Published in final edited form as:

Dev Psychol. 2009 January ; 45(1): 160–174. doi:10.1037/a0014538.

Multiple Memory Systems Are Unnecessary to Account for Infant Memory Development: An Ecological Model

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Abstract

How the memory of adults evolves from the memory abilities of infants is a central problem in cognitive development. The popular solution holds that the multiple memory systems of adults mature at different rates during infancy. The *early-maturing system* (implicit or nondeclarative memory) functions automatically from birth, whereas the *late-maturing system* (explicit or declarative memory) functions intentionally, with awareness, from late in the first year. Data are presented from research on deferred imitation, sensory preconditioning, potentiation, and context for which this solution cannot account and present an alternative model that eschews the need for multiple memory systems. The ecological model of infant memory development (N. E. Spear, 1984) holds that members of all species are perfectly adapted to their niche at each point in ontogeny and exhibit effective, evolutionarily selected solutions to whatever challenges each new niche poses. Because adults and infants occupy different niches, what they perceive, learn, and remember about the same event differs, but their raw capacity to learn and remember does not.

Keywords

multiple memory systems; infant memory development; potentiation; sensory preconditioning; ecological model of memory development

A central problem in cognitive development is how the memory of adults evolves from the memory abilities of infants. The widely accepted solution holds that dichotomous memory systems emerge hierarchically during the infancy period and eventuate in the adult-level mature capacity for learning and memory. In this article, we assess the current status of this solution and present recent data from studies of learning and memory from human infants for which multiple memory systems cannot account, whether they develop hierarchically or not. An alternative solution—an ecological model—was originally proposed by Spear (1984) but has received little or no attention in the literature on cognitive development. The model holds that infants and adults of all species exercise different behavioral adaptations to the current ecological niche and, over the course of evolution, have evolved the requisite physiological mechanisms to do so. By this account, normal ontogenetic changes in learning and memory do not demand explanation in terms of multiple memory systems.

Historical Perspective: Dichotomous Memory Systems

Scoville and Milner (1957) studied the cognitive, perceptual, and motor functioning of 10 patients who had become amnesic as a result of surgery that removed a portion of their medial

temporal lobe (MTL). The degree of amnesia was directly related to the extent of hippocampal removal. Patients with severe amnesia could not remember any new information beyond the span of their immediate memory but could remember events that had occurred up to 2–3 years before their surgery. Follow-up tests revealed that one severely amnesic patient (H. M.) exhibited normal learning and retention of new perceptual and motor skills despite being unaware of prior training (Corkin, 1968, 1984; Milner, Corkin, & Teuber, 1968). These findings were taken as evidence that the hippocampus is necessary for forming long-term memories that require knowledge and conscious awareness of a previous episode but is not necessary for forming long-term memories of perceptual and skill learning, which are acquired gradually and performed automatically, without awareness.

These dissociations were initially interpreted within the framework of a single memory system (Milner et al., 1968; Warrington & Weiskrantz, 1968) but later were attributed to dichotomous memory systems. The *explicit (declarative) memory system* depends on the integrity of a set of highly interconnected structures in the MTL (the hippocampus, dentate gyrus, and subiculum) plus adjacent cortical areas that surround the hippocampus and amygdala (the perirhinal cortex, the entorhinal cortex, and the parahippocampal cortex), whereas the *implicit (nondeclarative/procedural) memory system* consists of many different neuroanatomical areas in the MTL that are not integrated and are variously active when performing different indirect memory tests (Cohen & Eichenbaum, 1993; Cohen & Squire, 1980; Squire, 1992; Tulving & Schacter, 1990).

Drawing parallels between the memory abilities of infants and aging adults with amnesia, Schacter and Moscovitch (1984) advanced a Jacksonian account (Jackson, 1884/1958) of the development and demise of memory function. According to this account, the first memory system to develop in ontogeny is the last system to fail when the organism undergoes insult, as in amnesia; conversely, the last memory system to mature is the first to fail in adverse conditions. Since this influential chapter appeared a quarter-century ago, many developmental researchers have come to believe that the same, primitive memory system underlies memory processing in young infants and adults with amnesia and that a different, higher level system mediates memory processing in older children and healthy adults (e.g., K. Nelson, 1994). Moreover, the practice of inferring the learning and memory capacity of infants from the memory performance of amnesic adults has proceeded largely unchallenged. As Karmiloff-Smith (2002) cautioned, however, “the infant start state cannot be derived from the adult end state” (p. 91). To this we add, “especially not from an abnormal one.”

Richmond and Nelson (2007) wrote, “There is little debate about the development of implicit or procedural memory . . . [but] there is much debate as to the relative development of declarative memory” (p. 352). The latter debate has centered on the timing and nature of the presumed transition to the declarative memory system at the end of the first postnatal year (for reviews, see Bauer, 2004; Bauer, DeBoer, & Lukowski, 2007; Eichenbaum, 1997; Jones & Herbert, 2006a, 2006b). The authors proposed that maturation of the hippocampus (i.e., dentate gyrus) results in “adult-like explicit memory capabilities at around 8 months of age” (Richmond & Nelson, 2007, p. 351). Whether there is a transition has not been debated, and the ecological model of infant memory development excludes consideration of multiple memory systems in infancy altogether.

Ontogenetic changes in infant memory have been attributed to the hierarchical emergence of dichotomous memory systems (implicit and explicit memory) during the first year of life. We propose that this division is both conceptually and empirically flawed on a number of counts. First, the conceptual basis of classifying memory systems as implicit or explicit is conceptually ambiguous. Second, conscious awareness is not an appropriate conceptual basis for classifying a preverbal infant's memory as implicit or explicit. Third, assumptions of a one-to-one mapping

between processes and tests are wrong: No task is process pure. Fourth, classifying infant memory tasks as implicit and explicit is only descriptive and does not address the mechanism by which the memory is processed and extended. Fifth, the maturational status of infants' brains is not the rate-limiting step in their ability to form, maintain, and retrieve long-term memories. Sixth, dichotomous memory systems cannot account for a large amount of learning and memory data from human and nonhuman infants.

Taxonomic Classification of Memory Systems

Willingham and Goedert (2001) described four prerequisites of a classification taxonomy. First, it has a single and conceptually unambiguous basis—either neuroanatomical (structural) or cognitive (functional). Second, the classes of the taxonomy must specify which aspects of the conceptual basis are related to memory. If the conceptual basis is structural or neuroanatomical, for example, then the classes might specify brain areas (e.g., hippocampus, prefrontal cortex, cerebellum) that are directly related to memory. Third, there must be objective rules that specify how a memory is assigned to a particular class. If the conceptual basis is neuroanatomical, for example, then the rules would specify how memory is assigned to a particular neural substrate. (Is the classification based on damage to a particular neural substrate? Is it based on activation of the neural substrate during recall?) This prerequisite ensures that all scientists who use a particular taxonomy will classify the memory the same way. Fourth, there must be a method for evaluating the taxonomy. Willingham and Goedert offered two criteria: (a) the taxonomy is internally consistent, and (b) it is useful in inspiring theory.

An unambiguous taxonomic classification of memory systems requires a single, objective conceptual basis. For adults, the conceptual basis is either neuroanatomical or cognitive, but for infants, it currently is cognitive only and usually boils down to conscious awareness (Bauer, 1996, 2007; Mandler, 1990, 2007). Because preverbal infants cannot report whether they are consciously aware of having experienced a particular event before, however, conscious awareness is not a useful criterion for classifying an infant's memory as implicit or explicit.

The classification of dichotomous memory systems is ambiguous and mixes neuroanatomical features with cognitive features. Some researchers, for example, argue that a neuroanatomical feature such as hippocampal dependence indicates conscious awareness (Bowers & Schacter, 1990; Clark & Squire, 1998; Smith, Hopkins, & Squire, 2006; Squire, 1992), whereas others cite evidence of hippocampal processing without awareness and argue that the hippocampus processes stimulus relations and associations (Chun & Phelps, 1999; Davachi & Wagner, 2002; Eichenbaum, 1999; Hannula, Ryan, Tranel, & Cohen, 2007; Richmond & DeBoer, 2006; Ryan, Althoff, Whitlow, & Cohen, 2000). Further, although memory features *within* a taxonomic class are likely to be correlated, whether memory features *across* (independent) taxonomic classes are correlated is unclear. Currently there is no behavioral evidence to support the demand for two memory systems during infancy. With the advent of improved technology, there may be neurological evidence in the future.

Identifying a Task with a Process

A common fallacy in memory research is the practice of identifying a particular task with an underlying process. Just as automatic or unconscious processes can influence performance on direct tests (Jacoby, 1991), however, intentional or conscious processes can influence performance on indirect tests (McKone & Slee, 1997). Indirect tests that adults with amnesia can perform, for example, can also be completed implicitly and/or explicitly by healthy adults. The assumption that a task maps one to one onto a process is faulty.

Operant Conditioning

The mobile conjugate reinforcement task has been labeled a procedural memory task (Bauer, 1996; Bauer et al., 2007; Mandler, 1984, 1990; McDonough, 1995, quoted in Bower, 1995) and attributed to the early developing cerebellum and certain deep nuclei of the brainstem (Bauer, 2008; C. Nelson, 1995). In fact, the neurological correlates of the mobile task have never been examined, and the aforementioned brain areas are based on an analogy (see C. Nelson, 1995) to conditioned limb flexion in the adult cat (i.e., a classically conditioned escape response; Voneida, Chirstie, Bogdanski, & Choplo, 1990).

Procedural learning is defined as gradual or incremental learning as a result of reinforced practice. For instance, it took cats an average of 1,389 trials to acquire the conditioned limb-flexion response (Voneida et al., 1990). In the mobile task, however, learning is rapid—not gradual or incremental. Both 3- and 6-month-olds typically double or triple their baseline response rate within a few minutes (Hartshorn et al., 1998; Rovee & Rovee, 1969) and exhibit significant retention for 3 days at 3 months of age (after only 9 min of training) and for 5 days at 6 months of age (after only 6 min of training).

Applying the retrieval intentionality criterion (Schacter, Bowers, & Booker, 1989), 3- and 6-month-olds who were subjected to the same independent variables (e.g., interference, different study times or trials) during original training later performed differently on delayed recognition (explicit memory or direct) tests and reactivation or priming (implicit memory or indirect) tests (Rovee-Collier, 1997; Rovee-Collier, Hayne, & Colombo, 2001). In every instance, the initial manipulation impaired retention on the direct test but not on the indirect test. The same functional memory dissociations are obtained from amnesic and healthy (instructed) adults (Graf, Mandler, & Haden, 1982; Graf & Schacter, 1985). Procedural memory does not accommodate dissociations in the operant mobile task.

C. Nelson (1995), however, had suggested that infants' recognition of the mobile might be mediated by the hippocampus. Using the mobile task, we have found that 3-month-olds exhibit a behavioral phenomenon known as the *renewal effect*, which is the resumption of acquisition responding when the context that was associated with extinction is removed during testing (Cuevas, Learmonth, & Rovee-Collier, 2008). The renewal effect is dependent on an intact hippocampus (see Ji & Maren, 2007, for review). If, as proposed by Richmond and Nelson (2007), maturation of the hippocampus is the rate-limiting step for the onset of explicit memory, then it appears that the hippocampus is functionally mature by 3 months of age.

In the mobile and train tasks that we will describe, infants do not learn a skill (how to kick or lever press). Rather, operant training merely provides preverbal infants with a nonverbal response to indicate whether they subsequently recognize *incidental information* that was present during training, such as the context (Rovee-Collier & Cuevas, 2006) or the correlation between attributes on the mobile objects (Bhatt & Rovee-Collier, 1994, 1996). During acquisition, a ribbon strung from the infant's ankle to the hook holding the mobile enables kicks to move it. During baseline and the long-term retention test, the ribbon is detached from the mobile so that kicks cannot move the mobile (Figure 1). During the long-term test, infants are shown a mobile that is the same as before ("old") or differs in some way ("new"). Kicking significantly above baseline indicates that they recognize the mobile; baseline responding indicates that they do not. Because the mobile task is inappropriate for older infants, they learn an equivalent task in which lever-pressing moves a miniature train (Figure 2). During baseline and retention testing, the lever is deactivated.

Combining these two tasks reveals that the duration of retention increases linearly over the first 18 postnatal months (Figure 3; Hartshorn et al., 1998). This retention function is misleading, however, because even very young infants can remember after very long delays if

periodically reminded. For example, in one study, 2-month-olds learned the mobile task, were reminded every 3 weeks (six reminders total), and received a final retention test at 7.25 months of age, when the study ended. Although 2-month-olds typically forget the task after 1–2 days (Figure 3), all remembered it for 4.5 months after periodic reminding, and 4 of 6 infants remembered it for more than 5.25 months. An untrained yoked control group that received the same reminders exhibited no retention after any delay (Rovee-Collier, Hartshorn, & DiRubbo, 1999). Because most infants still remembered the mobile task when the study was terminated, Hartshorn (2003) repeated the study using the train task and beginning when the infants were 6 months of age. After only five spaced reminders, infants still exhibited significant retention when they were 2 years old—1.5 years after they were trained, despite receiving only one reminder in the preceding year—at 18 months! Again, untrained yoked control groups that received the same reminders exhibited no retention.

When the forgotten training memory is primed after children are between that ages of 2 years and 2 years 6 months, most children simply quit lever pressing when the train does not move during the 2-min test and tell the experimenter that the train is “broken” or needs batteries and to fix it (Hildreth & Hill, 2003; Hsu & Rovee-Collier, 2006). Although their verbal behavior confirms that the forgotten memory was reactivated, their rate of lever pressing (the “official” retention measure) does not. Obviously, the operant measure underestimates retention following reactivation at older ages.

Experiential variables (e.g., the number of prior retrievals or reminders), rather than maturational variables (e.g., infant age), determined the maximum duration of infants’ long-term retention at both 3 and 6 months of age. These findings stand in stark contrast with the assertion that portrays “the dentate gyrus of the hippocampus . . . as a rate-limiting variable in long-term memory” (Bauer, 2008, p. 27). In fact, given that a 6-month-old can exhibit long-term retention 1.5 years after original learning, it seems unlikely that the maturational status of the brain limits the duration of long-term retention. Infants were not tested after longer delays because the task was no longer age-appropriate—not because the infants had no longer exhibited retention. So what are the hypothesized maturational limits of infants’ memory? How meaningful is this notion if the memory of a 6-month-old can be measured 1.5 years later?

Deferred Imitation

Deferred imitation is characterized as an explicit memory task that is said to require the conscious recall of a specific prior episode (for review, see Bauer, 2004; Bauer et al., 2007; Mandler, 2007; Nelson, 1995; Richmond & Nelson, 2007). This characterization is based on four primary behavioral criteria (de Haan, Mishkin, Baldeweg, & Vargha-Khadem, 2006):

1. Memory formation occurs in a single trial.
2. By 1 year of age, infants do not need to practice immediately after the demonstration session to exhibit deferred imitation.
3. In deferred imitation tasks, there is evidence of memory in the absence of perceptual support from the information to be remembered.
4. Deferred imitation passes the “amnesia test.”

The first three criteria, however, are also met by infants as young as 3 months of age. For example, both 3- and 6-month-olds exhibit significant deferred imitation of a sequence of modeled actions after a single 60-s demonstration, and they do so after delays ranging from 1 day to 3 months (e.g., Barr, Dowden, & Hayne, 1996; Barr, Marrott, & Rovee-Collier, 2003; Barr, Vieira, & Rovee-Collier, 2001; Campanella & Rovee-Collier, 2005; Rovee-Collier & Barr, 2007; Townsend, 2007). Moreover, 3- and 6-month-olds exhibit deferred imitation after these delays without practicing the target actions immediately after the demonstration (e.g.,

Barr, Rovee-Collier, & Campanella, 2005; Bullman, Atkins, & Rovee-Collier, 2008; Campanella & Rovee-Collier, 2005; Townsend, 2007). If deferred imitation is considered to be a marker for the onset of explicit memory, then the explicit memory system must be present by 3 months of age.

The number of training trials affects task demands but does not determine which memory system or process is recruited. There is evidence of one-trial learning in classical conditioning (e.g., conditioned taste aversions), for example, which is considered a procedural (implicit) memory task. Moreover, Bunsey and Eichenbaum (1996) used a classical conditioning task to demonstrate that adult rats exhibited transitivity, flexibility, and relational memory, all of which are characteristics of explicit (declarative) memory. Despite the fact that rats required reinforced practice for multiple trials on each of multiple days until they attained a learning criterion on 3 of 4 consecutive days, their task performance was hippocampus dependent (i.e., animals with hippocampal lesions did not exhibit transitivity, flexibility, or relational learning).

The third criterion is infants' ability to exhibit deferred imitation in the absence of perceptual support (e.g., Bauer, 2002, 2004; Bauer et al., 2007). Because the explicit memory system was thought to mature at 9–10 months of age, infants were expected to exhibit deferred imitation for the first time at 9–10 months too. Bauer (2002) proposed that the production of ordered pairs on a deferred imitation test was essential for concluding that the neural substrate supporting long-term explicit memory was mature.

Even though early studies documented significant 24-hr deferred imitation by 6-month-olds (Barr et al., 1996; Barr & Hayne, 1996), Bauer argued that the infants had not demonstrated explicit memory because their ordered recall was not compelling: Only 25% of 6-month-olds exhibited ordered recall after 1 day, whereas 45% of 9-month-olds did so after 1 month (Carver & Bauer, 1999, 2001). She concluded, "Although we do not have data on 6-month-olds' ordered recall at retention intervals longer than 24 hr, based on the results at 24 hr, it is unlikely that the behavior would be readily apparent at appreciably longer intervals" (Bauer, 2002, p. 34). The "missing" data on 6-month-olds' ordered recall at retention intervals longer than 24 hr are presented in Table 1 and solidly refute this supposition. Table 1 summarizes the percentage of all 6-month-olds in all studies from our lab since 2001 who produced at least one ordered pair (maximum possible = 2) after test delays of 1–90 days. As can be seen, 83% of 6-month-olds exhibited ordered recall after 7 days, and an average of 50% and 67% in two multigroup studies exhibited ordered recall after 1 month (30–44 days)—a greater percentage than at 9 months. Thus, the production of ordered pairs does not predict the emergence of explicit memory at the end of the first postnatal year.

Evidence for the criterion of passing the "amnesia test" originated with McDonough, Mandler, McKee, and Squire (1995), who found that healthy, age-matched adults passed a deferred imitation test that patients with amnesia failed. Although the patients with amnesia had imitation scores and ordered recall scores that were significantly lower than those of age-matched controls, their imitation scores were marginally higher than baseline. The latter result, usually overlooked, led the authors to conclude that the amnesic patients had exhibited "some residual declarative memory capacity." Evidence of spared semantic memory has also been obtained from patients with developmental-onset amnesia (DA), which appears to result from hippocampal damage (Adlam, Vargha-Khadem, Mishkin, & de Haan, 2005). During a 24-hr test, DA patients had lower imitation scores than an age-matched control group but again produced more actions and ordered pairs than baseline. Vargha-Khadem et al. (2003) asked whether the age when brain damage was sustained affected the severity of amnesia. Adolescents with early onset DA (birth–3 months) surpassed those with late onset DA (6 years–14 years) on immediate memory tests but performed similarly on long-term memory tests (impaired episodic memory and spared semantic memory). The immediate-retention advantage

following brain damage in early infancy was attributed to the greater neuronal plasticity in the infant brain (Bayley, O'Reilly, Curran, & Squire, 2008; Isaacs et al., 2003).

Use of a baseline comparison is an important issue because developmental researchers and researchers who study patients with amnesia use different response criteria to define what constitutes successful deferred imitation. For infants, the response criterion is whether their production of the modeled actions significantly exceeds the baseline rate (spontaneous production) either within or between subjects. For amnesic patients, the “accepted” criterion is how they perform in comparison to a matched nonamnesic control group. If the baseline response criterion were applied to amnesic patients, however, then they would exhibit deferred imitation too. Using different standards of deferred imitation for infants and amnesic adults renders comparisons between them meaningless. Thus, upon closer inspection and analysis, deferred imitation does not pass the amnesia test.

In deferred imitation tasks, infants observe a sequence of target actions and then receive an opportunity to reproduce them after a delay. In elicited imitation tasks, a variant of deferred imitation, infants imitate the actions immediately (and often during the retention interval), and they receive verbal prompts during modeling and testing at all ages (Bauer, 2004). The latter procedures, however, introduce significant confounds. Immediate imitation facilitates “flexible” responding, and both interpolated imitation and verbal cues facilitate imitation after long retention intervals. Also, providing the same verbal cues to all ages obviously benefits older infants more (for reviews, see Hayne, 2004; Jones & Herbert, 2006a, 2006b).

Barr et al. (1996) developed a deferred imitation task for 6- to 24-month-olds in which an adult models three target actions on a fuzzy hand puppet wearing a same-color mitten. Infants who observe a demonstration lasting 60 s at 6 months or 30 s at 9–24 months exhibit deferred imitation 24 hr later. An infant's imitation score is the number of target actions (remove the mitten, shake it, attempt to replace the mitten) performed within 90–120 s of touching the puppet. Although older infants have higher imitation scores, some 6-month-olds imitate all three actions. Age-matched control groups who do not see the modeling event rarely produce the target actions spontaneously ($p = .13$). Retention of deferred imitation also increases linearly with age (Figure 3), but its retention function is shallower than the operant retention function because of differences in the training parameters. Again, this function shows no evidence of a discontinuity at the end of the first year, when the explicit memory system presumably emerges.

The deferred imitation retention function, like the operant retention function, is misleading. At all ages, the duration of retention is significantly affected by the number of times the memory of the demonstration has been retrieved and the time between successive retrievals. At 6 months, for example, infants remembered the demonstration for at least 10 weeks when they retrieved its memory on multiple occasions that were widely spaced (Barr et al., 2005). When 6-month-olds watched a 30-s demonstration (i.e., one retrieval) 24 hr after the original 60-s demonstration, they exhibited significant deferred imitation 7 days later. When 6-month-olds actively imitated the modeled actions 24 hr later (also one retrieval), all exhibited deferred imitation 10 days later, and all infants also exhibited deferred imitation both 30 days after modeling (i.e., two retrievals), when the test delay was doubled from 10 to 20 days, and 70 days after modeling (i.e., three retrievals), when the test delay was doubled again, from 20 to 40 days. This result was replicated with a new experimental group whose final deferred imitation test was 60 days after modeling. A control group that received the same regimen of tests as the experimental group but had not seen the target actions performed at baseline throughout. Because 6-month-olds otherwise remember the same target actions for only 1 day whether they imitate immediately after the demonstration or not (Barr & Hayne, 1996; Barr et al., 1996, 2001), their duration of retention is particularly impressive.

In a related study, Campanella and Rovee-Collier (2005) used repeated reactivations to document deferred imitation with 3-month-olds, who are motorically incapable of performing the target actions. Infants were exposed to Puppets A + B paired for 1 hr/day for 7 days in a sensory preconditioning paradigm, and on Day 8, the experimenter modeled the three target actions on Puppet B for 60 s. On Day 9 and five more times over the next 3 months, the infants were shown Puppet B for 30 s on the experimenter's stationary hand (a reactivation treatment). At 6 months of age, when infants had become sufficiently coordinated to perform the target actions, they were tested with Puppet A. Despite not seeing either the target actions or Puppet A for 3 months, infants exhibited significant deferred imitation. In contrast, both an unpaired A–B control group and a reactivation control group responded at baseline during the deferred imitation test. This result confirms that the maturational status of the infant's brain is not the rate-limiting factor in what an infant can learn and remember.

Experience profoundly affects retention in both operant-conditioning and deferred-imitation tasks. At both 3 and 6 months of age, the duration of long-term retention was determined by experiential variables (i.e., exposure to the puppet as a reminder, distribution of training, number and timing of memory retrievals). If the maximum duration of retention were determined by the maturational status of the infant brain, then experiential variables would be unable to extend deferred imitation from 1 day to 1–3 months.

Maturation of the Explicit Memory System or Experience?

Neuroanatomical studies of memory with patients with amnesia and healthy adults led proponents of dichotomous memory systems to hypothesize that infant memory undergoes a developmental transition when the explicit memory system emerges (Bauer, 2008; C. Nelson, 1995; Richmond & Nelson, 2007). A number of age-related changes in infant memory that have been attributed to maturation of the neural structures that support explicit memory, however, are experientially determined in young infants.

First, because amnesic adults can form long-term memories of procedural or skill learning only (Corkin, 1968, 1984), the characterization of the operant tasks used with infants as “procedural” was thought to “explain” their long-term retention (cf. Bauer, 1996; McDonough, quoted in Bower, 1995). But 6-month-olds remember—equally long or longer—an association that they formed between two objects they *merely observed* together, with no procedure or action involved. In operant tasks, infants of all ages remember at least twice as long if given two sessions instead of one, and their retention is prolonged exponentially—by weeks and even months—if the interval between the two training sessions is increased (Hsu, in press). Even 3-month-olds remember for as long as infants two to three times older, depending on the interval between training sessions. Thus, as unlikely as it may seem, the data indicate that prior experience, not the maturational status of an infant's brain, predicts the ability to form, maintain, and retrieve long-term memories.

Second, prior priming increases the duration of retention when infants are primed again. At 3 months, for example, a second prime increases retention from 1 week to 2 weeks (Hayne, 1990)—the same as in once-primed 6-month-olds. Similarly, prior priming increases the fluency of repetition priming as measured by the decreased latency of responding and accuracy. Although the speed of responding to a memory prime increases logarithmically over the first year of life (Hildreth & Rovee-Collier, 1999), 3-month-olds who were primed before respond to a second prime as rapidly as 6-month-olds had responded to the first prime (Hayne, Gross, Hildreth, & Rovee-Collier, 2000). Also, the minimum duration of exposure to a prime that successfully recovers a forgotten memory decreases from 2 min at 3 months to 1.8 s at 18 months (Hsu, Rovee-Collier, Hill, Grodkiewicz, & Joh, 2005). Priming the forgotten memory before, however, cuts the minimum duration of exposure to a second prime in half at 3 months,

regardless of when the first prime was presented or for how long it was exposed (Bearce & Rovee-Collier, 2006).

Finally, Hitchcock and Rovee-Collier (1996) primed the forgotten memory of 3-month-olds twice, using a novel cue or a novel context during the second prime. The second prime reactivated the memory when the context was novel—just as the first prime reactivates the memory of 12-month-olds when the context is novel (DeFrancisco & Rovee-Collier, 2008). During priming a third time, either a novel cue or a novel context reactivated the memory. The fact that prior priming eliminates the hyperspecificity that is a hallmark of implicit memory is a stark example of the pervasive contribution of experience to memory performance.

Representational Flexibility

Early accounts of conscious or explicit memory characterized it as “an elaborate network of associations that can be used with great flexibility for comparing items not previously experienced together during learning, and for guiding behavior in various situations, including explicit memory expression” (Eichenbaum, 1997, p. 554). Today, memory researchers view representational flexibility as a key feature of explicit memory. Eichenbaum (1997) defined representational flexibility as “a quality that permits inferential use of memories in novel situations” (p. 554). In a similar vein, Squire and Kandel (1999) stated that a representation is flexible if “animals can learn relations among stored items and then express this relational knowledge in novel situations” (p. 99). In both cases, *flexibility* referred to the inferential or relational aspect of explicit memory. In contrast, some developmental researchers have defined flexibility more loosely. Jones and Herbert (2006a; see also Bauer & Dow, 1994), for example, defined representational flexibility as “the ability to retrieve memories with cues and in contexts that are not identical to those originally encoded” (p. 200).

Because representational flexibility involves more than merely generalizing across cues or contexts in the adult literature but also entails the novel use of relational information (Eichenbaum & Cohen, 2001; Preston, Shrager, Dudukovic, & Gabrieli, 2004), we argue that research on representational flexibility with nonverbal subjects should be held to the higher standard (see Townsend, 2007, and Cuevas, Rovee-Collier, & Learmonth, 2006).

During sensory preconditioning (SPC), an association is formed between two stimuli or events that occur together, such that what is eventually learned about one of them generalizes to the other. *Preconditioning* refers to the fact that the association is formed between two contiguous external (sensory) stimuli or events in the absence of reinforcement, before formal conditioning occurs. Because associations are latent, however, the subsequent conditioning (training) procedure provides an overt means of expressing it. The SPC paradigm has three phases: (a) two neutral stimuli (S) are paired ($S1 + S2$), (b) a specific response (R1) is trained to one of the stimuli ($S1 \Rightarrow R1$), and (c) subjects are tested with the other stimulus (S2). If the trained response (R1) is produced to S2 ($S2 \Rightarrow R1$), then it can be concluded that an association was formed between S1 and S2 when they were paired in Phase 1. If S1 and S2 are preexposed separately (unpaired) in Phase 1, then no response transfer is possible.

Barr et al. (2003) used SPC and a deferred imitation task to study associative learning with 6-month-olds. In Phase 1, the experimental group was preexposed to two paired hand puppets (A + B) for 1 hr/day on 7 consecutive days (Figure 4). The control group was preexposed to the puppets equally long but separately, at different times of day. Otherwise, both groups were treated identically. In Phase 2 (1 day later), an adult modeled the target actions on one puppet ($A \Rightarrow R_A$); in Phase 3 (1 day after modeling), infants were tested with the other puppet (B). They found that the paired group imitated the target actions on the other puppet ($B \Rightarrow R_A$), but the unpaired group did not. The transfer of learning from A to B indicated that an $A \Leftrightarrow B$

association had been formed in Phase 1. Barr et al. (2003) also found that infants associated the paired puppets after 1-hr preexposure sessions on 2 consecutive days.

Bullman et al. (2008) found that infants successfully associated the paired puppets after a 1-hr preexposure session on 1 day. Merely viewing the paired puppets for a total of 1 hr over two temporally discrete sessions on 1 day enabled infants to remember the association for at least 14 days. Notably, 14 days is the same duration for which 6-month-olds exhibit retention after operant training on 2 consecutive days. These data reveal that relatively long retention by very young infants is not unique to operant conditioning or due to a special kind of “motor memory” or “action memory.”

Using a version of Barr et al.'s (2003) SPC procedure, Townsend (2007) preexposed infants to a new pair (instead of to same pair) of puppets for 1 hr/day on successive days. One member of each new pair had been preexposed the day before, while the other member was novel. In Phase 1, Townsend preexposed 6-month-olds to a different pair of puppets on each of 2 days (A + B, B + C). In Phase 2, he modeled the target actions on either Puppet C or Puppet A. In Phase 3, he administered a deferred imitation test with either Puppet A or Puppet C, respectively.

When tested for deferred imitation with Puppet A (the retrieval cue), infants presumably exploited a forward associative chain ($A \Rightarrow B \Rightarrow C$) and successfully imitated the actions that had been modeled on Puppet C. When tested for deferred imitation with Puppet C (the retrieval cue), infants presumably exploited a backward associative chain and imitated the actions that had been modeled on Puppet A ($A \Leftarrow B \Leftarrow C$; Figure 5, left panel). When another puppet pair (C + D) was added to the chain (i.e., $A-B-C-D$), and the target actions were modeled on Puppet D, infants imitated them also when tested with Puppet A, but they did not imitate when tested with a novel puppet (Puppet E; Figure 5, right panel). Finally, infants who saw Puppets A and B unpaired on the first day of Phase 1 failed to imitate the modeled actions on Puppet A, indicating that the integrity of the $A \Rightarrow B$ link of the chain was critical for successful indirect deferred imitation. The same result was obtained when infants were exposed to Puppet B alone (an extinction procedure) after the A–B association was formed (Group ExtB–B/A), after the A–B, B–C associations were formed (Group ExtB–C/A), or even after the demonstration on Puppet C (Group C–ExtB/A; Figure 5, left panel).

These findings suggested that infants had formed an associative chain in which successive puppet–puppet associations were linked by the common member (Puppet B). When one member of the chain was activated, the activation presumably spread along the chain to more remote members, allowing learned responding to transfer from the training stimulus to a stimulus that had never been directly paired with it. These findings are a classic example of representational flexibility.

An even more striking demonstration of representational flexibility with 6-month-olds was reported by Cuevas et al. (2006). They demonstrated that 6-month-olds formed an association between two objects that neither were perceptually present nor had ever appeared together when the representations of those objects were simultaneously activated in primary memory by associated retrieval cues. In this study, infants were simultaneously exposed to Puppets A and B (Phase 1) and were trained to kick to move a mobile in a distinctive context 24 hr later (Phase 2). By the end of Phase 2, infants had presumably formed two associations—one between Puppet A and Puppet B, and one between the mobile and the context. In Phase 3, infants were exposed to Puppet A (Puppet B not present) in the distinctive context (the mobile not present) to form an indirect Puppet B–mobile association (Figure 6). The new association was formed when Puppet A activated its associated memory of Puppet B, and the distinctive context activated its associated memory of the mobile. When the retrieved memory

representations of Puppet B and the mobile were simultaneously active in primary memory, they were associated, even though neither object was physically present. In Phase 4, the target actions were modeled on Puppet B in order to provide infants with an overt behavior for expressing the new association.

In a prior study, 6-month-olds had deferred imitation for 2 weeks when the demonstration was associated with an operant task that they remembered for 2 weeks (Barr et al., 2001). Cuevas et al. (2006) reasoned that if Puppet B and the mobile had been associated in absentia, then infants would similarly exhibit deferred imitation on Puppet B 2 weeks after the demonstration. They did. Infants formed a relatively enduring association between memory representations that were simultaneously activated in the absence of perceptual support.

These studies reveal that 3-month-olds rapidly form arbitrary associations between simultaneously present stimuli or events (Bhatt & Rovee-Collier, 1994, 1996; Campanella & Rovee-Collier, 2005). Six-month-olds form multiple associations in the same manner, link them in an associative chain over days, and use them to respond relationally in novel ways. A hierarchical, dichotomous memory systems account cannot accommodate these findings. According to this account, infants should not possess these capacities before the end of the first year or beginning of the second year of life, when the components of the explicit memory system—especially the hippocampus and associated cortex—mature (Eichenbaum, 1999). Furthermore, lesions to the hippocampus and surrounding area (i.e., fimbria, perirhinal cortex) produce deficits in SPC (Nicholson & Freeman, 2000; Port, Beggs, & Patterson, 1987; Port & Patterson, 1984; Talk, Gandhi, & Matzel, 2002; but see Ward-Robinson et al., 2001). Thus, SPC by very young infants is evidence of relational, hippocampal-dependent learning, which presumably characterizes explicit memory.

An Ecological Model of Memory Development

An ecological account of infant memory development does not attempt to force infant data to fit into a memory model that was developed to accommodate data from normal and abnormal adults. Very young infants of all species can learn and remember numerous associations between events that co-occur or share a common member or affordance (function). These associations can enter into relationships with previously acquired associations in a complex mnemonic network. As the network expands and becomes increasingly interconnected, their memory performance becomes increasingly flexible.

The widely embraced view that two different memory systems with different developmental trajectories account for learning and memory was derived from research with brain-damaged adults and has enjoyed few serious challenges over the years. An alternative ecological solution to the “central problem,” proposed by Spear (1984), was derived from psychobiological research with developing rat pups (Brasser & Spear, 2004; Rovee-Collier, 1983; Rovee-Collier & Gekoski, 1979; Rovee-Collier & Hayne, 1987; Spear, Kraemer, Molina, & Smoller, 1988; Spear & Kucharski, 1984). This account eschews a multiple memory systems account of infant memory development and instead recognizes that at each point in development, infants of all species epitomize a successful evolutionary adaptation. As such, they rapidly learn the relationships that define their niche and confer survival and reproductive advantage. As infants grow and change, their niche and the challenges it poses change too. As a result, infants’ behavioral adaptations to the new challenges and the physiological mechanisms that evolved to support them also change. To meet each new set of ecological demands, infants select particular aspects of episodes to learn and remember until their niche changes again.

In an ecological model, infants are not regarded as incomplete or imperfect adults who must “improve” and become more complete with age; rather, they are viewed merely as non-adults—as different organisms who occupy different ecological niches that pose different sets of

problems to solve (see Lehrman, 1953). As Kennedy (1967, p. 338) put it, "What is important . . . is that almost all mammals encounter a variety of environments during growth, and the optimal development of phenotype depends on adaptability to all rather than adaptation only to the final one." The learning and memory capacities of developing organisms do not become increasingly better or more adultlike, as is often said (e.g., Jones & Herbert, 2006a). Rather, at each stage of development, infants' learning and memory capacities are as good as they will ever be, but this fact is obscured because what infants and adults learn and remember about the same event differs. Moreover, infants can rapidly learn some associations that adults cannot learn at all.

The first evidence of such learning was obtained in studies of SPC and potentiation with preweanling rat pups (Brasser & Spear, 2004; Kucharski & Spear, 1985; Spear, 1984; Spear et al., 1988; Spear & Kucharski, 1984), and we have obtained parallel evidence with very young human infants. Our infant findings are reviewed in the following sections.

Sensory Preconditioning (SPC)

Cuevas, Bullman, and Rovee-Collier (2008) found developmental differences in how quickly infants formed associations during the preexposure phase of SPC. Specifically, 6-month-olds exhibited SPC when Puppets A and B were presented simultaneously for 1.9 min on a single occasion. However, 9- and 12-month-olds failed to exhibit SPC when the puppets were presented together for 15 min on a single occasion. Thus, younger infants formed associations between neutral stimuli (two puppets) faster than did older infants. From the perspective of neurological maturation, these findings seem counterintuitive. How would younger infants encode information faster than older infants if neurological development were related to the rate of encoding (see Bauer, 2008)? In an ecological model of memory development, memory processing is not assumed to improve with age.

Associations between neutral stimuli play a central role in the formation of the early associative network. We propose that by the time infants are 3 months of age, SPC is the primary mechanism via which they nonselectively pick up new information from the environment, associating whatever they see together and later using that association to transfer a learned response from one member of the association to the other. At 6 months of age, infants form new associations between what they see together rapidly (in < 2 min) and remember those new associations for at least 24 hr. Moreover, how quickly infants form associations during SPC is related to their current ecological niche. As a consequence of achieving independent locomotion, for example, 9- and 12-month-olds encounter an exponentially greater number and variety of neutral stimuli (e.g., objects, toys) than 6-month-olds and may do so rapidly as they navigate from one context to another. Rather than associating everything they pass with everything else, they are increasingly selective in the associations they form. This change is facilitated by the fact that 9- and 12-month-olds need be exposed to the neutral stimuli longer to either form the association or remember the association for 24 hr.

Research with rat pups (Chen, Lariviere, Heyser, Spear, & Spear, 1991; Cheslock, Varlinskaya, High, & Spear, 2003) has found developmental differences in the effective preexposure regimen for SPC. For newborn rat pups, *only* simultaneous preexposure produced SPC; at 12 days, *both* simultaneous and sequential preexposure produced SPC; at 21 days, *only* sequential preexposure produced SPC. Recently, Cuevas et al. (2008) also found that the developmental pattern of SPC in human infants at 6, 9, and 12 months of age parallels the findings with rat pups. For simultaneous preexposure, the puppets were displayed side by side in the infant's full view. For sequential preexposure, there was a specified delay (0-, 7.5-, 15-, 30-, or 60-s interstimulus interval [ISI]) between puppet presentations. Six-month-old infants exhibited SPC *only* after simultaneous preexposure, 9-month-olds exhibited SPC after *both* simultaneous and sequential preexposure (0-s ISI), and 12-month-olds exhibited SPC *only* after sequential

preexposure (7.5- and 30-s ISI). Furthermore, 9-month-olds exhibited SPC after a longer ISI (15 s) when presented with more paired presentations of the puppets.

Research with slightly older infants, 15- and 18-month-olds, however, revealed that human infants exhibit another associative shift in SPC during the second year of life. Using two different preexposure procedures (i.e., one 30-min session vs. two 15-min sessions), both Muentener (2004) and Cuevas (2007) found evidence of simultaneous SPC at 18 but not 12 months of age. Furthermore, 15-month-olds, like 12-month-olds, failed to exhibit simultaneous SPC (Cuevas, 2007). Taken together, the data suggest that the absence of simultaneous SPC is limited to 12 and 15 months of age, with both simultaneous and sequential SPC occurring at 9 and 18 months of age (Cuevas, 2007). Thus, the absence of simultaneous SPC at 12 and 15 months of age does not result from the onset of an explicit memory system. We propose that the developmental shifts in the effective preexposure regimen in the human infant are related to changes in the infant's ecological niche.

Unlike all other animals, the human infant has a protracted period during which he or she is unable to locomote independently (i.e., crawl, walk). The onset of independent locomotion changes the infant's niche and promotes the acquisition of sequential associations between neutral stimuli that are encountered in rapid succession during the preexposure phase of SPC. For instance, the 6-month-old infant's ecological niche is particularly suited for simultaneous SPC; they have not acquired independent locomotion and spend the majority of their time viewing the environmental surround, most likely learning "what goes with what." The onset of self-locomotion allows infants to actively encounter environmental stimuli successively, most likely learning "what comes next." Accordingly, the 9- and 12-month-old's ecological niche is well suited for sequential SPC. Nine months of age is a marked transitional stage at which infants form associations via both simultaneous and sequential SPC.

The infant's ecological niche may also be related to the absence of simultaneous SPC at 12 and 15 months of age. As a consequence of independent locomotion, 12- and 15-month-olds only form sequential associations between neutral stimuli (i.e., what comes next). Infants have limited resources, and we speculate that much of their time and energy is spent actively exploring their environment and using their new skill of independent locomotion. To this end, sequential preexposure mimics the 12- and 15-month-old's daily routine of actively moving between multiple places more than does simultaneous preexposure. We propose that the reemergence of simultaneous SPC at 18 months reflects the experienced walkers' ability to allocate resources to acquire both information about what goes with what and what comes next.

A hierarchical, dichotomous memory-systems account cannot accommodate these findings. According to such an account, the learning and memory capacities of developing organisms should become increasingly competent or adultlike (e.g., Jones & Herbert, 2006a).

Potentiation

When an event is learned better in the presence of a second event than alone, the enhancement is called *potentiation*. A cognitive account of potentiation holds that when two events occur simultaneously, they are associated in primary memory, and the memory strength that was previously accrued by one member of the association flows to the other. As a result, the first event is learned better, hence remembered longer. Any operation that strengthens the memory of the second event (e.g., retrieving it) will potentiate learning that occurs in its presence even more.

Potentiation of learning and retention are far superior in infant and preweanling rat pups than in adult rats, who often exhibit adverse effects (e.g., overshadowing or blocking) when learning about one event in the presence of another (Kucharski & Spear, 1985). Recently, we

documented potentiation effects with 6-month-old human infants when the target actions were modeled on the puppet in the presence of the train set after the infants had learned the train task. At 6 months of age, human infants exhibit deferred imitation of the modeled actions for 24 hr, but they remember the operant train task for 2 weeks. When the demonstration in the presence of the train set immediately followed operant training, deferred imitation was potentiated for 2 weeks—the same duration that they remember the train task—instead of only 24 hr (Barr et al., 2001). How did this occur? Apparently, when the representations of the previously learned train task and demonstration simultaneously occupied primary (active) memory, they were associated.

Because retrieving the memory of the train task 1 week after operant training doubles its retention from 2 to 4 weeks, we asked whether modeling the target actions in the presence of the train set 1 week after training would potentiate their deferred imitation longer too (Figure 7). It did. When the modeling event was associated with the retrieved memory of the train task, deferred imitation of the target actions was potentiated for 4 weeks too. Retrieving the memory of the train task 2 weeks after operant training quadruples its retention from 2 to 8 weeks. Likewise, when the target actions were modeled in the presence of the train set 2 weeks after operant training, the retrieved memory was strengthened even more, and deferred imitation was potentiated even longer. Now, 6-month-olds remembered the train task for 8 weeks, and deferred imitation was potentiated for 6 weeks after the demonstration (Rovee-Collier & Barr, 2007).

Considering that 6-month-olds can exhibit deferred imitation for only 24 hr when they see the same modeling event alone, the finding that they exhibited deferred imitation for 6 weeks is compelling evidence that the hippocampus or some other neuroanatomical structure that mediates deferred imitation and relational learning is functionally mature by 6 months, if not earlier (cf. Campanella & Rovee-Collier, 2005). In other words, how long young infants remember what they see depends on the meaningfulness of the context in which they see it. These findings have major implications for the benefits of varied experience and enriched environments in early infancy.

To summarize, if representational flexibility is a marker of explicit memory, then explicit memory is present by at least 6 months of age. If deferred imitation is the marker of explicit memory, then it is present by 3 months of age. And, if the formation of arbitrary associations, as in SPC, is the marker of explicit memory and hippocampal function, then it also is present by 3 months.

An Ecological Analysis of Infant Long-Term Memory

Proponents of dichotomous memory systems hold that the infant brain is too immature to encode, store, and retrieve declarative memories over the long term and that this capacity depends on brain structures that are not mature until the end of the first year of life (Bauer, 2004; Kagan & Hamburg, 1981; Liston & Kagan, 2002). Observations that infants were slower to learn and faster to forget than adults encouraged the view that these behavioral changes reflected ontogenetic changes in memory processes. From an ecological perspective, however, the underlying process does not change ontogenetically, but the content of what is learned and remembered does. Instead of asking *whether* infants remember over the long term, research in this tradition focuses on *what* they remember and under what conditions they remember it.

One mechanism underlying young infants' exuberant learning (and memory) is their ability to discriminate more and different aspects of the same event than do adults. That is, young infants can perceive aspects of an event that adults cannot. With culture-specific experience, however, infants' initially broad perceptual tuning narrows. Near the end of the first postnatal year, they can no longer perceive the same breadth of culture-general sights and sounds that they did

before. This phenomenon, known as *perceptual narrowing*, has now been documented in a number of domains, including the perception of speech sounds (Werker & Tees, 1984), faces (Pascalis, de Haan, & Nelson, 2002), and musical rhythms (Hannon & Trehub, 2005a, 2005b). In the latter case, for example, 6-month-olds discriminated changes in complex musical rhythms from nonnative cultures, but 12-month-olds and adults did not. Although the neural mechanisms that underlie perceptual narrowing are unknown, one possibility is that “the modification of neural circuits and synaptic connections with repeated use and disuse . . . may be operating to increase synaptic efficacy of environmentally relevant information” (Scott, Pascalis, & Nelson, 2007, p. 200).

What are infants likely to learn and remember? Spear (1984) speculated that infants are less selective than adults in the associations they form. As a result, they learn as much if not more than adults about a particular episode—and much more than could be useful later. From an ecological perspective, this rapid and exuberant learning is an adaptive strategy that cognitively equips the young of all species to respond effectively in new situations containing a member of an association, to form multiple associations between all elements of a multielement event, and to link prior associations with common members. A major drawback to their exuberant learning, however, is that infants learn too much. The problem then becomes how to prune the multitude of useless and possibly inappropriate associations.

One solution to this problem is *rapid forgetting*. Instead of being a memory deficit, infants’ rapid forgetting is an important way in which new memories are eliminated from the repertoire unless they are retrieved in the interim, which forestalls forgetting (a reinstatement procedure). Even a forgotten memory can be recovered, however, if it is primed by cues from the original encoding situation that are reencountered (a reactivation procedure). At all ages, infants forget the reactivated memory at the same rate as before. Thus, reactivating a memory essentially doubles its “life” (Hildreth & Rovee-Collier, 2002; Hsu et al., 2005).

There is an upper limit, however, to how long after encoding a forgotten memory can be reactivated. Although the absolute amount of time to the upper limit increases with age, the relative amount of time is a *constant* (4:1) *ratio* of the original duration of retention at all ages (Hildreth & Hill, 2003; Hsu, in press). Thus, reactivating a memory at the upper limit quadruples the life of a memory. The preceding data reveal that ontogenetic changes in infant memory cannot be due to an increased capacity for encoding, storage, or retrieval but to changes in what infants select to encode.

Another means of pruning excessive associations is rapid extinction. Both nonhuman and human infants not only exhibit rapid acquisition, but they also exhibit rapid extinction (Kucharski & Spear, 1985; Shafer & Rovee-Collier, 2008; Spear, 1979). Three-month-olds, for example, exhibit no spontaneous recovery unless extinction is delayed or the specific details of the original cue—but not its general features—are forgotten. In the latter case, novel details of a similar cue can be substituted for the old details in the original memory, updating it (Boller, Rovee-Collier, Gulya, & Prete, 1996; Galluccio & Rovee-Collier, 2005; Rovee-Collier, Adler, & Borza, 1994).

Dichotomous Memory Systems Redux

Many psychologists and neuroscientists attribute ontogenetic changes in infant memory to the hierarchical emergence of dichotomous memory systems (implicit and explicit memory) during the first year of life. We have argued that this division is both conceptually and empirically flawed on a number of counts:

1. The conceptual basis of classifying memory systems as implicit or explicit is conceptually ambiguous.

2. Classifying infant memory tasks as implicit and explicit is only descriptive and does not address the mechanism by which the memory is processed and extended.
3. Conscious awareness is not an appropriate conceptual basis for classifying a preverbal infant's memory as implicit or explicit.
4. Assumptions of a one-to-one mapping between processes and tests are wrong: No task is process pure.
5. The maturational status of infants' brains is not the rate-limiting step in their ability to form, maintain, and retrieve long-term memories.
6. Dichotomous memory systems cannot account for a large amount of learning and memory data from human and nonhuman infants. These data strip dichotomous memory systems of their descriptive utility.

Finally, we propose that at every point in development, organisms are perfectly adapted to meet the ecological challenges posed by their changing niche. As ecological demands change, so do their adaptive strategies and the physiological mechanisms that evolved to support them. By this account, adults and infants are different organisms who meet different ecological demands with adaptive solutions that are different but equally effective. As a result, infants and adults select to learn different things about the same event, and infants can even learn some associations that adults cannot learn at all. Observation of normal ontogenetic changes in learning and memory does not demand explanation in terms of dichotomous memory systems.

Acknowledgments

This research was supported by National Institute of Mental Health Grant MH32307 to Carolyn Rovee-Collier. We are indebted to Norman E. Spear for numerous stimulating conversations about ontogenetic differences in stimulus selection over the last 30 years.

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Figure 1.

Experimental arrangement used with 2- to 6-month-olds in the operant mobile task, shown here with a 3-month-old. From left to right: (a) Baseline—The ankle ribbon and mobile are connected to different hooks, and kicks do not move the mobile; (b) Acquisition—Kicks conjugately move the mobile via an ankle ribbon connected to the mobile hook; (c) Immediate retention test/long-term retention test—The ankle ribbon and mobile are again connected to different hooks. During the test, infants who recognize the mobile kick to move it, even though they cannot.

Figure 2.

Experimental arrangement used with 6- to 24-month-olds in the operant train task, shown here with a 6-month-old. Each lever press moves the toy train for 2 s (1 s for older infants) during acquisition; during baseline and all retention tests, the lever is deactivated, and presses do not move the train. From "Infant Memory," by C. Rovee-Collier and K. Cuevas, 2008, in J. Byrne (Series Ed.) and H. L. Roediger, III (Vol. Ed.), *Learning and memory: A comprehensive reference*. Vol. 2: Cognitive psychology of memory (Figure 5, p. 692). Copyright 2008 by Elsevier. Reprinted with permission.

Figure 3.

Standardized reference functions for the maximum duration of retention (in weeks) of infants who were trained and tested in the operant mobile and train tasks and the deferred imitation (puppet) task using a standardized procedure with age-calibrated parameters. Differences in the slopes of the two functions are due solely to different training parameters. (From "The Ontogeny of Long-Term Memory Over the First Year-and-a-Half of Life," by K. C. Hartshorn, P. Rovee-Collier, R. S. Gerhardstein, T. L. Bhatt, P. J. Wondoloski, P. J. Klein, et al., 1998, *Developmental Psychobiology*, 32 (Figure 11, p. 83). Copyright 1998 by Wiley Periodicals. Reprinted with permission.

Figure 4.

A 6-month-old infant during a paired preexposure to Puppet A and Puppet B at sensory preconditioning (*left panel*), demonstration of the target actions on Puppet A (*middle panel*), and the deferred imitation test on Puppet B (*right panel*).

Figure 5.

Mean imitation scores of independent groups of 6-month-old infants. When tested for deferred imitation with Puppet A (the retrieval cue), infants presumably exploited a forward associative chain ($A \Rightarrow B \Rightarrow C$) and successfully imitated the actions that had been modeled on Puppet C. When tested for deferred imitation with Puppet C (the retrieval cue), infants presumably exploited a backward associative chain and imitated the actions that had been modeled on Puppet A ($A \Leftarrow B \Leftarrow C$; left panel). When another puppet pair (C + D) was added to the chain (i.e., $A-B-C-D$), and the target actions were modeled on Puppet D, infants imitated them also when tested with Puppet A, but they did not imitate when tested with a novel puppet (Puppet E; right panel). Infants who saw Puppets A and B unpaired in Phase 1 failed to imitate the modeled actions on Puppet A, indicating that the integrity of the $A \Rightarrow B$ link of the chain was critical for successful indirect deferred imitation. The same result was obtained when infants were exposed to Puppet B alone (an extinction procedure) after the $A-B$ association was formed (Group ExtB-B/A). An asterisk indicates that the mean imitation score of a group was significantly greater than the mean test score of the pooled baseline control group ($p < .05$). Error bars = 1 SE.

Figure 6.

Exposing Puppet A in the distinctive mobile training context established an association between Puppet B and the mobile, even though Puppet B and the mobile were not physically present when the association was formed. The association was formed when Puppet A and the context simultaneously activated the associated memories of Puppet B and the mobile, respectively.

Figure 7.

Experimental arrangement used with 6-month-old infants in studies in which the demonstration and train task are associated. The target actions were modeled on the puppet with the train set in view. Testing for imitation occurred in this same context. From “Mediated Imitation in 6-Month-Olds: Remembering by Association” by R. Barr, A. Vieira, and C. Rovee-Collier, 2001, *Journal of Experimental Child Psychology*, 79 (Figure 4, p. 238). Copyright 2001, Elsevier. Reprinted with permission.

Evidence of Ordered Recall in 6-Month-Old Infants

Table 1

Percentage of 6-month-old infants who also exhibited deferred imitation and ordered recall after a delay											
Length of delay (in days)											
1											
Study	Percent	Range (%)	Percent	Range (%)	Percent	Range (%)	Percent	Range (%)	Percent	Range (%)	Percent
Barr et al., 2001	33		33	0–67	17						
Barr et al., 2002						29	20–33				
Barr et al., 2003	50				42	33–50					
Barr et al., 2005	42	17–67	23	0–50	40	14–83	67	50–83	9	0–17	
Campanella & Rovee-Collier, 2005	39	33–44									27 ^a
Cuevas et al., 2006	50		83		29						
Learmonth et al., 2004	44	17–67									
Learmonth et al., 2005	44	17–83									
Rovee-Collier & Barr, 2007			25	17–33	33		50	33–67			
Townsend, 2007	45	25–63									

Note. Range values refer to range of multiple groups tested after the same delay.

^a Infants were 3 months old at the time of demonstration.