long-term declarative memory over the first two years of life.

Explaining Age-Related Changes in Long-Term Declarative Memory

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Ultimately, several sources of variance will be implicated in the explanation of age-related changes in long-term declarative memory. They will range from changes in the neural processes and systems and basic mnemonic processes that permit memories to be formed, retained, and later retrieved, to the social forces that shape what children ultimately come to view as important to remember about events and even how they express their memories. For purposes of this review, we focus on "lower-level" mechanisms of

Age at Exposure (in months)	Percentage of Infants Showing Evidence of Ordered Recall After Various Delays					
	24 Hours	1 Months	6 Months	12 Months		
6	25%	?				
9		45%	?			
13		78%	39%	39%		
20		100%	83%	67%		

Table 10.3 Changes in the Reliability of Recall Memory Over the First Two Years of Life

change—those at the level of neural systems and basic mnemonic processes. We begin with a brief review of the neural network thought to subserve declarative memory in the adult and what is known about its development. We then examine the basic mnemonic processes of encoding, consolidation, storage, and retrieval, and evaluate their contributions to age-related changes in long-term declarative memory (see Bauer, 2004, 2006b, for expanded versions of this discussion).

The Neural Substrate of Declarative Event Memory and Its Development

The Substrate of Declarative Memory

In adult humans, the formation, maintenance, and retrieval of declarative memories over the long term depends on a multicomponent neural network involving temporal and cortical structures (e.g., Eichenbaum & Cohen, 2001; Markowitsch, 2000; Zola & Squire, 2000). As schematically illustrated in Figure 10.1, upon experience of an event, sensory and motor inputs are registered in multiple brain regions distributed throughout the cortex (i.e., primary somatosensory, visual, and auditory cortices). Inputs from these primary sensory areas are sent (projected) to sensory association areas that are dedicated to a single modality (somatic sensation, vision, or audition), where they are integrated into whole percepts of what the object or event feels like, looks like, and sounds like, respectively. The unimodal sensory association areas in turn project to polymodal (also termed multimodal) posterior-parietal, anterior-prefrontal, and limbic-temporal association areas where inputs from the different sense modalities converge.

Ultimately, the association areas are the long-term storage sites for memories. Yet between initial registration and commitment to long-term storage there is



FIGURE 10.1. Schematic representation of the input and output pathways of the hippocampal formation. Hippo, hippocampus; D.G., dentate gyrus. Adapted from Kandel, Schwartz, and Jessell (2000, Figure 62.5, p. 1232) and Zola and Squire (2000, Figure 30.1, p. 487).

substantial additional processing. That processing generally is described as involving integration and stabilization of the inputs from different cortical regions and is thought to be performed by medial temporal lobe structures—in particular, the hippocampus—in concert with the association cortices. Whereas integration and stabilization processes begin upon registration of a stimulus, they do not end there. The process of stabilization of a memory trace, termed *consolidation*, continues for hours, days, months, and perhaps even years. Importantly, throughout the consolidation period, memories are vulnerable to disruption and interference. Eventually, cortical structures alone are responsible for storage of memories over the long term. Prefrontal structures are implicated in the retrieval of memories after a delay. Thus, long-term recall requires multiple cortical regions, including prefrontal cortex; temporal structures; and intact connections between them.

Development of the Neural Network for Declarative Memory

At a general level, the time course of changes in behavior reviewed earlier is consistent with what is known about developments in the temporalcortical network that supports declarative memory (Bauer, 2002, 2004, 2006b; C. A. Nelson, 2000). In the human, many of the medial temporal lobe components of the declarative memory network develop early. As reviewed by Seress (2001), the cells that make up most of the hippocampus are formed early in gestation and by the end of the prenatal period, virtually all have migrated to their adult locations. By approximately 6 postnatal months, the number and density of synapses have reached adult levels, as has glucose utilization in the temporal cortex (e.g., Chugani, 1994).

In contrast to early maturation of most of the hippocampus, development of the dentate gyrus of the hippocampus is protracted (Seress, 2001). It is not until 12 to 15 postnatal months that the morphology of the dentate gyrus appears adultlike. Maximum density of synaptic connections in the dentate gyrus also is reached relatively late. The density of synapses increases dramatically (to well above adult levels) beginning at 8 to 12 postnatal mo248nths and reaches its peak at 16 to 20 months. After a period of relative stability, excess synapses are pruned until adult levels are reached at about 4 to 5 years of age (Eckenhoff & Rakic, 1991).

There is reason to believe that the protracted development of the dentate gyrus is consequential. As already noted, information about events and experiences that originally is distributed across regions of cortex converges on medial temporal structures (see Figure 10.1). One of those structures the entorhinal cortex—provides two "routes" for the transfer of information into the hippocampus. The "long route" (indicated by dotted lines in Figure 10.1) involves projections from entorhinal cortex into the hippocampus, by way of the dentate gyrus; the "short route" (indicated by solid line in Figure 10.1) bypasses the dentate gyrus. Whereas short route

processing may support some forms of memory (C. A. Nelson, 1995, 1997), rodent data suggest that adultlike memory behavior depends on processing of information through the dentate gyrus (Czurk, Czh, Seress, Nadel, & Bures, 1997; Nadel & Willner, 1989). This implies that maturation of the dentate gyrus of the hippocampus is a rate-limiting variable in the early development of declarative memory (Bauer, 2002, 2004, 2006b; Bauer et al., 2003; C. A. Nelson, 1995, 1997, 2000).

The association areas also develop slowly (Bachevalier, 2001). For instance, it is not until the 7th prenatal month that all six cortical layers are apparent. The density of synapses in prefrontal cortex increases dramatically beginning at 8 postnatal months and peaks between 15 and 24 months. Pruning to adult levels is delayed until puberty (Huttenlocher, 1979; Huttenlocher & Dabholkar, 1997; see Bourgeois, 2001, for discussion). Although the maximum density of synapses may be reached as early as 15 postnatal months, it is not until 24 months that synapses develop adult morphology (Huttenlocher, 1979). Other maturational changes in prefrontal cortex, such as myelination, continue into adolescence, and adult levels of some neurotransmitters are not seen until the second and third decades of life (Benes, 2001).

The network that supports declarative memory can be expected to function as an integrated whole only once each of its components, as well as the connections between them, achieve a level of functional maturity. "Functional maturity" is reached when the number of synapses peaks; "full maturity" is achieved as the number of synapses is pruned to adult levels (Goldman-Rakic, 1987). Adoption of this metric leads to the prediction of (a) emergence of declarative memory by late in the first year of life (with the increase in formation of new synapses in both dentate gyrus and prefrontal cortex), (b) significant development over the second year (continued synaptogenesis through 20 to 24 months), and (c) continued (albeit less dramatic) development for years thereafter (due to protracted selective reduction in synapses both in the dentate gyrus and in the prefrontal cortex).

What are the consequences for behavior of the slow course of development of the network that supports long-term declarative memory? At a general level, we may expect that as the neural substrate develops, the behavior develops as well (and vice versa, of course). More specifically, we may ask how changes in the medial temporal and cortical structures, and their interconnections, produce changes in memory representations. To address this question, we must consider "how the brain builds a memory," and thus, how the "recipe" for a memory might be affected by changes in the underlying neural substrate. In other words, we must consider how developmental changes in the substrate for memory relate to changes in the efficacy and efficiency with which information is encoded and stabilized for long-term storage, in the reliability with which it is stored, and in the ease with which it is retrieved.

Changes in Basic Mnemonic Processes

Encoding

Association cortices are involved in the initial registration and temporary maintenance of experience. Because prefrontal cortex in particular undergoes considerable postnatal development, it is reasonable to assume that there may be changes in encoding processes over the first years of life. Consistent with this suggestion, we have found age-related differences in encoding that are related to age-related differences in long-term recall. In a longitudinal study, relative to when they were 9 months of age, infants at 10 months of age showed more robust encoding and more robust recall. To test encoding, we recorded infants' ERPs as they looked at photographs of props used in multistep sequences to which they had just been exposed, interspersed with photographs of props from novel sequences. The amplitudes of responses to newly encoded stimuli at 10 months were larger than those of the same infants at 9 months; there were no differences in responses to novel stimuli. The differences at encoding were related to differences at recall. One month after each ERP, we used imitation to test long-term recall of the sequences. The infants had higher rates of recall of the sequences to which they had been exposed at 10 months, relative to the sequences to which they had been exposed at 9 months (Bauer et al., 2006).

Age-related differences in encoding do not end at 1 year of age. Relative to 15-month-olds, 12-month-olds require more trials to learn multistep sequences to a criterion (learning to a criterion indicates that the material was fully encoded). In turn, 15-month-olds are slower to achieve criterion relative to 18-month-olds (Howe & Courage, 1997). Indeed, across development, older children learn more rapidly than younger children (Howe & Brainerd, 1989).

Whereas age-related differences in encoding are apparent throughout the first 2 years, they alone do not account for the age trends in long-term declarative memory. Even with levels of encoding controlled statistically (Bauer et al., 2000), by matching (Bauer, 2005a), or by bringing children of different ages to the same learning criterion (Howe & Courage, 1997), older children have higher levels of long-term ordered recall relative to younger children. Findings such as these strongly suggest that changes in postencoding processes also contribute to developmental changes in declarative memory.

Consolidation and Storage

Although separable phases in the life of a memory trace, at the level of analysis available in the existing developmental data, consolidation and storage cannot be effectively separated. For this reason, we discuss them in tandem. As reviewed earlier, medial temporal structures are implicated in the consolidation process by which new memories become "fixed" for long-term storage; cortical association areas are the presumed long-term storage sites.

Even in a mature, intact adult, the changes in synaptic connectivity associated with memory trace consolidation continue for hours, weeks, and even months after an event. Throughout this time, memory traces are vulnerable: Lesions to medial temporal structures inflicted during the consolidation period result in deficits in memory, whereas lesions inflicted after a trace has consolidated do not (e.g., Kim & Fanselow, 1992; Takehara, Kawahara, & Kirino, 2003). Consolidation may be an even more vulnerable process for the developing organism. Not only are some of the neural structures themselves relatively undeveloped (i.e., dentate gyrus and prefrontal cortex), but the connections between them are still being created and thus are not fully effective and efficient. As a consequence, even once children have successfully encoded an event, they remain vulnerable to forgetting. Younger children may be more vulnerable than older children (Bauer, 2005a).

To examine the role of consolidation and storage processes in long-term declarative event memory in 9-month-old infants, Bauer et al. (2003) combined ERP measures of encoding (i.e., immediate ERP tests), ERP measures of consolidation and storage (i.e., 1-week delayed ERP), and deferred imitation measures of recall after 1 month. After the 1-month delay, 46% of the infants showed ordered recall and 54% did not. The differences in long-term recall were not due to differential encoding: Across the groups, infants' ERPs to the old and new stimuli were different, strongly implying that they had encoded the sequences. In spite of apparently successful encoding, at the 1-week delayed recognition test, the infants who would go on to recall the events recognized the familiar props, whereas infants who would not evidence ordered recall did not. Moreover, the size of the difference in the delayed-ERP response predicted recall performance 1 month later. These data strongly imply that at 9 months of age, consolidation and storage processes are a source of individual differences in mnemonic performance.

In the second year of life, there are behavioral suggestions of between-age group differences in consolidation and/or storage processes, as well as a replication of the finding among 9-month-olds that intermediate-term consolidation and/or storage failure relates to recall over the long term. In Bauer et al. (2002), 16- and 20-month-olds were tested for recall of multistep sequences immediately (as a measure of encoding) and after 24 hours. Over the delay, the younger children forgot a substantial amount: They produced only 65% and 57% of the target actions and ordered pairs of actions (respectively) that they had learned just 24 hours earlier. Among the older children, the amount of forgetting was not statistically reliable. These observations suggest age-related differences in the vulnerability of memory traces during the initial period of consolidation.

The vulnerability of memory traces during the initial period of consolidation is related to the robustness of long-term recall. This is apparent from another of the experiments in Bauer et al. (2002), this one involving 20-month-olds only. The children were exposed to sequences and then tested on some of the sequences immediately, some after 48 hours (a delay

after which, based on Bauer et al., 1999, some forgetting was expected), and some after 1 month. Although the children exhibited high levels of initial encoding (measured by immediate recall), they showed significant forgetting after both 48 hours and 1 month. The robustness of memory after 48 hours predicted 25% of the variance in recall 1 month later; variability of encoding did not predict significant variance. This finding is a conceptual replication of that observed with 9-month-olds in Bauer et al. (2003). In both cases, the amount of information lost to memory during the period of consolidation predicted the robustness of recall 1 month later.

Retrieval

Retrieval of memories from long-term stores is thought to depend on prefrontal cortex. Because prefrontal cortex undergoes a long period of postnatal development, retrieval processes are a likely candidate source of age-related differences in long-term recall. Unfortunately, there are few data with which to evaluate their contribution because in most studies, there are alternative candidate sources of age-related change. For instance, in studies in which imitation is deferred until after some delay (e.g., Hayne, Boniface, & Barr, 2000; Liston & Kagan, 2002), because no measures of learning are obtained (i.e., no immediate imitation) it is impossible to know whether developmental differences in long-term recall are due to retrieval processes or possibly to encoding processes. Moreover, even when indices of encoding are available, with standard testing procedures, it is difficult to know whether a memory representation is intact but has become inaccessible with the cues provided (retrieval failure) or whether it has lost its integrity and become unavailable (consolidation or storage failure). Implication of retrieval processes as a source of developmental change requires that encoding be controlled and that memory be tested under conditions of high support for retrieval. One study in which these conditions were met was Bauer et al. (2003; i.e., ERPs indicated that the events had been encoded; the suggestion of consolidation and/or storage failure was apparent on a recognition test). The results, described in the preceding section, clearly implicated consolidation and/or storage, as opposed to retrieval.

Another study that permits assessment of the contributions of consolidation and/or storage relative to retrieval processes is Bauer et al. (2000), in which children of multiple ages (13, 16, and 20 months) were tested over a range of delays (1 to 12 months). Because immediate recall of half of the events was tested, measures of encoding are available. There also was high support for retrieval: (a) children were reminded of the sequences both by the props and by verbal labels; and (b) after the test of delayed recall, the ultimate in retrieval support was provided—*the sequences were demonstrated again* and savings in relearning was assessed. When it accrues, savings (a reduction in the number of trials required to relearn a stimulus relative to the number required to learn it initially) is thought to result

because the products of relearning are integrated with an existing (though not necessarily accessible) memory trace (Ebbinghaus, 1885/1964). Conversely, absence of savings is attributed to storage failure: There is no residual trace upon which to build. In developmental studies, age differences in relearning would suggest that the residual traces available to children of different ages are differentially intact.

To eliminate encoding processes as a potential source of developmental differences in long-term recall, in a reanalysis of the data from Bauer et al. (2000), subsets of 13- and 16-month-olds and subsets of 16- and 20-month-olds were matched for levels of encoding (as measured by immediate recall; Bauer, 2005a). Performance after the delays then was examined. In both comparisons, the younger children remembered less than the older children. Moreover, in both comparisons, levels of relearning by the older children were higher than those by the younger children (Bauer, 2005a). Together, the findings strongly implicate storage as opposed to retrieval processes as the major source of age-related differences in delayed recall.

Summary

Ultimately, a number of factors will be found to explain age-related variance in long-term declarative memory in the first years of life. At present, developments in the basic mnemonic processes of encoding, consolidation and storage, and retrieval are one of the few sources of change to be evaluated. Examination of their relative contributions implicates consolidation and storage as a major source of developmental change. This conclusion is consistent with the loci of developments in the neural substrate of declarative memory. Late in the first year and throughout the second year of life there are pronounced changes in the temporal lobe structures implicated in integration and consolidation of memory traces. A likely consequence is changes in the efficiency and efficacy with which information is stabilized for storage, with resulting significant behavioral changes in resistance to forgetting.

Are Changes Indicative of Development of a Particular Memory System?

In opening this chapter, we made the argument that the type of memory we study corresponds to long-term declarative (or explicit) memory in adults. We further argued that the age-related functional changes that we see in this type of memory are related to developments in the neural structures and the network that supports it. Yet the functional changes we observe in children's performance on presumably declarative imitation-based tasks are not unlike those charted with other measures. A prime example is conjugate reinforcement: There are similarities in performance on reinforcement and imitation-based tasks (see chapter 9, this volume), even though they are thought to tap different memory systems. At first glance, this may seem counterintuitive: If the tasks assess different memory systems, why the similarities? After describing some of the apparent parallels between the tasks, we discuss their likely sources and their implications for the multiple memory systems perspective.

Conjugate Reinforcement and Imitation: Vanilla and Chocolate Pudding?

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In the most commonly used conjugate reinforcement task, a mobile is suspended above an infant's crib or sling seat. Researchers measure the baseline rate of infant kicking and then arrange the testing apparatus such that as the infant kicks, the mobile moves. Infants quickly learn the contingency between their own kicking and the movement of the mobile. Once the conditional response is acquired, a delay is imposed, after which the mobile again is suspended above the infant; the infant's leg is not attached to the mobile. If the posttraining rate of kicking is greater than the baseline rate, memory is inferred (see Rovee-Collier & Hayne, 2000, for a description of this and related procedures).

There are *apparent* similarities in the content, function, and rules by which memory seems to operate in conjugate reinforcement and imitationbased tasks. In both tasks, infants learn about and remember objects. In reinforcement tasks, this is apparent in reduced rates of kicking to mobiles on which some of the elements differ between training and test, thereby demonstrating memory for the objects on the training mobile. In imitationbased tasks, memory for objects is apparent when infants reenact specific actions using props and also when they select from an array the objects previously used to produce a sequence (e.g., Bauer & Dow, 1994). Memory for order information-which elsewhere has been highlighted as clear evidence of recall (e.g., Bauer, 2004, 2005b; Carver & Bauer, 2001)-also seems to be common across the tasks. For instance, Gulya, Rovee-Collier, Galluccio, and Wilk (1998) exposed infants to an ordered "list" of three mobiles. One day later, infants exhibited higher rates of kicking when they saw Mobile 1 before Mobile 2 than they did when they saw Mobile 3 before Mobile 2, thereby showing sensitivity to order information.

There also are apparent similarities across the tasks in the rates of learning: In both tasks learning is relatively rapid and older infants acquire new information at a faster rate than younger infants. In reinforcement tasks, 2- and 3-month-old infants learn the contingency between kicking and the movement of the mobile over two to three 15-minute sessions (Rovee-Collier, 1990). By 6 months of age, learning is accomplished over two or three sessions only 10 minutes in length (e.g., Borovsky & Rovee-Collier, 1990). As noted earlier, rapid—even one-trial—learning also is apparent in imitation-based tasks. Yet younger infants (e.g., 6-month-olds) require more exposures to test sequences than older infants (e.g., 9- and 14-month-olds).

Finally, with regard to the apparent rules by which memory seems to operate, there also seem to be similarities across the tasks. With respect to the elephant in the room of declarative memory-consciousness-neither task can claim a definitive address. The participants in these paradigms do not declare that they are consciously aware that their current behavior is influenced by prior experience. Neither do they verbally express their memories. (Though as noted earlier, once they develop language, children talk about multistep sequences experienced months previously, when they were preverbal infants. We are not aware of any evidence of later verbal accessibility of memory for the conjugate-reinforcement training experience.) Moreover, in both paradigms, there seem to be developmental changes in the extent to which memory is context dependent. In reinforcement tasks, young infants show marked decrements in performance if the conditions of training and testing vary even slightly. With increased age, greater deviation is tolerated (see Rovee-Collier & Hayne, 2000, for a review). Hayne and her colleagues have reported similar age-related changes in susceptibility to interference associated with changes in the props used in imitation-based tasks (Hayne, MacDonald, & Barr, 1997; Hayne et al., 2000; Herbert & Hayne, 2000). On the other hand, other laboratories have observed that in imitation-based tasks, memory is robust to changes between the encoding and retrieval contexts (Baldwin et al., 1993; Barnat et al., 1996; Bauer & Dow, 1994; Bauer & Fivush, 1992; Hanna & Meltzoff, 1993; Klein & Meltzoff, 1999; Lechuga et al., 2002; McDonough & Mandler, 1998; Meltzoff, 1988).

Likely Sources of Across-Task Similarities

If reinforcement and imitation-based tasks are indicative of different memory systems, why are there so many apparent similarities between them? There are two answers to this question. First, some of the similarities are delusive. An example is the demonstration of memory for temporal order in the two tasks. In the reinforcement task, sensitivity to temporal order is demonstrated by a higher rate of kicking to a chain of stimuli presented in the same (e.g., Mobile 1 before Mobile 2) relative to a different (i.e., Mobile 3 before Mobile 2) order than originally encountered. The response is not unlike that in another test of nondeclarative or implicit learning, Serial Reaction Time. In Serial Reaction Time tasks, a pattern is established by, for example, a series of lights that are turned on and off in a particular pattern. The participant follows the pattern on a keyboard. As the pattern is repeated, children and adults show facilitated performance in the form of decreased reaction times. If the pattern is changed, performance is disrupted (i.e., longer reaction times; e.g., Thomas & Nelson, 2001). Facilitated and disrupted performance is observed even among participants who profess no awareness that there even was a pattern. This example makes clear that the type of sensitivity to temporal order apparent in the reinforcement task occurs even in the absence of conscious awareness.

Although sensitivity to temporal patterns is sufficient for performance in reinforcement tasks, it is not sufficient for temporally ordered recall of a modeled sequence. In imitation tasks, infants and children watch as a model uses props to demonstrate a sequence of actions. The test of memory for order information is not whether participants increase or decrease their rate of responding when order is violated, but whether they reproduce the temporal order, from memory. The task requires that order information be encoded during presentation of the sequence and then retrieved from memory. In this it is akin to memory for a spoken utterance. Once the utterance is produced, it is no longer perceptually available. The only way it can be reproduced by another is if the other encoded it into memory and then retrieved it. Such tasks cannot be performed by individuals with damage to the neural structures implicated in declarative memory. Whereas individuals with medial temporal lobe amnesia have normal short-term memory for digits and sentences, delays as short as 10 minutes produce severe impairments (e.g., Reed & Squire, 1998). Such individuals also have difficulty on imitation-based tasks (McDonough et al., 1995). In short, careful analysis of task differences makes clear that the demands imposed by reinforcement tasks are in critical ways different from those imposed by imitation-based tasks. Thus, similarities across the task may be more apparent than real.

The second answer to the question of why, if reinforcement and imitation-based tasks are indicative of the operation of different memory systems, there are so many apparent similarities in memory as tested in them, is that we should expect—rather than be surprised by—similarities in mnemonic behavior even as it "crosses" different memory systems. In all its manifestations, memory involves taking in information that is out in the environment at the moment and preserving it beyond its physical duration. The mechanisms by which this feat is accomplished are highly conserved across evolution and within species, across brain regions and systems.

At the cellular and molecular level, the best (indeed, only viable) mechanism for learning and memory is long-term potentiation (LTP). LTP was first discovered in and is best characterized in the hippocampus. Critically, however, it takes place throughout the brain, including in the neocortex, amygdala, neostriatum, cerebellum, and even spinal cord (Eichenbaum & Cohen, 2001). Across brain regions, it operates in the roughly the same manner. Early LTP, which is initiated by brief stimulus exposure (in the form of a high-frequency stimulus train known as a *tetanus*), results in rapid but temporary changes in the probability of synaptic firing. In hippocampal slices, this activation lasts anywhere from 1 to 3 hours. Late LTP is initiated by multiple stimulus chains that result in the synthesis of new proteins, which in turn produce morphological changes, including growth of new dendritic spines on postsynaptic neurons. In hippocampal slices, late LTP can last for 24 hours or more; in intact animals, it can last for days and even weeks. Evidence that LTP is a means by which information is stabilized for long-term storage in the hippocampus comes from mice that have been

genetically altered in such a way that late-phase LTP is blocked (see Eichenbaum & Cohen, 2001, for a review). Just like patients with medial temporal lobe damage, the animals have normal short-term memory, but they are unable to consolidate new learning. Assuming that LTP is the fundamental mechanism for learning and memory, the fact that it has been shown to operate in highly similar fashion throughout the brain leads to expectations of similarities, rather than differences, in the factors that affect the encoding, consolidation, and storage of information.

There also is reason to expect similarities in mnemonic behavior at the level of memory systems. The reason is that the same neural structures may participate in multiple memory networks. For instance, as the storage site for most memories, the cerebral cortex is implicated in multiple memory systems. To the extent that declarative and nondeclarative memory tasks share a structure, there may be similarities in function. Importantly, there also are differences in the behavior of a structure as a consequence of the other structures in the network (e.g., Stanton, 2000). In essence, a structure behaves in a particular way as a function of the "crowd" with which it runs. The hippocampus is an excellent case in point. Whereas the hippocampus is classically involved in declarative memory, it also is part of a larger circuit, along with the cerebellum, that mediates modification of adaptive reflexes. As part of these different networks, it is differentially involved in different tasks. We provide illustrations of each of these principles.

Hippocampal Involvement in Different Memory Networks

The involvement of the hippocampus in long-term declarative memory is incontrovertible: Legions of studies have documented that individuals with damage to the hippocampus are impaired on a range and variety of tasks that meet the criterion for tests of declarative memory. Involvement of the hippocampus in declarative memory is further supported by research with animal models and by results from neuroimaging studies (see Eichenbaum & Cohen, 2001; Schacter et al., 2000; Zola & Squire, 2000, for reviews).

There also is strong evidence that the hippocampus is involved in some forms of conditioning, including trace eyeblink conditioning. As illustrated in Figure 10.2A, in trace eyeblink conditioning an organism is presented with an auditory or visual conditioned stimulus (CS) that terminates some number of milliseconds before the onset of a periocular shock or puff of air to the eye (i.e., the unconditioned stimulus, US). Because the CS and US do not overlap, the task requires formation of a short-term memory trace for the CS that persists over the empty interval. Successful trace conditioning critically depends upon the cerebellum, its related circuitry, and the hippocampus (e.g., Krupa, Thompson, & Thompson, 1993; Thompson, 1986). Removing the hippocampus before training abolishes the acquisition of the learned responses (Moyer, Deyo, & Disterhoft, 1990; Solomon, Vander



FIGURE 10.2. Schematic representation of the temporal parameters of trace (A) and standard delay (B) conditioning (based on Figure 1 in Herbert, Eckerman, & Stanton, 2003).

Schaaf, Thompson, & Weisz, 1986). On the rare occasion when animals do perform conditioned responses, they are not adaptively timed to avoid the impact of the US (Moyer et al., 1990; Port, Mikhail, & Patterson, 1985; Port, Romano, Steinmetz, Mikhail, & Patterson, 1986).

Within a Memory System, Differential Involvement of the Hippocampus in Different Tasks

Whereas declarative memory depends on the hippocampus (e.g., Squire et al., 1993), different declarative memory tasks may make different demands on the structure. In the context of imitation-based tasks, this point is made via work with a population at risk for memory impairment: infants born to mothers with diabetes. Infants of mothers with diabetes are exposed prenatally to several chronic metabolic risk factors, including iron deficiency, hypoglycemia (low glucose levels), and hypoxemia (insufficient oxygenation of the blood). Although all three of these risk factors impact

neurobehavioral development (see Nold & Georgieff, 2004, for review), data from rodents indicate that prenatal iron deficiency *selectively* damages the hippocampus (de Ungria et al., 2000; Jorgenson, Wobken, & Georgieff, 2003; Rao, Tkac, Townsend, Gruetter, & Georgieff, 2003) and alters cellular processes as well (e.g., long-term potentiation: see Jorgensen et al., 2003). The effects of prenatal iron deficiency are apparent on tasks known to be mediated by the hippocampus (e.g., swim distance on the Morris water maze and radial arm maze behavior; Felt & Lozoff, 1996; Schmidt, Waldow, Salinas, & Georgieff, 2004, respectively); they are exacerbated if the animal is also hypoxic (Rao et al., 1999) as is the case in the intrauterine environment of infants of mothers with diabetes.

Using imitation-based tasks, we compared performance of 12-month-old infants of mothers with diabetes to that of a control group (DeBoer, Wewerka, Bauer, Georgieff, & Nelson, 2005). Recall after a 10-minute delay differed between the groups: Infants of mothers with diabetes showed impaired performance on ordered recall, relative to the control group. In contrast, the groups did not differ on immediate imitation (of different sequences). Relative to delayed imitation, immediate imitation may make fewer demands on the hippocampus because the to-be-remembered information is kept active in temporary storage. When imitation must be delayed, the information must be consolidated (a hippocampally mediated process), stored (in distributed cortical areas), and subsequently retrieved.

There also is evidence that the extent of damage to the hippocampus may alter performance on imitation-based tasks. Infants of mothers with diabetes were divided into two groups: those who experienced severe and those who experienced moderate iron deficiency (based on levels of fetal iron stores taken at birth). At 12 months of age, both subgroups showed impaired recall after 10 minutes. The infants in the severely iron deficient group also showed impaired performance when tested immediately. This finding makes the point that the involvement of the hippocampus in declarative memory tasks may be best conceptualized not as simply "on" or "off" but as a continuum of activation with more demanding tasks requiring higher levels of contribution from this structure.

A continuum of hippocampal involvement also is apparent in conditioning tasks. As reviewed earlier, the hippocampus is necessary for normal performance in trace eyeblink conditioning. It also plays a nonessential—though modulatory—role in standard delay conditioning in which an auditory or visual CS overlaps and coterminates with the US (see Figure 10.2, Panel B). In this task, learning is faciliated by induction of LTP in the hippocampus prior to training (Berger, 1984). Conversely, learning is slowed in animals given drugs that interfere with hippocampal function (Moore, Goodell, & Solomon, 1976). Yet lesioned animals eventually learn the contingency such that their performance does not differ from that of controls (e.g., Ivkovich & Stanton, 2001). These data indicate the modulatory role played by the hippocampus, even on a task that is not absolutely dependent on it.

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Implications for the Multiple Memory Systems Perspective

There are a number of apparent similarities in performance and developmental changes across tasks thought to tap declarative and nondeclarative memory. Whereas some of the similarities are more apparent than real, others are more substantive. They do not, however, imply that the distinction between different forms of memory is irrelevant for the developmental literature. First, at the cellular and molecular levels, we should expectrather than be surprised by—similarities in performance across tasks. The basic mechanisms of learning and memory are the same across species, ages, and brain regions: Neurons do not discriminate; they do not know in what type of memory they are participating. Second, a systems-level analysis also leads to the expectation of similarities across tasks. Similarities are to be expected because in some cases, the same structure (e.g., the hippocampus) participates in multiple memory networks. Moreover, within a network, the same structure may play different roles as a function of task demands. As a result of these basic principles, we should expect to find similarities in memory behavior across systems as well as differences in mnemonic behavior within systems.

On the Horizon

The perspective taken in this chapter is that "what develops" in early memory are different memory systems, reasonably specialized for different mnemonic tasks. We argue that the specific type of memory we study corresponds to long-term declarative (or explicit) memory in adults. We further argue that age-related changes in overt behavior that we see in this type of memory across the first years of life are the result (in part) of developments in the neural structures implicated in memory, and in the networks of structures that support different types of memory. With this perspective, a number of undertakings appear on the horizon.

One enterprise for future research is to gain more descriptive information on age-related changes in long-term declarative memory. To date we have learned a great deal about the temporal extent, the robustness, and the reliability of memory in populations of infants and children of different ages. However, we have only begun to learn how changes in the basic mnemonic processes of encoding, consolidation and storage, and retrieval contribute to the observed age-related changes. Future research should be aimed at explicating these processes and the developmental changes therein. In addition, it will be important to further develop conceptual links between age-related changes in these basic processes and developments in the neural substrates that presumably underlie them. The links should guide hypotheses as to the individual and combined contributions of the

processes to long-term memory, and how they might change over the course of development (see Bauer, in press, for discussion).

Another avenue for future research is to gain more information about basic brain development in the young human. In the last decade of the 20th century, our knowledge of prenatal brain development and the genetic, cellular, and molecular events that guide it exploded. For example, whereas only a few years ago the means by which neuroblasts navigated their way to the cortex were mysterious indeed, now we have identified a great many of the proteins and signaling systems that accomplish the feat. Over the same period of time, knowledge of postnatal developments also increased, though not as substantially. The task is complicated for obvious practical and ethical reasons. As a result, we must look forward to more powerful imaging techniques of both gray matter and white matter tracts, and to continued progress in research on animal models of human brain development, for insights into development of the neural structures and connections that permit memory for past events.

As we conduct more fine-grained analyses of mnemonic behavior and as we gain more information about neural developments, we will be afforded opportunities for further progress in mapping relations between function and structure. Progress in evaluating relations between structure and function also will be made by making more frequent use in the developmental literature of one of the most powerful techniques in adult neuropsychology—the lesion method. The work described earlier on infants born to mothers with diabetes is an excellent example of this approach. In this population, there is strong reason to believe that there is a relatively focal lesion in the hippocampus. Careful study of the consequences of such lesions for mnemonic behavior in infancy and beyond promises to be very illuminating.

Also needed in the study of relations between structure and function in development are converging tests of relations. At this point, the number of tasks that clearly tap long-term declarative memory in infancy is limited. Development of additional techniques and their use with infants and children in the first years of life is very important in order to test hypotheses regarding the mechanisms of development.

Finally, a task for future research is to begin to determine how different memory networks "talk" to one another. As Eichenbaum and Cohen (2001) pointed out, different memory systems operate in parallel. It is only when we disrupt one or another that we see the "joints" that separate them. In experimental research, we often try to force the joints in order to isolate one particular mnemonic process or system. After completing the nondeclarative serial reaction time task, for example, individuals are typically questioned in a debriefing session to determine whether they had explicit knowledge of the sequence during learning (e.g., Curran, 1997). This process attempts to isolate those who learned nondeclaratively or implicitly, thereby ensuring that the findings were not "contaminated" by explicit awareness. This control is noteworthy in that performance in nondeclarative tasks may be facilitated by

declarative learning and memory (in serial reaction time tasks, Curran & Keele, 1993; in trace eyeblink conditioning, Manns, Clark, & Squire, 2000). These examples make clear that the networks that support different types of mnemonic behavior are not isolated from one another. In day-to-day life, organisms make use of the full range of resources available to them to adapt to and thrive in their environments. Developing humans are no exception.

Conclusion

Within a relatively short space of time, the field has moved from considering the mnemonic life of infants and preverbal children as relatively discontinuous with that of older children and adults to recognizing essential continuities in mnemonic processes across the span of development. The change in perspective was made possible by development of nonverbal means of assessing declarative or explicit memory, which in verbal children and adults is typically assessed verbally. Addition of ERPs to the methodological arsenal has allowed for refinement of the description of developmental change. The combination of behavioral and electrophysiological techniques makes it possible to ask questions at the level of overt behavior and at the level of the basic mnemonic processes presumably contributing to it. The new perspective also facilitates the search for explanations of developmental change by closing the distance between levels of analysis. Joint consideration of changes in function and in underlying neural structures brings into sharper focus many of the questions to be addressed in future research and also hints at the form of their answers.

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Note

1. The pudding metaphor is borrowed from Maratsos (1998), who discussed the conceptual pitfalls of considering heterogeneous domains such as language to be essentially homogeneous, or qualitatively the same throughout.

References

- Adlam, A.-L. R., Vargha-Khadem, F., Mishkin, M., & de Haan, M. (2005). Deferred imitation of action sequences in developmental amnesia. *Journal of Cognitive Neuroscience*, 17, 240–248.
- Bachevalier, J. (2001). Neural bases of memory development: Insights from neuropsychological studies in primates. In C. A. Nelson & M. Luciana (Eds.), *Handbook of developmental cognitive neuroscience* (pp. 365–379). Cambridge, MA: MIT Press.
- Baldwin, D. A., Markman, E. M., & Melartin, R. L. (1993). Infants' ability to draw inferences about nonobvious properties: Evidence from exploratory play. *Child Development*, 64, 711–728.
- Barnat, S. B., Klein, P. J., & Meltzoff, A. N. (1996). Deferred imitation across changes in context and object: Memory and generalization in 14-monthold children. *Infant Behavior and Development*, 19, 241–251.
- Barr, R., Dowden, A., & Hayne, H. (1996). Developmental change in deferred imitation by 6- to 24-month-old infants. *Infant Behavior and Development*, 19, 159–170.
- Bauer, P. J. (2002). Long-term recall memory: Behavioral and neurodevelopmental changes in the first 2 years of life. *Current Directions in Psychological Science*, 11, 137–141.
- Bauer, P. J. (2004). Getting explicit memory off the ground: Steps toward construction of a neuro-developmental account of changes in the first two years of life. *Developmental Review*, 24, 347–373.
- Bauer, P. J. (2005a). Developments in declarative memory: Decreasing susceptibility to storage failure over the second year of life. *Psychological Science*, 16, 41–47.
- Bauer, P. J. (2005b). New developments in the study of infant memory. In
 D. M. Teti (Ed.), *Blackwell Handbook of Research Methods in* Developmental Science (pp. 467–488). Oxford, UK: Blackwell.
- Bauer, P. J. (2006a). Event memory. In W. Damon (Ed.-in-Chief) & D. Kuhn & R. Siegler (Vol. Eds.), Handbook of Child Psychology: Vol. 2. Cognition, Perception, and Language (6th ed., pp. 373–425). New York: Wiley.
- Bauer, P. J. (2006b). *Remembering the times of our lives: Memory in infancy and beyond*. Mahwah, NJ: Erlbaum.
- Bauer, P. J. (in press). Toward a neuro-developmental account of the development of declarative memory. *Developmental Psychobiology*.
- Bauer, P. J., Cheatham, C. L., Strand Cary, M., & Van Abbema, D. L. (2002). Short-term forgetting: Charting its course and its implications for longterm remembering. In S. P. Shohov (Ed.), Advances in psychology research (Vol. 9, pp. 53–74). Huntington, NY: Nova Science.
- Bauer, P. J., & Dow, G. A. (1994). Episodic memory in 16- and 20-month-old children: Specifics are generalized, but not forgotten. *Developmental Psychology*, 30, 403–417.
- Bauer, P. J., & Fivush, R. (1992). Constructing event representations: Building on a foundation of variation and enabling relations. *Cognitive Development*, 7, 381–401.
- Bauer, P. J., & Hertsgaard, L. A. (1993). Increasing steps in recall of events: Factors facilitating immediate and long-term memory in 13.5- and 16.5month-old children. *Child Development*, 64, 1204–1223.

- Bauer, P. J., Hertsgaard, L. A., & Wewerka, S. S. (1995). Effects of experience and reminding on long-term recall in infancy: Remembering not to forget. *Journal of Experimental Child Psychology*, 59, 260–298.
- Bauer, P. J., Kroupina, M. G., Schwade, J. A., Dropik, P. L., & Wewerka, S. S. (1998). If memory serves, will language? Later verbal accessibility of early memories. *Development and Psychopathology*, 10, 655–679.
- Bauer, P. J., & Shore, C. M. (1987). Making a memorable event: Effects of familiarity and organization on young children's recall of action sequences. *Cognitive Development*, 2, 327–338.
- Bauer, P. J., Van Abbema, D. L., & de Haan, M. (1999). In for the short haul: Immediate and short-term remembering and forgetting by 20-month-old children. *Infant Behavior and Development*, 22, 321–343.
- Bauer, P. J., Van Abbema, D. L., Wiebe, S. A., Strand Cary, M., Phill, C., & Burch, M. M. (2004). Props, not pictures, are worth a thousand words: Verbal accessibility of early memories under different conditions of contextual support. *Applied Cognitive Psychology*, 18, 373–392.
- Bauer, P. J., Wenner, J. A., Dropik, P. L., & Wewerka, S. S. (2000). Parameters of remembering and forgetting in the transition from infancy to early childhood. *Monographs of the Society for Research in Child Development*, 65(4, Serial No. 263).
- Bauer, P. J., Wiebe, S. A., Carver, L. J., Lukowski, A. F., Haight, J. C., Waters, J. M., et al. (2006). Electrophysiological indices of encoding and behavioral indices of recall: Examining relations and developmental change late in the first year of life. *Developmental Neuropsychology*, 29, 293–320.
- Bauer, P. J., Wiebe, S. A., Carver, L. J., Waters, J. M., & Nelson, C. A. (2003). Developments in long-term explicit memory late in the first year of life: Behavioral and electrophysiological indices. *Psychological Science*, 14, 629–635.
- Bauer, P. J., Wiebe, S. A., Waters, J. M., & Bangston, S. K. (2001). Reexposure breeds recall: Effects of experience on 9-month-olds' ordered recall. *Journal of Experimental Child Psychology*, 80, 174–200.
- Benes, F. M. (2001). The development of prefrontal cortex: The maturation of neurotransmitter systems and their interaction. In C. A. Nelson & M. Luciana (Eds.), *Handbook of developmental cognitive neuroscience* (pp. 79–92). Cambridge, MA: MIT Press.
- Berger, T. W. (1984). Long-term potentiation of hippocampal synaptic transmission affects rate of behavioral learning. *Science*, *224*, 627–630.
- Borovsky, D., & Rovee-Collier, C. (1990). Contextual constraints on memory retrieval at six months. *Child Development*, *61*, 1569–1583.
- Bourgeois, J.-P. (2001). Synaptogenesis in the neocortex of the newborn: The ultimate frontier for individuation? In C. A. Nelson & M. Luciana (Eds.), *Handbook of developmental cognitive neuroscience* (pp. 23–34). Cambridge, MA: MIT Press.
- Carver, L. J., & Bauer, P. J. (1999). When the event is more than the sum of its parts: Nine-month-olds' long-term ordered recall. *Memory*, 7,147–174.
- Carver, L. J., & Bauer, P. J. (2001). The dawning of a past: The emergence of long-term explicit memory in infancy. *Journal of Experimental Psychology: General*, 130, 726–745.

- Cheatham, C. L., & Bauer, P. J. (2005). Construction of a more coherent story: Prior verbal recall predicts later verbal accessibility of early memories. *Memory*, 13, 516–532.
- Chugani, H. T. (1994). Development of regional blood glucose metabolism in relation to behavior and plasticity. In G. Dawson & K. Fischer (Eds.), *Human behavior and the developing brain* (pp. 153–175). New York: Guilford.
- Collie, R., & Hayne, H. (1999). Deferred imitation by 6- and 9-month-old infants: More evidence of declarative memory. *Developmental Psychobiology*, 35, 83–90.
- Curran, T. (1997). Effects of aging on implicit sequence learning: Accounting for sequence structure and explicit knowledge. *Psychological Research/Psychologische Forschung*, 60(1–2), 24–41.
- Curran, T., & Keele, S. W. (1993). Attentional and nonattentional forms of sequence learning. Journal of Experimental Psychology: Learning, Memory, and Cognition, 19, 189–202.
- Czurkó, A., Czéh, B., Seress, L., Nadel, L., & Bures, J. (1997). Severe spatial navigation deficit in the Morris water maze after single high dose of neonatal X-ray irradiation in the rat. *Proceedings of the National Academy of Science, USA, 94*, 2766–2771.
- DeBoer, T., Wewerka, S., Bauer, P. J., Georgieff, M. K., & Nelson, C. A. (2005). Explicit memory performance in infants of diabetic mothers at 1 year of age. *Developmental Medicine and Child Neurology*, 47, 525–531.
- de Ungria, M., Rao, R., Wobken, J. D., Luciana, M., Nelson, C. A., & Georgieff, M. K. (2000). Perinatal iron deficiency decreases cytochrome c oxidase (CytOx) activity in selective regions of neonatal rat brain. *Pediatric Research*, 48, 169–176.
- Ebbinghaus, H. (1964). *On memory* (H. A. Ruger & C. E. Bussenius, Trans.). New York: Dover. (Original work published 1885)
- Eckenhoff, M., & Rakic, P. (1991). A quantitative analysis of synaptogenesis in the molecular layer of the dentate gyrus in the rhesus monkey. *Developmental Brain Research*, 64, 129–135.
- Eichenbaum, H., & Cohen, N. J. (2001). From conditioning to conscious recollection: Memory systems of the brain. New York: Oxford University Press.
- Felt B., & Lozoff, B. (1996). Brain iron and behavior of rats are not normalized by treatment of iron deficiency anemia during early development. *Journal of Nutrition*, 126, 693–701.
- Goldman-Rakic, P. S. (1987). Circuitry of primate prefrontal cortex and regulation of behavior by representational memory. In F. Plum (Ed.), *Handbook of physiology, the nervous system, higher functions of the brain* (Vol. 5, pp. 373–417). Bethesda, MD: American Physiological Society.
- Gulya, M., Rovee-Collier, C., Galluccio, L., & Wilk, A. (1998). Memory processing of a serial list by young infants. *Psychological Science*, 9, 303–307.
- Hanna, E., & Meltzoff, A. N. (1993). Peer imitation by toddlers in laboratory, home, and day-care contexts: Implications for social learning and memory. *Developmental Psychology*, 29, 702–710.

Hayne, H., Boniface, J., & Barr, R. (2000). The development of declarative memory in human infants: Age-related changes in deferred imitation. *Behavioral Neuroscience*, 114, 77–83.

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- Hayne, H., & Herbert, J. (2004). Verbal cues facilitate memory retrieval during infancy. *Journal of Experimental Child Psychology*, 89(2), 127–139.
- Hayne, H., MacDonald, S., & Barr, R. (1997). Developmental changes in the specificity of memory over the second year of life. *Infant Behavior and Development*, 20, 233–245.
- Herbert, J. S., Eckerman, C. O., & Stanton, M. E. (2003). The ontogeny of human learning in delay, long-delay, and trace eyeblink conditioning. *Behavioral Neuroscience*, 117(6), 1196–1210.
- Herbert, J., & Hayne, H. (2000). Memory retrieval by 18–30-month-olds: Agerelated changes in representational flexibility. *Developmental Psychology*, 36, 473–484.
- Howe, M. L., & Brainerd, C. J. (1989). Development of children's long-term retention. *Developmental Review*, 9, 301–340.
- Howe, M. L., & Courage, M. L. (1997). Independent paths in the development of infant learning and forgetting. *Journal of Experimental Child Psychology*, 67, 131–163.
- Huttenlocher, P. R. (1979). Synaptic density in human frontal cortex: Developmental changes and effects of aging. *Brain Research*, *163*, 195–205.
- Huttenlocher, P. R., & Dabholkar, A. S. (1997). Regional differences in synaptogenesis in human cerebral cortex. *Journal of Comparative Neurology*, *387*, 167–178.
- Ivkovich, D., & Stanton, M. E. (2001). Effects of early hippocampal lesions on trace, delay, and long-delay eyeblink conditioning in developing rats. *Neurobiology of Learning and Memory*, 76, 426–446.
- Jorgenson, L. A., Wobken, J. D., & Georgieff, M. K. (2003). Perinatal iron deficiency alters apical dendritic growth in hippocampal CA1 pyramidal neurons. *Developmental Neuroscience*, 25, 412–420.
- Kandel, E. R., Schwartz, J. H., & Jessell, T. M. (2000). *Principles of neural science* (4th ed.). New York: McGraw-Hill.
- Kim, J. J., & Fanselow, M. S. (1992). Modality-specific retrograde amnesia of fear. Science, 256, 675–677.
- Klein, P. J., & Meltzoff, A. N. (1999). Long-term memory, forgetting, and deferred imitation in 12-month-old infants. *Developmental Science*, 2, 102–113.
- Köhler, S., & Moscovitch, M. (1997). Unconscious visual processing in neuropsychological syndromes: A survey of the literature and evaluation of models of consciousness. In M. D. Rugg (Ed.), *Cognitive neuroscience* (pp. 305–373). London: UCL Press.
- Krupa, D. J., Thompson, J. K., & Thompson, R. F. (1993). Localization of a memory trace in the mammalian brain. *Science*, 260, 989–991.
- Lechuga, M. T., Marcos-Ruiz, R., & Bauer, P. J. (2001). Episodic recall of specifics and generalisation coexist in 25-month-old children. *Memory*, 9, 117–132.
- Liston, C., & Kagan, J. (2002). Memory enhancement in early childhood. *Nature*, 419, 896.
- Mandler, J. M. (2004). Two kinds of knowledge acquisition. In J. M. Lucariello, J. A. Hudson, R. Fivush, & P. J. Bauer (Eds.), *The development*

of the mediated mind: Sociocultural context and cognitive development. Essays in honor of Katherine Nelson (pp. 13–32). Mahwah, NJ: Erlbaum. Mandler, J. M., & McDonough, L. (1995). Long-term recall of event sequences in infancy. Journal of Experimental Child Psychology, 59, 457–474.

- Manns, J. R., Clark, R. E., & Squire, L. R. (2000). Awareness predicts the magnitude of single-cue trace eyeblink conditioning. *Hippocampus*, 10(2), 181–186.
- Maratsos, M. (1998). The acquisition of grammar. In W. Damon (Ed.-in-Chief), & D. Kuhn & R. S. Siegler (Vol. Eds.), *Handbook of child psychology: Vol. 2. Cognition, perception, and language* (5th ed., pp. 421–466). New York: Wiley.
- Markowitsch, H. J. (2000). Neuroanatomy of memory. In E. Tulving & F. I. M. Craik (Eds.), *The Oxford handbook of memory* (pp. 465–484). New York: Oxford University Press.
- McDonough, L., & Mandler, J. M .(1998). Inductive generalization in 9- and 11-month-olds. *Developmental Science*, *1*, 227–232.
- McDonough, L., Mandler, J. M., McKee, R. D., & Squire, L. R. (1995). The deferred imitation task as a nonverbal measure of declarative memory. *Proceedings of the National Academy of Sciences, USA, 92*, 7580–7584.
- Meltzoff, A. N. (1988). Imitation of televised models by infants. *Child Development*, 59, 1221–1229.
- Meltzoff, A. N. (1995). What infant memory tells us about infantile amnesia: Long-term recall and deferred imitation. *Journal of Experimental Child Psychology*, *59*, 497–515.
- Moore, J. W., Goodell, N. A., & Solomon, P. R. (1976). Central cholinergic blockage by scopolamine and habituation, classical conditioning, and latent inhibition of the rabbit's nictitating membrane response. *Physiological Psychology*, *4*, 395–399.
- Moyer, J. R., Jr., Deyo, R. A., & Disterhoft, J. F. (1990). Hippocampectomy disrupts trace eye-blink conditioning in rabbits. *Behavioral Neuroscience*, 104 (2), 243–252.
- Nadel, L., & Willner, J. (1989). Some implications of postnatal maturation of the hippocampus. In V. Chan-Palay & C. Köhler (Eds.), *The hippocampus—new vistas* (pp. 17–31). New York: Alan R. Liss.
- Nelson, C. A. (1995). The ontogeny of human memory: A cognitive neuroscience perspective. *Developmental Psychology*, 31, 723–738.
- Nelson, C. A. (1997). The neurobiological basis of early memory development. In N. Cowan (Ed.), *The development of memory in childhood* (pp. 41–82). Hove, UK: Psychology Press.
- Nelson, C. A. (2000). Neural plasticity and human development: The role of early experience in sculpting memory systems. *Developmental Science*, *3*, 115–136.
- Nelson, K., & Ross, G. (1980). The generalities and specifics of long-term memory in infants and young children. In M. Perlmutter (Ed.), New directions in child development—children's memory (pp. 87–101). San Francisco: Jossey-Bass.
- Nold, J., & Georgieff, M. (2004). Infants of diabetic mothers. *Pediatric Clinics* of North America, 51, 619–637.
- Piaget, J. (1952). *The origins of intelligence in children*. New York: International Universities Press.

Pillemer, D. B. (1998). What is remembered about early childhood events? *Clinical Psychology Review, 18,* 895–913.

- Pillemer, D. B., & White, S. H. (1989). Childhood events recalled by children and adults. In H. W. Reese (Ed.), Advances in child development and behavior (Vol. 21, pp. 297–340). Orlando, FL: Academic Press.
- Port, R. L., Mikhail, A. A., & Patterson, M. M. (1985). Differential effects of hippocampectomy classically conditioned rabbit nictitating membrane response related to interstimulus interval. *Behavioral Neuroscience*, 99(2), 200–208.
- Port, R. L., Romano, A. G., Steinmetz, J. E., Mikhail, A. A., & Patterson, M. M. (1986). Retention and acquisition of classical trace conditioned responses by rabbits with hippocampal lesions. *Behavioral Neuroscience*, 100(5), 745–752.
- Rao, R., de Ungria, M., Sullivan, D., Wu, P., Wobken, J. D., Nelson, C. A., et al. (1999). Perinatal iron deficiency increases the vulnerability of rat hippocampus to hypoxic ischemic insult. *Journal of Nutrition*, 129, 199–206.
- Rao, R., Tkac, I., Townsend, E. L., Gruetter, R., & Georgieff, M. K. (2003). Perinatal iron deficiency alters the neurochemical profile of the developing rat hippocampus. *Journal of Nutrition*, 133, 3215–3221.
- Reed, J. M., & Squire, L. R. (1998). Retrograde amnesia for facts and events: Findings from four new cases. *Journal of Neuroscience*, 18, 3943–3954.
- Rovee-Collier, C. (1990). The "memory system" of prelinguistic infants. In A. Diamond (Ed.), *The development and neural bases of higher cognitive functions* (pp. 517–536). New York: New York Academy of Science.
- Rovee-Collier, C. (1997). Dissociations in infant memory: Rethinking the development of implicit and explicit memory. *Psychological Review*, 104, 467–498.
- Rovee-Collier, C., & Hayne, H. (2000). Memory in infancy and early childhood. In E. Tulving & F. I. M. Craik (Eds.), *The Oxford handbook of mem*ory (pp. 267–282). New York: Oxford University Press.
- Schacter, D. L., Wagner, A. D., & Buckner, R. L. (2000). Memory systems of 1999. In E. Tulving & F. I. M. Craik (Eds.), *The Oxford handbook of memory* (pp. 627–643). New York: Oxford University Press.
- Schmidt, A. T., Waldow, K. J., Salinas, J. A., & Georgieff, M. K. (2004). The long-term behavioral effects of fetal/neonatal iron deficiency on a hippocampally dependent learning task in the rat [Abstract]. *Pediatric Research*, 55, 279A.
- Seress, L. (2001). Morphological changes of the human hippocampal formation from midgestation to early childhood. In C. A. Nelson & M. Luciana (Eds.), *Handbook of developmental cognitive neuroscience* (pp. 45–58). Cambridge, MA: MIT Press.
- Simcock, G., & Hayne, H. (2002). Breaking the barrier? Children fail to translate their preverbal memories into language. *Psychological Science*, 13, 225–231.
- Solomon, P. R., Vander Schaaf, E. R., Thompson, R. F., & Weisz, D. J. (1986). Hippocampus and trace conditioning of the rabbit's classically conditioned nictitating membrane response. *Behavioral Neuroscience*, 100(5), 729–744.

- Squire, L. R., Knowlton, B., & Musen, G. (1993). The structure and organization of memory. *Annual Review of Psychology*, 44, 453–495.
- Stanton, M. E. (2000). Multiple memory systems, development and conditioning. Behavioural Brain Research, 110, 25–37.
- Takehara, K., Kawahara, S., & Kirino, Y. (2003). Time-dependent reorganization of the brain components underlying memory retention in trace eyeblink conditioning. *Journal of Neuroscience*, 23, 9897–9905.
- Thomas, K. M., & Nelson, C. A. (2001). Serial reaction time learning in preschool- and school-age children. *Journal of Experimental Child Psychol*ogy, 79, 364–387.
- Thompson, R. F. (1986). The neurobiology of learning and memory. *Science, 233,* 941–947.
- Travis, L. (1997). Goal-based organization of event memory in toddlers. In P. W. van den Broek, P. J. Bauer, & T. Bourg (Eds.), *Developmental spans* in event comprehension and representation: Bridging fictional and actual events (pp. 111–138). Mahwah, NJ: Erlbaum.
- Zola, S. M., & Squire, L. R. (2000). The medial temporal lobe and the hippocampus. In E. Tulving & F. I. M. Craik (Eds.), *The Oxford handbook of memory* (pp. 485–500). New York: Oxford University Press.