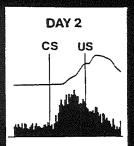
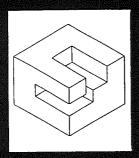
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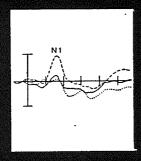


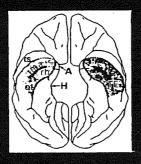


The Development and Neural Bases of Higher Cognitive Functions

Editor Adele Diamond







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Rate of Maturation of the Hippocampus and the Developmental Progression of Children's Performance on the Delayed Non-Matching to Sample and Visual Paired Comparison Tasks^a

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INTRODUCTION

This paper addresses two questions: (a) Does the hippocampal formation, and the memory function dependent upon it, mature early or late? (b) Why is it that a variety of cognitive abilities appear to be present earlier when assessed by where subjects look than by where subjects reach?

The traditional view is that the hippocampus matures late. It has been suggested, for example, that we do not have access to memories of the earliest years of life ("infantile amnesia") because the memory system dependent on the hippocampus (the system required for memories to which we have conscious access) is not yet mature during those early years (Nadel & Zola-Morgan, 1984; Schacter & Moscovitch, 1984; Bachevalier & Mishkin, 1984). This view of hippocampal maturation is based primarily on anatomical studies in the rat. Further support for this view came a few years ago when it was found that monkeys could not succeed until relatively late in infancy on one of the classic tests of hippocampal memory function, delayed non-matching to sample. Recent work from our laboratory and from that of Overman shows that children, too, are not able to succeed on the delayed non-matching to sample test until very late in infancy.

The traditional view of hippocampal maturation will be questioned in this paper,

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however. Evidence from the rat brain may have led to misleading conclusions about the rate and timing of hippocampal maturation in the primate brain. Primates are born more mature than rodents, and emerging evidence from anatomical studies in the monkey suggests that the hippocampus matures quite early in primates. Moreover, human infants and infant monkeys are able to succeed on a memory test very similar to delayed non-matching to sample, the visual paired comparison test, from earliest infancy.^d

This brings us, then, to the puzzle that is examined in the second half of the paper: If the memory function dependent on the hippocampal formation matures early, why does success on a criterial test of this hippocampal function, the delayed non-matching to sample test, appear so late? Delayed non-matching to sample and visual paired comparison seem to be very similar tests; why does success on delayed non-matching to sample appear so much later than success on visual paired comparison? One possibility might be that success on these two tasks depends on different neural systems that mature at different rates. For example, it might have been that the visual paired comparison task requires only implicit memory, whereas the delayed non-matching to sample task requires explicit memory.^e However, both in infants and adults, each task appears to depend on the explicit memory system subserved by the hippocampal neural circuit. It might have been that explicit memory becomes available to, or integrated with, the visual system earlier than it does the reaching system. That is, in infants, the eyes may know something before the hands. Indeed, other cognitive competencies (such as knowledge or memory of a hidden object) have long appeared to develop late when assessed by reaching, but have recently been shown to develop early when assessed by where infants look. However, as will be described below, we have constructed a version of delayed non-matching to sample (requiring reaching) on which infants succeed from the very earliest age they can be tested at delays fully as long as those on which they succeed in the visual paired comparison task (which requires only looking).

Evidently, delayed non-matching to sample requires some ability other than explicit memory, not required by visual paired comparison, which accounts for the late appearance of success on the task. That ability might involve *motor planning* enabling older infants to execute means—end action sequences required by delayed non-matching to sample but not by visual paired comparison. It might be the ability to deduce an abstract rule or the ability to demonstrate during explicit testing

^cSee description of the task in Part I. Briefly, delayed non-matching to sample is a recognition memory task where a sample object is presented, and then after a delay the subject is shown two objects, one matching the now familiar sample and one new (non-matching) object. The correct response is for the subject to reach to the new, non-matching object. Delayed non-matching to sample is used, rather than delayed matching to sample, because monkeys have a natural preference for novelty (Harlow, 1950; Brush, Mishkin & Rosvold, 1961; Mishkin, Prockop & Rosvold, 1962; Gaffan, Gaffan & Harrison. 1984) and so learn delayed non-matching to sample much more readily than delayed matching to sample. The same is true for human infants (Overman, this volume) and infant monkeys (Bachevalier, this volume).

dSee description of task in Part 1. Here, as in delayed non-matching to sample, a sample stimulus (the "familiarization stimulus") is presented. After a delay, the subject is given the choice of looking at the now familiar stimulus or at a new stimulus, not previously seen. "Success" on visual paired comparison, as on delayed non-matching to sample, is defined as consistent choice of the novel (non-matching) stimulus. Because when given a choice between an old, familiar stimulus and something new, human infants and monkeys tend to choose something new, memory of the previously presented stimulus is inferred from consistent choice of the new stimulus.

^eImplicit memory can be demonstrated in behavior without any conscious awareness of the "memory" on the part of the person (see, e.g., Schacter, this volume). Explicit memory is, roughly, memory of which the subject is aware. Explicit memory appears to depend upon the functions of the hippocampal neural system and is severely impaired in adults with amnesia, although amnesic adults demonstrate relatively normal implicit memory (see, e.g., Zola-Morgan & Squire, this volume).

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something which can readily be shown in a "free play" situation much earlier. It might involve the symbolic and representational skills necessary to understand that the object one sees and initially acts upon is not the reward, but only stands for the reward. It might involve resistance to interference required by delayed non-matching to sample but not by visual paired comparison. Or, it might involve faster speed of processing in encoding visual stimuli as the sample stimulus is present much more briefly in delayed non-matching to sample than in visual paired comparison. We are currently in the process of testing these hypotheses. Regardless of which is correct, one fact appears clear: Although delayed non-matching to sample is a test of the memory function dependent on the hippocampus in adult monkeys and humans, the developmental progression of improved performance on the task in infants does not chart the developmental progression of this memory function or neural circuit, even though the same task is used with infants and adults.

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The hippocampus appears to mature early in primates; the memory function dependent on that neural system appears to be present early (as seen by performance on the visual paired comparison task). Improved performance with age on delayed non-matching to sample must, then, be charting the developmental progression of some other ability. In adult humans or monkeys, hippocampal damage leaves this other ability intact but impairs memory, impairing performance on the task at long delays but not at very brief ones. Here is an instance where a task has been linked to a specific neural circuit in infant monkeys, adult monkeys, and human adults, and where the developmental progression in human infants and infant monkeys has been charted. While one might have thought that the developmental progression of improved performance on the task corresponds to maturation of the hippocampal neural circuit, that conclusion turns out to be unjustified. This is an important illustration of the care that must be taken in drawing conclusions about developmental brain-behavior relationships.

PART I: DOES THE HIPPOCAMPAL FORMATION, AND THE MEMORY FUNCTION DEPENDENT ON IT, MATURE EARLY OR LATE?

Evidence for the Traditional View of Hippocampal Maturation

Anatomical Evidence of Late Hippocampal Maturation in the Rat

There is considerable evidence of prolonged postnatal maturation of the hippocampus, particularly the subarea called the dentate gyrus, in the rat f For example, while the vast majority of the pyramidal cells in the hippocampus proper are present at birth, the vast majority of the granule cells in the dentate gyrus of the rat are generated after birth (Altman & Das, 1965; Altman, 1967; Bayer & Altman, 1974; 1975; Altman & Bayer, 1975; Trice & Stanfield, 1986). The timetable is approxi-

fThe hippocampus consists of two parts: Ammon's horn (fields CA1-4; often called the hippocampus proper) and the dentate gyrus (also called the dentate fascia). Different cell types are found in these two subregions: Pyramidal cells characterize Ammon's horn, while the smaller granule cells are found in the dentate gyrus.

mately 15% of the dentate gyrus granule cells present at birth, 40% present by 4 days of age, 60% present by day 8, 87% present by 16 days.8

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The story for synaptogenesis in the rat dentate gyrus is much like the story for neurogenesis—it occurs primarily postnatally. Fewer than 1% of the synapses seen in the molecular layer of the dentate gyrus in the adult rat are present at 4 days of age. The greatest rate of increase is estimated to occur between days 4 and 11, when the number of synapses doubles almost daily. Still, only 5% of the synapses are present even by day 11. Sometime between 11-25 days of age, essentially all the synapses in the molecular layer of the dentate gyrus have been formed (Crain, Cotman, Taylor & Lynch, 1973). (These synapses represent input from the entorhinal cortex to granule cells in the dentate gyrus.)

Similarly, there is biochemical evidence of late development. Acetylcholinestrase activity is barely noticeable in the rat hippocampus before 3-4 days of age. It becomes more pronounced in the dentate gyrus by 6-8 days of age, increases sharply between 10-20 days of age, and takes on the full adult pattern by 35 days of age (Ritter, Meyer & Wenk, 1972; Matthews, Nadler, Lynch & Cotman, 1974). The high concentration of zinc in the hippocampus associated with the projection from dentate gyrus granule cells onto pyramidal cells in fields CA2-4 of the hippocampus proper (the mossy fiber projection) does not become apparent until rats are 18-22 days old (Crawford & Connor, 1972).

Finally, physiological evidence that anatomical connections are, in fact, functional has not been found earlier than 3 weeks of age for the projection from the septum to the hippocampus and not before 1 month of age for the projection from entorhinal cortex to the hippocampus in the rat (Nikitina, 1974).

This is impressive converging evidence, derived from a variety of measures and techniques, that the hippocampus (especially the dentate gyrus) shows a protracted postnatal development in the rat.

The Standard Delayed Non-Matching to Sample Task Defined

The delayed non-matching to sample task assesses recognition memory for objects. First a sample object is presented at the center of the testing area. In order to insure that the subject has seen the sample, the subject must displace it to retrieve a reward underneath. Then an opaque screen is lowered and a delay typically within the range of 10 sec to 2 min is imposed. The screen is then raised revealing the familiar sample object and a new object the subject has never seen before (one to the left of midline and the other to the right). The subject must displace one of the objects, and if he or she displaces the new object (i.e., the one that does not match the object presented before the delay) a hidden reward is revealed for the subject to retrieve. The left-right position of the new and familiar objects is varied randomly Over trials

^gRats are elderly by 1 year and rarely live much past 24-30 months. They are mature by somewhere between 45-120 days. Thus, by 16 days of age the average rat has lived as large a percentage of his or her lifespan as has the average person by the age of 3 years.

The testing procedure currently used, with different junk objects on every trial ("trial-unique stimuli"), was independently devised by Gaffan (1974) and by Mishkin & Delacour (1975). Delayed non-matching to sample is used because monkeys find it so difficult to learn delayed *matching* to sample, given their natural preference to reach to the new object (Harlow, 1950; Brush, Mishkin & Rosvold, 1961; Mishkin, Prockop & Rosvold, 1962; Gaffan, Gaffan & Harrison, 1984).

Success on Delayed Non-Matching to Sample Depends on Hippocampal Function

The delayed non-matching to sample task is a sensitive measure of the memory functions dependent on the medial temporal lobe, in particular the memory functions of the hippocampus. Performance on delayed non-matching to sample is impaired in monkeys following lesions of the hippocampus plus neighboring structures including the amygdala (Mishkin, 1978; Zola-Morgan, Squire & Mishkin, 1982); by lesions of the hippocampus plus adjoining perirhinal cortex but excluding the amygdala (Zola-Morgan, Squire & Amaral, 1989a; 1989c); by lesions limited to the hippocampal formation alone^h (Mahut, Zola-Morgan & Moss, 1982; Zola-Morgan & Squire, 1986; Zola-Morgan, Squire & Amaral, 1989a); and by lesions limited to regions adjoining, and strongly interconnected with, the hippocampal formation (perirhinal and parahippocampal cortices: Zola-Morgan, Squire & Amaral, 1989c; rhinal sulcus: Murray, Bachevalier & Mishkin, 1989).

Monkeys with lesions to any of these areas perform the task well at brief delays (5–10 sec); hence when the memory demands are minimal they are capable of learning and performing the task well. They fail, however, at longer delays (15–60 sec), and their performance progressively deteriorates as a function of the length of delay. This strongly suggests that the reason monkeys with lesions to the hippocampal system fail delayed non-matching to sample is because of the memory requirements of the task. It had once been thought that involvement of the amygdala was also critical for success on the task, but as indicated in the paragraph above, that no longer appears to be the case (see also Zola-Morgan & Squire, this volume).

Importantly, delayed non-matching to sample performance is also impaired in human adults with amnesia (Squire, Zola-Morgan & Chen, 1988). Amnesic patients, like monkeys with hippocampal lesions, perform well when delays are brief on delayed non-matching to sample and on other tasks, but perform more and more poorly as the delay increases. Amnesia is a memory disorder in which the hippocampal system is strongly implicated (e.g., Squire, 1986; Squire & Cohen, 1984).

In short, the hippocampus and related structures appear to subserve a memory function in human adults and monkeys. Damage to the hippocampus and related structures results in impaired performance on the delayed non-matching to sample task in adult monkeys, and apparently in human adults (although complete anatomical evidence on the actual site of brain damage is not yet available for all amnesic patients tested). The reason hippocampal damage results in impaired delayed

non-matching to sample performance in these populations appears to be because of the memory requirements of the task: Performance is excellent at brief delays and declines as a linear function of delay.

Success on Delayed Non-Matching to Sample Appears Relatively Late in Development

When a 10-sec delay is used, 3-month-old infant monkeys fail delayed non-matching to sample. Infant monkeys finally succeed at the task with delays of 10 sec by the age of 4 months. At longer delays (30, 60, and 120 sec), even 1-year-old monkeys do not perform as well on delayed non-matching to sample as do 3-year-old adult monkeys (Bachevalier & Mishkin, 1984; Bachevalier, this volume). This is consistent with a widely held hypothesis that hippocampal function matures late (e.g., Douglas, 1967; 1975; Altman, Brunner & Bayer, 1973; O'Keefe & Nadel, 1978; Nadel & Zola-Morgan, 1984; Schacter & Moscovitch, 1984).

Human infants also cannot succeed on delayed non-matching to sample until relatively late. Even with a brief 5-sec delay, they do not succeed until roughly 21 months of age. This is true whether they are tested with a procedure closely resembling that used with amnesic patients (Squire *et al.*, 1988), as we have done (Diamond, Towle & Boyer, in prep.), or with a procedure more closely resembling that used with monkeys (e.g., Zola-Morgan & Squire, this volume; Bachevalier, this volume), as Overman has done (see Overman, this volume).

In our procedure, we tell the children that we have hidden a reward and want to see if they can find it. As is done with amnesic patients and monkeys, we do not tell the children the principle determining which response is correct. During the first part of each trial, a sample object covering a small reward is presented at the midline. After the child displaces the object and finds the reward, a screen is positioned between subject and testing area for the delay period. Then a new object and the familiar sample are presented to the right and left of midline (with the reward hidden under the new object), and the child is encouraged to displace one of the objects to find the reward. If the child reaches incorrectly, he or she is not permitted to try again, but the experimenter removes the other object and shows the child where the reward had been.

A new pair of objects is used on every trial, drawn from a pool of 75 junk objects. The left-right position of the novel and familiar objects is varied across trials according to a pseudorandom schedule (Gellerman, 1933). Each child is first trained on the basic task using a 5-sec delay, as is done with amnesic patients and monkeys. The training trials continue until the child is correct on 5 trials in a row. Then the

¹It should be noted, however, that once they could succeed with delays of 10 sec, all groups of monkeys (4 and 7 months of age, and 1 and 3 years of age) succeeded at all delays (30, 60, and 120 sec), performing at roughly the 90% level or better. The performance of the 3 younger groups was significantly worse than the adults because the adults performed near 100% so consistently, not because the younger groups were failing the task.

Delayed matching to sample is more difficult for human infants and infant monkeys than is delayed non-matching to sample, just as is true for adult monkeys. Thus, although success on delayed non-matching to sample appears quite late, success on delayed matching to sample appears much later still in human infants (see Overman, this volume) and in infant monkeys

(see Bachevalier, this volume).

^hDeficits from lesions of the hippocampal formation alone are as severe as those resulting from lesions of the hippocampal formation plus the amygdala, but not as severe as those resulting from lesions of the hippocampal formation plus perirhinal cortex (Zola-Morgan-Squire & Amaral, 1989b; 1989c).

delay is increased to 30 sec. When children aged 3, 4, or 5 years were tested, delays of 60 sec were also used. Subjects aged 12, 15, 18, 21, 24, 27, or 30 months received a total of 25 trials, while those tested also at 60 sec received a total of 30 trials.

Although infants did not reliably succeed on delayed non-matching to sample until 21 months of age, almost all infants aged 21 months or older passed criterion at the 5-sec delay, and most went on to succeed at the 30-sec delay as well. The difference between performance at 18 and 21 months was dramatic: Only 67% of the 18-month-olds passed criterion at 5 sec versus 92% of 21-month-old infants (Diamond *et al.*, in prep.). (See TABLE 1.) A delay of 60 sec was used only with the older subjects (3–5 years of age); all older subjects succeeded at all delays.

Even as late as 18 months, the mean percent correct on delayed non-matching to sample with only a 5-sec delay was a mere 71%. Against the background of the dramatic memory abilities infants can demonstrate (see, e.g., in this volume: Melt-

TABLE 1. Performance on Delayed Non-Matching to Sample by Age and Delay

	-	5-Sec Delay		30-Sec Delay
Ages	Mean Number of Trials to Criterion	Percent Passing Criterion	Percent Correct	Percent Correct
12 months ^b	17	50	66	$65 (N = 6)^c$
15 months	11	67	67	64 (N = 8)
18 months	16	67	71	81 (N = 8)
21 months	10	92	80	80 (N = 11)
24 months	9	92	87	86 (N = 11)
27 months	7	100	85	90
30 months	8	100	85	90
3 years	6	100	93	96
4 years	5	100	98	99
5 years	5	100	94	95

"Criterion = 5 correct responses in a row. For subjects who never reached criterion (6 subjects at 12 months, 4 subjects each at 15 and 18 months, and 1 subject each at 21 and 24 months), the total number of trials they were tested (25) was used in calculating the mean here.

zoff; Mandler; Rovee-Collier; Diamond), success on delayed non-matching to sample appears very late indeed.

Evidence for a New View of Hippocampal Maturation

Anatomical Evidence of Early Hippocampal Maturation in Primates

Neurogenesis generally, and the generation of dentate gyrus granule cells in particular, occurs before birth to a much larger extent in primates than in rats. For example, approximately 80% of the dentate gyrus granule cells in the rhesus monkey are generated before birth, as compared to only about 15% in the rat. Most of the

remaining granule cells in the monkey dentate gyrus are generated during the first 3 months of life (i.e., by what is roughly equivalent to 9 months of age in humans) (Rakic & Nowakowski, 1981), as opposed to most granule cells in the rat brain not being present until what is roughly equivalent to 3 years of age in humans (the third week of life in the rat). In contrast to the considerable neurogenesis reported in the dentate gyrus of adult rats, there is no evidence of production of new neurons in the dentate gyrus of the rhesus monkey after puberty (Eckenhoff & Rakic, 1988). In short, there is postnatal neurogenesis in the dentate gyrus in the monkey, but it appears to be much less pronounced and much earlier than in the rat.

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Emerging biochemical evidence is fully consistent with this. While there are substantial differences in the distribution of both opiate and muscarinic receptor binding sites in the neocortex of newborn versus adult rhesus monkeys, the distribution of these receptors appears adult-like in all respects in subcortical and allocortical structures (including the hippocampus) at birth (Bachevalier, Ungerleider, O'Neill & Friedman, 1986; O'Neill, Friedman, Bachevalier & Ungerleider, 1986; Bachevalier, this volume).

If anything, the dentate gyrus shows even earlier maturation in the human than it does in the monkey (Conel, 1939; Rakic & Sidman, 1968; Bogolepova, 1970; Sidman & Rakic, 1973; 1982; Kostovic, 1975; Purpura, 1975a; 1975b). For example, Conel's (1939) work clearly shows the presence of granule cells in the human dentate gyrus at birth. Similarly, Purpura (1975b) reports results on a 35-week post-conception preterm infant where the granule cells in the dentate gyrus were already present. Purpura also presents much evidence that, in dendritic growth and in the development of pyramidal neurons, the hippocampus matures earlier and faster during the prenatal period than does visual cortex. Indeed, in primates, the hippocampus (including the dentate gyrus) appears to mature earlier than do most regions of neocortex, although there is some overlap.

Kretschmann. Kammradt, Krauthausen, Sauer & Wingert (1986) report results on volume of the entire hippocampus (not broken down by Ammon's horn and dentate gyrus). They report that the human hippocampus is nearly 40% mature by birth, 50% mature by 1–1½ months, and fully mature by 15 months of age. This is a very early maturational timetable compared with that for prefrontal cortex, which is not thought to be fully mature until at least 10 years of age. It is also very early compared with the timetable of hippocampal maturation in the rat. Extrapolating from the rat data, people had assumed (erroneously, it now appears) that the hippocampus probably does not reach full maturity in humans until 3–5 years of age (e.g., Douglas, 1967). In short, in primates, the hippocampus appears to mature relatively early.

The Visual Paired Comparison Task Is Similar to Delayed Non-Matching to Sample

Visual paired comparison (also called "preferential looking") is another measure of recognition memory. In broad outline, the visual paired comparison task is quite similar to the delayed non-matching to sample task. Here, as in delayed non-matching to sample, a sample is presented during the first part of the trial (called the "familiarization phase"). Following a delay, the sample stimulus is presented again, paired with a novel stimulus (one stimulus presented to the left and the other to the

 $[^]hN = 12$ for all ages.

Only subjects who passed criterion at 5 sec were tested at 30 sec.

^kPrimates are more mature at birth in most regards than are rodents.

right). As in delayed non-matching to sample, memory of the sample is inferred by the subject choosing the non-matching (novel) stimulus. The logic here is that if subjects are given enough time with a stimulus to get bored with it (i.e., to habituate to it), when given a choice between looking at the same stimulus again or something new, subjects will choose the new stimulus—provided they remember the first stimulus. ("Choice" is indicated here by preferentially looking at a stimulus, rather than by reaching and displacing it.)

Success on Visual Paired Comparison Appears Very Early in Development

The visual paired comparison test was first devised to study human infants (Fantz, 1964; 1967; Fagan, 1970; this volume), and it has been widely used. Much evidence now exists that by 4 months, human infants succeed on the visual paired comparison task at delays of 0–15 sec (e.g., Pancratz & Cohen, 1970; Welch, 1974; Caron, Caron, Minichiello, Weiss & Friedman, 1977). Indeed, infants of only 2–3

TABLE 2. Age at Which Success First Appears on the Visual Paired Comparison and Delayed Non-Matching to Sample Tasks

Subjects	Visual Paired Comparison	Delayed Non-Matching to Sample
Humans	Infants reliably choose the novel stimulus by 4 months of age at delays of at least 10 sec.	Infants do not reliably choose the novel stimulus until 21 months of age at delays of only 5 sec.
Monkeys	Infant monkeys reliably choose the novel stimulus by 2 weeks of age at delays of at least 10 sec.	Infant monkeys do not reliably choose the novel stimulus until 4 months of age at delays of 10 sec.

NOTE: Success on the visual paired comparison task appears much earlier in humans and monkeys than does success on the delayed non-matching to sample task.

months succeed at delays of 0 sec (Saayman, Ames & Moffett, 1964; Fantz, Fagan & Miranda, 1975; Caron et al., 1977). Although it has yet to be demonstrated using the visual paired comparison paradigm, visual recognition memory of the sample has been demonstrated even in newborn human infants (e.g., Friedman, 1972a, 1972b; Friedman, Bruno & Vietze, 1974; Werner & Siqueland, 1978). Moreover, given sufficient familiarization time and simple stimuli that can be easily scanned, that differ markedly from one another along several dimensions, and that have some importance to the infant (such as a person's face), infants of at least 5 months (e.g., Fagan, 1970, this volume) show evidence of recognition memory in the visual paired comparison task after delays of weeks, and there is reason to believe that, under the right circumstances, infants of 2 months or younger could succeed on the task with delays of 24 hours or more (Martin, 1975).

Similarly, in contrast to their performance on delayed non-matching to sample, infant monkeys succeed on visual paired comparison at a very early age (see Table 2). Infant monkeys succeed on the visual paired comparison task with a 10-sec delay by 15 days of age (Brickson & Bachevalier, 1984; Hagger, Brickson & Bachevalier,

1985; Bachevalier, this volume). Recall that they cannot succeed on delayed non-matching to sample with a 10-sec delay until approximately 130 days of age (4 months).

If delayed non-matching to sample and visual paired comparison are so similar, why are human infants and infant monkeys able to succeed on visual paired comparison months earlier than they can succeed on delayed non-matching to sample? One possibility is that these two tasks might require different kinds of memory. While the type of memory required for delayed non-matching to sample depends on the hippocampus, the memory functions required for visual paired comparison might not be dependent on the hippocampus. For example, the visual paired comparison task might require implicit or procedural memory (i.e., memory functions not dependent on the hippocampus), whereas the delayed non-matching to sample task is thought to require explicit or declarative memory (memory functions dependent on the hippocampus; e.g., Schacter, 1987, this volume; Squire & Cohen, 1984). However, as discussed in the section below, lesions of the hippocampus plus neighboring structures including the amygdala impair visual paired comparison performance, just as they do delayed non-matching to sample performance.

Success on Visual Paired Comparison Appears to Depend on Hippocampal Function

In both infant and adult monkeys, performance on the visual paired comparison task is impaired by lesions of the hippocampus plus the amygdala and neighboring structures (Brickson & Bachevalier, 1984; Bachevalier, this volume; Saunders, 1989). The results for infant monkeys are particularly dramatic because of how young the monkeys were and because the lesions were performed in two stages. Lesions are normally bilateral and performed in one stage (that is, the homologous structure on both sides of the brain is usually removed within the same surgical session). Brickson and Bachevalier removed the hippocampus + amygdala in one hemisphere when the monkeys were 7 days of age and waited until the monkeys were 21 days old to operate on the other hemisphere. When lesions are made in two stages, they often have a weaker effect than do lesions performed in one stage, and sometimes produce no deficit at all. Similarly, unilateral lesions often produce a weaker effect than bilateral lesions, and sometimes produce no deficit at all.

Brickson and Bachevalier found that infant monkeys of only 15 days of age and with only unilateral lesions of the hippocampus + amygdala failed to look preferentially at the novel stimulus when tested on visual paired comparison. Similarly, 30-day-old infant monkeys with bilateral lesions of the hippocampus + amygdala performed in two stages and adult monkeys with bilateral lesions of the hippocampus + amygdala performed in one stage failed to show a novelty preference on visual paired comparison.

These results are in marked contrast to those obtained when inferior temporal

Results reported in this paper are all for rhesus and cynomolgus monkeys. It should be noted, however, that Gunderson and her colleagues have been investigating performance during infancy on visual paired comparison in pigtailed monkeys. Gunderson finds evidence of recognition memory on the visual paired comparison task in infant pigtailed monkeys of at least 3 weeks with delays of 3 sec (Gunderson, Grant-Webster & Sackett, 1989) and in infant pigtailed monkeys aged $1\frac{1}{2}$ months ($6\frac{1}{2}$ - $17\frac{1}{2}$ weeks) with a 24-hour delay (Gunderson & Swartz, 1985; performance at the individual ages not reported).

cortex (area TE) is lesioned (Hagger, Brickson & Bachevalier, 1985). TE is a visual association area. Lesions of area TE in the adult monkey produce deficits on visual paired comparison, but lesions of area TE in the infant (performed in two stages at 7 and 21 days of age) do not. Infants of 15 and 30 days still look preferentially at the novel stimuli during visual paired comparison testing following lesions of area TE. This suggests that TE is not yet mature during the first month of life, hence lesioning the area does not impair infants' performance.

Not only does success on visual paired comparison appear very early in development, but hippocampal-amygdalar lesions impair visual paired comparison performance from the very earliest age, just as these lesions do in the adult. All of this suggests that the hippocampal system may mature very *early*, in direct contrast to the conclusion one would draw from the results on delayed non-matching to sample.^m The conclusion drawn from the delayed non-matching to sample results was based solely on the developmental progression in performance, however, not on the effects of early lesions on performance.

If there were results demonstrating that early lesions of the hippocampus + amygdala spared performance on delayed non-matching to sample, whereas later lesions impaired performance, that would be evidence suggesting that the hippocampal system might be late maturing. This type of evidence does not exist, however. Rather, the opposite result is found: Early lesions of the hippocampus + amygdala appear to have the same detrimental effect on delayed non-matching to sample performance as do lesions of these structures in adulthood. The same infant monkeys who received lesions of the hippocampus + amygdala in two stages on postnatal days 7 and 21 and were impaired on visual paired comparison were also impaired on delayed non-matching to sample at 10 months of age (the youngest age they were tested on delayed non-matching to sample postoperatively), although they were unimpaired on control tasks (see Bachevalier, this volume). Similarly, Mahut & Moss (1986) found that bilateral lesions restricted to the hippocampal formation performed in one stage at only 2 months of age yielded deficits even years later when the monkeys were tested on delayed non-matching to sample, although performance on control tasks was unimpaired. In contrast, monkeys who have received early lesions of area TE show no deficit at 10 months on delayed non-matching to sample, just as they show no deficit at 1 month on visual paired comparison—although TE lesions in adulthood produce deficits on both tasks (see Bachevalier, this volume). These lesion results would seem to suggest that the hippocampus, unlike the cortical area TE, matures early, at least in the monkey.

Evidence Suggesting That the Memory Requirements of Delayed Non-Matching to Sample Are Not Why Success on the Task Appears So Late in Development

Well before 21 months of age infants can succeed on all manner of tasks at delays much longer than a mere 5 sec (e.g., $A\overline{B}$ [see Diamond, this volume], deferred

^mIt should be noted, however, that the individual contributions of the hippocampus, amygdala, and surrounding areas to visual paired comparison performance have yet to be investigated. It may be that while the hippocampal system, rather than the amygdala, is critical for delayed non-matching to sample, the amygdala, rather than the hippocampus, might be critical for visual paired comparison.

imitation [see Meltzoff, this volume; Mandler, this volume], cued recall of conjugately reinforced footkicks [see Rovee-Collier, this volume], and, of course, visual paired comparison [see Fagan, this volume]). When children finally succeed on delayed non-matching to sample with delays of 5 sec, they are also typically able to succeed, in that same session, at delays of 30 sec (Diamond *et al.*, in prep.). Note how similar the percent correct is at the 5- and 30-sec delays at every age in TABLE 1 above.

Overman (this volume), too, found little difference in performance by delay length (over delays of 10, 30, 60, and 120 sec) in children at any age. Bachevalier's results in infant monkeys are similar (Bachevalier, this volume): Once infant monkeys could succeed at the shortest delay used (10 sec), they could succeed at all delays (30, 60, and 120 sec), performing at roughly the 90% level or better throughout.

It would seem that some ability required for delayed non-matching to sample other than memory, and not dependent on the hippocampus, is late-developing and accounts for why success appears so late on this task. While it is true that success on delayed non-matching to sample requires hippocampal involvement, and it is true that success on delayed non-matching to sample appears relatively late in development, it does not appear to be true that the late emergence of success on this task is due to late maturation of the hippocampus, or to the memory ability it subserves. Indeed, even monkeys with the most extensive damage to the hippocampus + perirhinal, parahippocampal, entorhinal cortex, and amygdala do not show deficits on delayed non-matching to sample at delays of 10 or 15 sec, much less delays of 5 sec (the delay at which human infants fail). Damage to this neural circuit does not produce deficits on any comparable task at delays that brief. Errors at such brief delays are due to some other cause.

Infants have never been tested, to my knowledge, on non-matching to sample, with no delay and the sample present throughout. Given the above pattern of results, however, I would predict that even when the need to remember the sample is removed altogether (by having the sample remain in view) infants would still fail the task until almost 21 months of age.

PART II: WHY IS IT THAT A VARIETY OF COGNITIVE ABILITIES APPEAR TO BE PRESENT EARLIER WHEN ASSESSED BY WHERE SUBJECTS LOOK THAN BY WHERE SUBJECTS REACH?

If the failure of infant monkeys and human infants to succeed on delayed non-matching to sample until quite late in infancy at delays of only 5–10 sec is *not* due to late maturation of the hippocampal system and is *not* due to the memory requirements of the task, what is it about the task that makes it so difficult? Why should success appear so much later here than on visual paired comparison given that the two tasks are so similar? Indeed, why in general, does success on reaching measures appear so much later than success on visual measures?

Before addressing these questions directly, I would like to present another example of a puzzling décalage where success on reaching measures appears later

than success on visual measures. It is possible that the key to solving this second puzzle may be related to the key to the delayed non-matching to sample mystery.

Infants' Understanding That Objects They Cannot See Are Still There, As Assessed by Looking and by Reaching

Human infants younger than $7\frac{1}{2}$ -8 months do not seem to know that an object is still there once it is hidden, judging by their much-replicated failure to reach for a hidden object. Indeed, they fail to reach for an occluded object even if the object creates a large bulge under a cloth cover, even if the experimenter squeaks or rattles the toy behind a screen or under a cover, and even if the infant was in the process of reaching for the toy when it was covered (e.g., Piaget, 1954 [1937]; Uzgiris & Hunt, 1970; Gratch & Landers, 1971; Uzgiris & Benson, 1980; Wishart & Bower, 1984). (Note that by 5 months of age infants are able to reach for free-standing objects and to remove cloths.) This set of results has been so convincing and so well replicated that it has been taken as fact for years that infants below $7\frac{1}{2}$ -8 months do not know that an object is still there once it is hidden.

Yet infants of only 3–5 months do seem to know that a hidden object is still there when looking rather than reaching is the dependent measure (Baillargeon, Spelke & Wasserman, 1985; Baillargeon, 1987). Baillargeon habituated infants to the movement of a screen back and forth through a 180° arc, like a drawbridge. A box was then placed behind the screen. In one test condition, infants were shown the screen moving along its arc only partially, stopping when it reached the hidden box (possible event). In the other condition, the screen moved through its full 180° arc, as though the box were no longer there (impossible event). Infants of 4 and 5 months, and some infants of 3 months, looked longer at the impossible than at the possible event, suggesting that they knew the box hidden behind the screen was still there. When no box was placed behind the screen, the opposite results were obtained. Predictably, infants looked longer when the screen stopped before completing its 180° arc (same movement as in the possible condition above) than when the screen repeated the boring 180° arc to which they had habituated. Thus, the presence of an object that the infants could no longer see behind the screen significantly affected their looking time; infants seemed to expect the screen to stop when it reached the object and were surprised (looked longer) when the screen continued beyond this point (see Fig. 1 & TABLE 3). Indeed, Baillargeon has gone on to demonstrate that infants of at least 51/2 months remember a good deal about the appearance and characteristics of the hidden object (e.g., Baillargeon & Graber, 1988).

Why is it that infants seem to remember that an object is behind a screen at 3–5 months when judged by their looking, but not until 7½–8 months when judged by their reaching? Similarly, why is it that infant monkeys of only 15 days can demonstrate that they remember a stimulus by where they look (in the visual paired comparison task), but cannot demonstrate until at least 4 months that they remember a stimulus by where they reach (in the delayed non-matching to sample task)?

One possibility is that because vision matures earlier than reaching (and because reaching requires both the visual system and the arm movement system), cognitive abilities might become integrated with the visual system before they become integrated with reaching. Perhaps when a cognitive competence appears it is not generally accessible, but becomes incorporated first into one response system and

then another. This kind of reasoning is consistent with the plethora of findings in neuropsychology showing that whether or not a brain-damaged patient is judged to have certain cognitive abilities often depends on which response system is used to measure those abilities (e.g., explicit verbal recognition or recall vs. implicit demonstration in behavior [Schacter, 1987; this volume; Squire & Cohen, 1984]; response of left or right hand to information shown to only one eye in split brain patients [Gazzaniga, 1970; 1985]). This reasoning is also consistent with the notion that

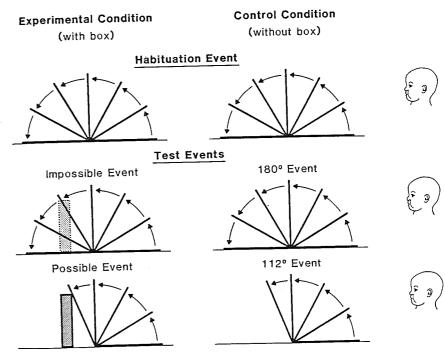


FIGURE 1. Illustration of the testing paradigm used by Baillargeon, Spelke, and Wasserman (1985). All infants were habituated to the movement of the screen through a 180° arc. Infants in the control condition looked very little when the screen continued to move 180°. They looked much longer when the screen moved only 112°. Infants in the experimental condition saw a box placed so that it would block the screen's movement beyond 112°. Even though these infants had been habituated to the same 180° movement of the screen before the box was introduced, and even though the box could not be seen once the screen started its movement, infants in the control condition looked much longer when the screen moved 180° now that the box was behind it, and they looked very little when the screen moved 112°.

cognitive capacities first appear in narrow contexts and then become generalized during development (e.g., Rozin, 1976). But note that this also suggests that "I" (as an infant) don't know or remember something. Rather, early in development, my eyes may know it, but my hands may not.

Alternatively, perhaps competencies have been demonstrated earlier with visual measures than with reaching measures because the reaching measures have involved

TABLE 3. Looking Responses of 4–5-Month-Old Infants to the Movement of a Screen after They Had Habituated to the Screen Moving 180° by Whether or Not a Solid Object Was Placed behind the Screen after Habituation^a

Condition	Infants' Responses to Movement of Screen 180°	Infants' Responses to Movement of Screen 112°	
No object behind screen Solid object behind screen	Looked little (bored) Looked long (surprised)	Looked long (surprised) Looked little (bored)	

Note: Once the screen was raised 90° or more, the object was no longer visible. Based on Baillargeon, Spelke & Wasserman (1985) and Baillargeon (1987).

an additional task demand, the need to execute a means-end action sequence. A means-end action sequence involves first acting on, or in relation to, one object (e.g., removing a cover, displacing a stimulus, or detouring around a barrier), and then acting on another object (e.g., retrieving a reward). When visual fixation is the dependent measure, subjects need only look at what interests them. This is a simple, direct response; they do not look at something in order to obtain anything else. If subjects remember the stimulus to which they habituated during the familiarization period, they will look at something new given the choice (as they do on visual paired comparison). If the unexpected happens they will look longer than if there is nothing surprising (as they do in Baillargeon's paradigm). When reaching is the dependent measure, however, studies have required subjects to act in relation to one object in order to obtain another object. Thus, subjects remove a cover, or detour around a screen, to obtain a hidden toy, or they must displace an object to obtain the reward beneath it (as in delayed non-matching to sample). This is a complicated, indirect response; subjects must act on one object to obtain another, rather than acting on an object to obtain that object itself. This would suggest that the critical variable may not be looking versus reaching, but rather simple, single-action responses versus more complicated, two-action responses. The complicated responses require some planning or forethought; simple, direct responses do not. Perhaps the additional requirement of executing a sequence of actions can account for why abilities appear later when measured by reaching than by looking. Evidence consistent with this interpretation is that infants begin to reach for hidden objects at about the same age that they first demonstrate other means-end action sequences (e.g., pulling a cloth closer to retrieve a distant toy on the cloth) (Piaget, 1954 [1937]; Willatts, 1987).

TABLE 4.

Dependent Measure	Visual Response Required	Reaching Response Required
Only a simple, direct	Visual paired comparison	
response required (reward = stimulus)	Baillargeon's visual habitu- ation paradigms	
A two-part, indirect response required		Delayed non-matching to sample
(reward hidden under stim- ulus)		Uncovering a hidden object

As you can see from TABLE 4, the visual paired comparison task and Baillargeon's visual habituation procedure both use looking as the dependent measure and both require only a simple, direct response. Whereas, the delayed non-matching to sample task and uncovering a hidden object both use reaching as the dependent measure and both require acting on one object to retrieve another object. Vision, single response, and reaching, two-part response, are completely confounded, so it is not possible from this set of results to determine which of the two variables is more critical.

The Delayed Non-Matching to Sample Task (with a New, Simple Procedure)

To test between the two interpretations (that the critical difference is (a) looking versus reaching or (b) a simple response versus a response requiring two sequences of action) we modified the testing procedure for delayed non-matching to sample so that only a single action sequence was required. In this way, reaching could be dissociated from means—end action. Instead of subjects displacing a stimulus object to obtain the reward beneath it, the stimulus object was the reward itself. Subjects reached to the stimulus object to obtain that object, just as subjects look at a stimulus in visual paired comparison because they are interested in that stimulus, not to obtain anything else.

We were able to use the novel object as its own reward because infants have a natural preference for novelty (e.g., Fantz, 1964; Fagan 1970; 1973; Cohen & Gelber, 1975). This enabled us to use almost identical procedures for visual paired comparison and delayed non-matching to sample (single action). In both tasks, infants were presented with an object (the sample) until they got bored with it (habituated), a delay ensued, and then the sample and a novel object were presented simultaneously (one to the left and one to the right). Since infants prefer novelty, the prediction was that if the infant remembered the sample, he or she would choose to look at, or reach for, the new object. The primary difference between the tasks was that in delayed non-matching to sample (single action) infants reached for an object during familiarization and test while in visual paired comparison infants only looked at the object(s) during familiarization and test.

We tested infants on delayed non-matching to sample (single action) and on visual paired comparison (Diamond, in prep.). If infants could still withstand longer delays at younger ages on visual paired comparison than on delayed non-matching to sample (single action), it would suggest that the need to execute a means—end response sequence is not what makes the standard version of delayed non-matching to sample more difficult than visual paired comparison. If, on the other hand, the developmental progression on delayed non-matching to sample (single action) were found to be comparable to that for visual paired comparison, it would suggest that the critical variable is not which modality or motor system is used to make the response.

Pretesting

In order to minimize differences between the testing procedures for visual paired comparison and delayed non-matching to sample (single action), the same 10 pairs of

trial-unique objects were used for both tasks. This meant that visual paired comparison was administered using 3-dimensional objects, rather than the more typically used 2-dimensional stimuli (such as black and white abstract designs or photos of faces).

Preliminary work was necessary to find objects meeting the following criteria: (1) infants up to 1 year of age had never seen them before (so the objects would be truly novel), (2) sufficiently interesting that infants would reach for, or look at, them, and (3) sufficiently boring that when given another chance infants would reach for, or look at, something else. Moreover, we wanted the two objects in each pair to be roughly equal in interest because if infants greatly preferred one of the objects, and that object served as the sample, infants might still reach for, or look at, that object during the test choice.

The 10 object pairs selected are pictured in Figure 2. Each object is highly discriminable from the object with which it is paired. TABLE 5 presents data on infants' preferences (expressed by which object they reached for) when both members of each pair were presented with no prior familiarization period or delay. As you can see in TABLE 5, the objects in each pair were quite equal in preference at each age, judging by where infants reached (Diamond, in prep.).

Infants' preference for novelty has often been demonstrated with visual measures, but it was not a foregone conclusion that a similar preference would appear in reaching. For example, after 9 months of age, infants often show a longer latency to reach for novel than familiar objects, which could have shown up here as preference for the familiar, and under 9 months they often impulsively reach for whichever object they see first, which could have shown up here as no effect of familiarization (e.g., Schaffer & Parry, 1970; Schaffer, Greenwood & Parry, 1972). One can see from TABLE 6, however, which presents results from delayed non-matching to sample (single action) pre-testing with a 0-sec delay, that infants at each age did show a robust novelty preference in their reaching for all our pairs of objects. Because infants demonstrate this when no delay is used, a failure to demonstrate it after a delay can be attributed to forgetting.

Experimental Design

We tested 120 human infants: 20 infants (10 M & 10 F) \times 2 tasks \times 3 ages (Diamond, in prep.). All infants were healthy and full-term, and all were tested in our laboratory. On both visual paired comparison and delayed non-matching to sample (single action), 20 infants were tested at the age of 6 months and at 9 months of age.ⁿ In addition, 20 4-month-old infants (range = 17(1)-21(0) weeks; mean = 19(8) weeks) were tested on visual paired comparison to establish comparability with other studies using that task. Infants of 4 months cannot retrieve free-standing objects and so could not be tested on delayed non-matching to sample. Twenty infants were tested on delayed non-matching to sample (single action) at 12

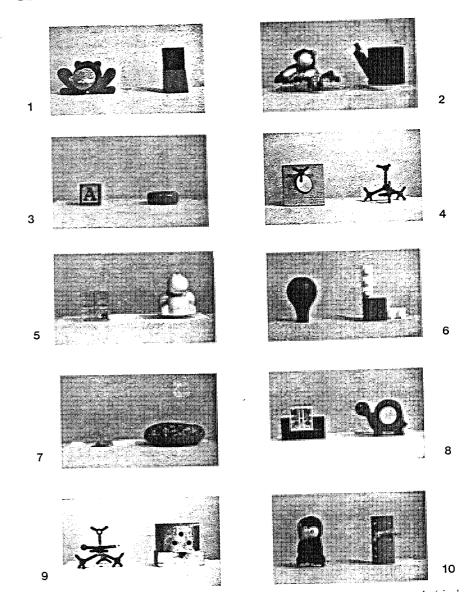


FIGURE 2. The stimulus pairs used for testing both delayed non-matching to sample (single action) and visual paired comparison.

months of age (range = 52(0)–55(6); mean = 53(5) weeks) in case performance on this task lagged behind performance on visual paired comparison. In sum, a total of 60 infants at 3 different ages were tested on each task (4, 6, and 9 months of age for visual paired comparison; 6, 9, and 12 months of age for delayed non-matching to sample).

[&]quot;For 6-month-olds: range = 25 weeks (5 days) to 29(0) weeks; mean = 27(2) weeks for VPC and 27(4) weeks for DNMS. For 9-month-olds: range = 39(0) to 43(0) weeks; mean = 40(4) weeks for VPC and 40(5) weeks for DNMS.

TABLE 5. Percent of Infants Reaching for the Object Shown on the Right for Each Pair Pictured in FIGURE 1

		Age in	Months	
Pair	$\frac{6}{(N=38)}$	8 (N = 36)	(N = 39)	(N = 30)
1	66	67	64	73
2	42	67	54	48
3	50	55	67	54
4	58	50	41	67
5	55	44	36	37
6	50	67	56	48
7	45	58	46	54
8	55	50	51	48
9	63	44	51	54
10	50	47	56	50

Regardless of the task, each infant received 10 trials, 2 trials each at delays of 10 sec, 15 sec, 1 min, 3 min, and 10 min. Each of the first 5 trials was at a different delay, counterbalanced across infants within experimental condition (Latin square design). The delays were presented in reverse order over the last 5 trials. Which member of an object pair served as the sample was counterbalanced across infants within condition. The test pairs were always presented as pictured in FIGURE 2. In half the sessions, the object serving as the sample was: R (object on the right on trial 1), R, L, L, R, L, R, Thus, there were 5 orders of delay × left or right object defined as the familiar \times 2 tasks \times 2 sexes, at each of 3 ages. All infants were tested twice at all 5 delays (10, 15, 60, 180, and 600 sec).

An infant-controlled procedure was used to determine habituation during the

TABLE 6. Percent Reaching for the Non-Matching Object when Both Objects Were Presented 0 Sec after Sample Presentation

		Age in Months	
Pair	6 $(N = 10)$	9 (N = 10)	12 $(N = 10)$
1	100	100	70
2	80	90	90
3	100	90	80
4	80	100	100
5	60	100	90
6	100	50	100
7	100	80	100
8	80	100	90
9	100	70	90
10	100	80	90

 $^{^{}o}$ It had been intended that the two shortest delays be 0 and 10 sec. However, analysis of the videotape records revealed that the delays actually used were longer than intended. The actual delays were 10 and 15 sec.

familiarization period of each trial. That is, we presented the sample until a standard level of habituation was reached rather than for a standard length of time. We did this to reduce subject attrition and because we were interested in memory once the subject had processed the stimulus.

Each trial consisted of two parts separated by a delay:

Sample Presentation (Familiarization Period). The experimenter presented an object for the infant to play with (delayed non-matching to sample) or look at (visual paired comparison) until the infant tired of the object (reached habituation criterion).

For visual paired comparison, the object was moved continually from left to right, out of reach, until the infant looked away from the sample 3 times for periods of at least 3 sec each. Each time, if the infant did not look back at the object after 3 sec, the experimenter recaptured the infant's attention. Visual fixation was monitored by an observer looking at the session on a television screen and seated at a computer keyboard. The duration of each "look away" was timed by computer.

For delayed non-matching to sample, the same procedure for determining habituation was used, except that here infants could indicate boredom not only by looking away but by discarding the object as well. The discarded object was returned to the infant each time until the end of the familiarization period. The familiarization period ended after the child had discarded the toy 4 times, looked away for 3 periods of at least 3 sec each, or any combination of the two totaling 4.

Immediately following familiarization, the delay began. During the delay period, infants were allowed to crawl around the room, climb onto the testing table, feed, interact with parent or experimenter, or play with two large toys that were introduced before testing and that were very different from the small stimulus objects.

Test Phase (Paired Presentation). After the delay, the experimenter asked the parent to again center the child at the center marker on the table and to close his or her own eyes (to avoid biasing the infant's response). The pair of objects was then presented.

For visual paired comparison, the objects were presented out of reach, one to the left and one to the right, and moved back and forth at the same speed along the horizontal plane on their respective sides. The objects were presented for a total of 20 sec, with their left-right placement reversed after 10 sec.

For delayed non-matching to sample, the objects were presented side by side at the midline to insure that the infant saw both objects. Movement of each object along the horizontal plane encouraged the infant to visually track each object. Once the infant had clearly seen both objects, each object was placed at the boundary of the infant's reach and 20.5 cm from the midline. Placing the objects just barely within reach forced the infant to stretch to grasp an object, and so discouraged reaching simultaneously for both objects. Once the infant had touched an object, the other object was removed.

^pIf the sample is presented for a standard amount of time, that time will be too short for some children to have habituated and too long for others so that they become cranky and fidgety. With an infant-controlled procedure, the sample is presented until each child has reached the habituation criterion (e.g., looked away 3 times for at least 3 sec each time).

Results

Infants were able to succeed on delayed non-matching to sample (single action) and to withstand delays fully as long on this task as on visual paired comparison from the youngest age at which they could be tested. "Success" on a task is defined as a significant tendency to reach for, or look at, the novel (non-matching) object. We judged success on delayed non-matching to sample (single action) by the percent of infants reaching for the novel object. We judged success on visual paired comparison by (a) the difference in fixation time to the novel and familiar objects (percent of fixation to the novel object) and (b) the percent of infants fixating the novel object at least 67% of the time (to yield a measure more comparable to that used for delayed non-matching to sample). Results for the first 5 trials (first trial at each delay) were comparable to results for the last 5 trials (second trial at each delay) and so are combined in the analyses discussed below.

TABLE 7. Percent of Infants Choosing the Non-Matching (Novel) Object by Age, Task, and Delay

	4 Moi	ths Old	6 Mor	nths Old	9 Moi	nths Old	12 Mo	nths Old
Delays	VPC	DNMS	VPC	DNMS	VPC	DNMS	VPC	DNMS
10 sec	70**		90**	85**	80**	85**		90** 85**
15 sec	55 60		60 75**	80** 70**	80** 80**	85** 90**		85**
1 min 3 min	50		70**	65*	65*	85**		90**
10 min	50		60	70**	70**	80**		85**

Note: VPC = visual paired comparison; DNMS = delayed non-matching to sample (single action). Choice of novel object in VPC = looked at novel object 67% of time during 20-sec paired presentation. Choice of novel object in DNMS = reached for novel object.

Subjects were tested on VPC at 4, 6, and 9 months of age. Subjects were tested on DNMS at 6, 9, and 12 months. All N's = 20. Each subject was tested on only 1 task and at only 1 age. All received 2 trials at each delay; these 2 scores are averaged for each subject.

Significance levels (binomial distribution): 90% = 0.0002, 85% = 0.0008, 80% = 0.004, 75% = 0.01, 70% = 0.03, 65% = 0.065, 60% = 0.10, 55% = 0.15

Infants of 4 months succeeded on visual paired comparison *only* at the shortest delay (10 sec), failing even at delays of only 15 sec (see TABLES 7 & 8). These results for 4-month-old infants accord well with the results found in other studies. Pancratz and Cohen (1970) report that 4-month-old infants showed a significant novelty preference after a delay of 15 sec but not at 5 min (no intermediate delays tried). Stinson (1971) found that 4-month-olds showed recognition memory of a visual stimulus after 15 sec, but not at the next longer delay (30 sec). Finally, Albarran (1987), in a study using 3-dimensional objects, such as were used here, found that 4-month-olds succeeded on visual paired comparison after a delay of 10 sec but not at the next longer delay (1 min).

At 6 months of age, infants succeeded on visual paired comparison at delays of 10 sec and 1 min, and failed with a 10-min delay. They showed a tendency to prefer the novel object at 15 sec, but this did not reach statistical significance (see TABLES 7 & 8). As judged by percent of fixation to the novel, they failed at the 3-min delay,

TABLE 8. Fixation Times to Non-Matching (Novel) and Matching (Familiar) Objects in the Visual Paired Comparison Task by Age and Delay

ne Visual Paired Compariso Delay	4 Months Old	6 Months Old	9 Months Old
pelay of 10 Sec			
Mean fixation time to novel	10.33	10.11	10.79
Mean fixation time to	7.92	6.48	6.48
Percent of time fixating	57%	63%	62%
Significance of difference in fixation	t = 2.22 $p = 0.03$	t = 4.96 p < 0.0001	t = 3.97 p = 0.0008
Delay of 15 Sec Mean fixation time to novel object	9.98	10.17	10.63
Mean fixation time to familiar object	8.72	8.42	7.22
Percent of time fixating	53%	54%	59%
Significance of difference in fixation	t = 1.07ns	t = 1.57 ns	t = 3.81 $p = 0.001$
Delay of 1 Min Mean fixation time to novel object	11.29	11.03	10.81
Mean fixation time to familiar object	8.48	7.13	8.02
Percent of time fixating novel	55%	60%	57%
Significance of difference in fixation	t = 1.85 $p = 0.08$	t = 3.10 $p = 0.006$	t = 2.78 $p = 0.01$
Delay of 3 Min Mean fixation time to novel object	10.06	10.01	10.06
Mean fixation time to familiar object	9.41	8.25	7.69
Percent of time fixating novel	51%	55%	57%
Significance of difference in fixation	t = 0.57ns	t = 1.32	t = 2.32 $p = 0.03$
Delay of 10 Min Mean fixation time to novel object	10.29	9.66	10.99
Mean fixation time to familiar object	8.98	8.09	8.21
Percent of time fixating novel	53%	54%	57%
Significance of difference in fixation	t = 1.40	t = 1.37 ns	t = 2.68 $p = 0.01$

^aPercent of time fixating novel = (mean fixation time to novel) divided by (mean fixation time to novel + mean fixation time to familiar).

although as judged by percent of infants meeting the 67% fixation criterion, they just barely passed at the 3-min delay. Infants of 6 months succeeded on delayed non-matching to sample (single action) at all delays, although the percent of infants reaching for the novel object at the longer delays (1, 3, and 10 min) was just barely significant (see TABLE 7). Thus, performance of 6-month-old infants on delayed non-matching to sample (single action) was at least as good as their performance on visual paired comparison, and there is some suggestion that their performance was better. We conclude that 6-month-old infants could clearly succeed on both tasks at delays up to 1 min and that a delay of 3 min was probably just at the limit of their ability on visual paired comparison. Clearly, at roughly the earliest age when infants can reach for free-standing objects, they can succeed at delayed non-matching to sample. Indeed, they succeed at quite long delays.

At 9 months of age, infants succeeded on both tasks at all delays. Results for all dependent measures are in complete agreement (see TABLES 7 & 8).

Thus, allowing the stimulus object to serve as its own reward totally eliminated any suggestion that infants succeed earlier on visual paired comparison than on delayed non-matching to sample. We had not expected that requiring only a simple, one-part response on delayed non-matching to sample would so effectively eliminate developmental differences in when infants could succeed on the two tasks. Had we expected this, we would (a) have used longer delays (as there was probably a ceiling effect at 9 months of age—although the results at 6 months suggest that if differences were found at still longer delays they would have been in the direction of superior performance on delayed non-matching to sample [single action] as compared to visual paired comparison), and (b) we would not have needed to test subjects at 12 months of age. Predictably, given the success of the 9-month-old infants, infants of 12 months succeeded at all delays on delayed non-matching to sample (single action) (TABLE 7).

The correlation between where infants were looking as they reached and where they reached in the delayed non-matching to sample task was 0.98. Results for which object infants looked at are the same as the results for where they reached.

Conclusions from Delayed Non-Matching to Sample (Simple Procedure) and Visual Paired Comparison Testing: Vision versus Reaching and Single-Action Sequence versus Two-Action Means-End Sequence

From the earliest age reaching could be tested (6 months), infants showed evidence of memory on delayed non-matching to sample (single action) (reaching as the dependent measure) at delays every bit as long as those they could tolerate on visual paired comparison (looking as the dependent measure). This would seem to eliminate the possibility that recognition memory might first become available to the visual system and only later to reaching. Here is evidence of early memory at long delays using reaching as the dependent measure. We conclude from this that the critical difference between delayed non-matching to sample (standard, two-action procedure) and visual paired comparison is not reaching versus looking.

We cannot conclude, however, that the critical difference between the two tasks is necessarily that delayed non-matching to sample (standard procedure) requires planning and executing a 2-action sequence, whereas visual paired comparison requires only a simple, direct response. This might be the critical difference. Indeed, the difficulty of planning or executing a 2-action means-end sequence could also account for why infants will not reach around a screen, or pull off a cover, to retrieve a hidden object until roughly 8 months, although earlier at only 4 or 5 months they can indicate that they know a hidden object is still there on visual habituation tasks. It is certainly reasonable to suppose that the need to string two responses together might complicate things, requiring as it does a certain degree of planning and temporal organization in behavior. There are, however, a number of dimensions on which delayed non-matching to sample (simple procedure) and visual paired comparison are similar to one another and different from delayed non-matching to sample (standard procedure). Any one of these dimensions could potentially be the critical one (see the section below). Also, why should success on delayed non-matching to sample (standard procedure) appear so very much later than success on visual paired comparison (21 months vs. 4 months) when success in retrieving a hidden object appears only a few months later than when knowledge of hidden objects can be demonstrated in visual habituation paradigms (8 months vs. 4 months)? Why, too, should success on delayed non-matching to sample appear so much later than success in retrieving a hidden object (21 months vs. 8 months)? The complication posed by the need to execute a means-end action sequence might be sufficient to account for the hidden object findings, and for part of what makes delayed non-matching to sample (standard procedure) so difficult, but even if it is part of the answer, it is unlikely to be the whole story.

DIAMOND: RATE OF MATURATION OF HIPPOCAMPUS

Possible Alternative Explanations for the Late Appearance of Success on Delayed Non-Matching to Sample

Stimulus ≠ Reward

One possibility is that what makes delayed non-matching to sample so difficult is that the stimulus for which the subject reaches is not the reward. The stimulus stands for the reward. This is more abstract than if the object is itself the reward. In delayed non-matching to sample, subjects must act on the stimulus to obtain something else which is not even visible until after they act. In the visual paired comparison and visual habituation paradigms, subjects look at something because it is intrinsically interesting, not because of its relationship to anything else. Similarly, when infants uncover a cloth to retrieve the object beneath, the thing they initially see and reach for (the cloth) is not the reward. Here, too, they must act on one thing to obtain another. To dissociate (a) a simple, direct response versus an indirect. 2-action sequence from (b) whether the subjects must act on one thing to obtain another versus the stimulus is its own reward, we constructed a jack-in-the-box apparatus for testing delayed non-matching to sample (see TABLE 9, lines 1 and 2). Here, the objects are affixed to trays on the top of the apparatus and cannot be removed. However, in reaching for the object, if the object is moved at all, a jack-in-the-box pops up behind it (much to the infant's delight). The jack-in-the-box is the reward, not the object for which the infant reaches, but only one action is required—the act of starting to retrieve the object causes the jack-in-the-box to spring up. We are presently testing infants on this in our laboratory.

TABLE 9. Task Characteristics or Requirements of Delayed Non-Matching to Sample That Are *Not* Present in Visual Paired Comparison

Task Characteristics or Requirements	Baillargeon vs. Uncovering	Jack-in-the-Box
(1) Two-action sequence	applies	should succeed
(2) Stimulus ≠ reward	applies	should fail
(3) Deduce an abstract rule	doesn't apply	should fail
(4) Explicit testing/negative feedback	??	should fail, but could give reward regardless
(5) Quick speed of encoding visual stimuli	applies	should succeed, but could give short exposure
(6) Interference between sample and test	?? perhaps, cover	should fail, but could give no reward after sample

Abstract Rule

Mishkin has proposed that delayed non-matching to sample is more difficult than visual paired comparison because the former requires attending to the abstract quality of novelty and learning an abstract rule ("reach to the stimulus that does not match the sample") whereas the latter requires only doing what comes naturally. To explore whether children fail delayed non-matching to sample (standard procedure) because of difficulty deducing the rule, we told subjects, aged 12, 15, 18, 21, 24, 27, and 30 months, what the rule was at the outset of testing (Diamond et al., in prep.). That is, on each of 3 preliminary trials, when the two objects were presented in the test phase of the trial we said, "The [reward] is hidden under the new one. Can you find it? Look under the thing you have never seen before." Most subjects over 12 months of age succeeded on 2 out of 3 of these preliminary training trials (percent correct at each age from 15-24 months = 83%; 12-month-olds performed at chance and probably did not understand the verbal prompt). Infants of 15 and 18 months performed slightly better on the test trials following this training than they did when they had to deduce the rule themselves (69% vs. 63% correct at 5-sec delay at 15 months; 79% vs. 70% correct at 5-sec delay at 18 months). This effect is very modest and does not reach statistical significance.

Explicit Testing

A closely related hypothesis to that offered by Mishkin is that when there is a formal testing situation, where it is possible to be wrong, the performance of infant monkeys and young children deteriorates. On visual paired comparison and delayed non-matching to sample (simple procedure), there is no wrong answer. The subject can look at, or have, whichever object he or she chooses. It feels more like a play situation than a test. In contrast, when the standard delayed non-matching to sample task is administered, subjects are only rewarded when they reach to the novel stimulus. Here it is clear they are being tested, and that there are right and wrong

answers. After all, amnesic patients often cannot recall information when explicitly tested, but can show that they have some memory of that information on subtle measures where they do not know they are being tested. If explicit testing and/or negative feedback is what makes delayed non-matching to sample so relatively difficult, then the jack-in-the-box condition should also be difficult. Presumably if there was no feedback about right or wrong responses (i.e., if the jack-in-the-box popped up regardless of which object the subject chose, or if rewards were hidden under both objects in the standard delayed non-matching to sample task), then if this explanation is correct, subjects should succeed much earlier here than when feedback is provided. That is, their spontaneous preference might lead them to choose the new object most of the time, even though they do not do this when they try to "think about" what they are doing, or what they are supposed to do.

Brief Presentation Time

In standard delayed non-matching to sample testing, the subject sees the sample initially for only a few seconds (roughly 2–5 sec): The subject displaces the sample to retrieve the reward and then the screen comes down immediately. In contrast, in delayed non-matching to sample (simple procedure), the object is typically present for about 70 sec, and infants typically look at it for 40–50 sec (see TABLE 10). Similar looking times at the sample were found when we administered the visual paired comparison task (TABLE 10). In other studies using the visual paired comparison task, the sample has been presented for anywhere from 10 sec to 2 min (see Fagan, this volume)—all longer than the 2–5 sec it is available in standard delayed non-matching to sample. Perhaps the difference in the amount of time subjects are given to encode the sample stimulus accounts for why success on visual paired comparison appears earlier than success on delayed non-matching to sample.

We know that information processing time decreases dramatically with age; younger children need much longer to process a stimulus than do older children. Studies of visual paired comparison have often shown that if the sample is only presented briefly no novelty preference is found (e.g., Hunter & Ames, 1975; Caron et al., 1977; Lasky, 1980; Rose, Gottfried, Melloy-Carminar & Bridger, 1982). Moreover, the time needed to encode the sample decreases with age during infancy (e.g., Caron et al., 1977; Werner & Perlmutter, 1979; Rose et al., 1982). so if the sample is presented only briefly, younger children would be more adversely affected than older children.

TABLE 10. Means of Total Visual Fixation Time of Sample during the Familiarization Period by Age and Task

	Age in Months			
Task	4	6	9	12
Visual paired comparison task	53.0	34.5	35.1	
Delayed non-matching to sample task simple procedure		53.8	43.3	40.3

Similarly, when an object is hidden, the infant sees the object and the hiding procedure for only a few seconds. In Baillargeon's visual habituation procedures, however, the infant sees this repeated over and over again many times. Differences in time available to process what is happening might be important in understanding why infants show that they know the hidden object is there earlier in Baillargeon's tasks than when allowed to uncover a hidden object.

With the jack-in-the-box apparatus we will be able to see if presentation time makes a critical difference in delayed non-matching to sample performance. Before, it was not possible to test this with young infants. If the object is not its own reward (as in the standard delayed non-matching to sample procedure), then infants do not want to spend a long time looking for it. From their perspective it is teasing to try to make them look at it, but not let them have it. If infants are allowed to have the object (as in delayed non-matching to sample [simple procedure]) then they do not want to relinquish it as soon as they have gotten it (i.e., within 2–5 sec of seeing it). However, it takes about 30 sec to affix the objects to the trays on the jack-in-the-box apparatus. Infants will watch during this time without fussing at not being able to have the object, because they can see that we are getting it ready for them (this allows for a long presentation time). By having a screen in place while the sample is being attached to the apparatus, we can make the presentation time brief.

Yet, there are already indications that length of presentation time may not be the critical variable either. (1) Bachevalier reports (see discussion following this paper) that even though the sample stimulus was present for 30 sec during visual paired comparison testing, infant monkeys generally looked at it for only about 2–5 sec.⁹ This is about as long as they saw the sample during delayed non-matching to sample testing. Yet, she found that infant monkeys could succeed on visual paired comparison as early as 2 weeks of age, but could not succeed on delayed non-matching to sample until at least 4 months of age. (2) In our own work, 4-month-old human infants looked at the sample longer during visual paired comparison testing than did older infants (53 sec vs. 35 sec; see TABLE 10 above), and all were equated on level of habituation before the sample object was removed, yet the 4-month-olds still failed to look longer at the novel object except at the very shortest delay, unlike the older infants (see TABLE 8 above).

Interference

A final possible explanation for the late appearance of success on standard delayed non-matching to sample might be that retrieval of the reward after the sample is displaced interferes with, or masks, the memory of the sample object. Gaffan. Shields, and Harrison (1984) found that monkeys performed better on the delayed matching to sample task when they received no reward during initial sample

presentation. Perhaps the reason performance was so much better here was because the last thing subjects saw before the delay was the sample, rather than having their attention drawn away from the sample to the reward.

There is much evidence, however, that recognition memory on visual measures is quite robust despite the presence of stimuli interspersed between sample and test even in very young infants (e.g., Caron & Caron, 1968; Fagan, 1971; Martin, 1975; Bornstein, 1976). If interference is a problem, then children should fail the new jack-in-the-box condition, for here too a reward is interposed after the sample. They should succeed, however, (if the problem is interference from the reward between sample and test) if nothing happens after they touch the sample (i.e., the jack-in-the-box does not pop up, or no reward waits underneath the sample in the standard delayed non-matching to sample procedure).

SUMMARY

Although it has been widely speculated that the hippocampus, and the type of memory dependent upon the hippocampus, develops late in primates just as it does in rats (e.g., Nadel & Zola-Morgan, 1984; Bachevalier & Mishkin, 1984; Schacter & Moscovitch, 1984), the evidence to date would not seem to support this. Instead, there is behavioral evidence of very early recognition memory and anatomical evidence of very early hippocampal maturation in human and non-human primates. It is true, however, that the standard delayed non-matching to sample task, which requires recognition memory, is not mastered until quite late. The reason for this late mastery would appear to be the late emergence of some other ability required for the task, not recognition memory. The candidates for what that ability might be are (1) the capacity to plan and execute an indirect, two-action sequence, (2) the capacity to understand that the object stands for the reward, but is not the reward itself, (3) the ability to deduce an abstract rule, (4) the ability to make explicit on testing what can be shown implicitly during play, (5) the ability to quickly encode visual stimuli (speed of encoding), and (6) the ability to resist interference. Only empirical work will enable us to decide among these candidate abilities; that work is currently underway.

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^qBachevalier's looking times for infant monkeys are much shorter than ours for human infants. That may be because, until our habituation criterion was met, we re-directed subjects' attention back to the sample stimulus if they looked away for more than 3 sec, whereas Bachevalier did not bring subjects' attention back to the stimulus if they looked away.

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DISCUSSION

N. Fox (*University of Maryland, College Park, MD*): What exactly did you ask the children to do on the two delayed non-matching to sample tasks you gave? How did you word your instructions to them?

A. DIAMOND (University of Pennsylvania, Philadelphia, PA): We asked them to find the reward. We did not tell them where or how to find it. There is also something else we did that is like what is done in testing amnesic patients on delayed non-matching to sample: After the 3-, 4-, and 5-year-olds had reached criterion at 5 sec, or after 10 trials at 5 sec, we asked them to state the rule. The wording we used for the children was, "How did you know where to find the reward?" Here, they had been getting it right 5 times in a row, and most would go on to get all 15-25 trials correct, yet the 3-year-olds could not tell you how they knew where to look. They would say, "I know 'cause I know." The 4-year-olds can tell you, though. The 4-year-olds also describe it in terms of turn-taking, which was interesting. They would say, "Each one gets a turn. The reward was under this one when it was presented all by itself, so the reward must be under the other one now." In terms of performance, however, the 3-year-olds, even though they couldn't state the rule, were performing every bit as well as the 5-year-olds. Everybody was above 90% correct. There was no significant difference by age in performance between 3 and 5 years. Although amnesic patients, in the second test that is described in the paper by Larry [Squire], Stuart [Zola-Morgan], and Karen [Chen], can't state the rule, at the short delay of 5 sec they are fine. So I don't think that the amnesics don't know the rule.

Fox: That wasn't really my question. My intent was to compare the tasks that you are giving both the infants in the second year of life and to the 3- to 5-year-olds with Bill [Overman's] task, and my understanding is that, in addition to the direct versus indirect (i.e., the object as its own reward versus displacing the object to get the hidden reward), a difference here is that you gave instructions in your task. And Bill gave no instructions whatsoever, as I understand it.

It would seem to me that is a *major* difference between the two sets of data, because Bill has 1,000 trials for an 18-month-old with absolutely no instructions and you have 25 trials with children of the same age with instructions. So aside from direct versus indirect and this and that and everything else, there is an issue of instruction.

DIAMOND: No. We do not instruct the children in the rule governing the correct choice. All we do is make the situation approximate more closely normal social

interaction. Bill Overman's testers extend their hands from behind a screen hiding the rest of the person and move the stimulus toward the child without saying a word. We have the tester sit opposite the child as people normally sit and say to the child as the stimulus is pushed forward, "See if you can find the reward." This "instruction" is superfluous; all of Bill's subjects, even the youngest, figure out immediately to pick up the stimulus to see what is underneath. Children do this spontaneously on their own. Our tester speaks primarily to make conversation so that the situation does not seem so strange to the child; people do not normally interact soundlessly. To say to the child, "The reward is under the new object," is to instruct the child in the task. However, to say, "We have hidden the reward under one of these objects. Can you find it?" does not tell the child anything that even the youngest children do not readily realize for themselves. There is no age difference, and no difference between Bill's results and mine, in whether children pick up the stimulus to look for what is underneath. All do so readily with or without this "instruction." It is remarkable that given all of the procedural differences between Bill's study and mine, Bill's data and my data are in exact agreement. For the age range that we studied, we find the same changes over age and the same things that don't change over age. Our results are extremely comparable. When Bill and I have studied children of the same age (he didn't study the very young babies, and he didn't study 5-year-olds) we have gotten exactly comparable results, despite dramatically different testing procedures.

Fox: I didn't see 1,000 trials on yours, though. I saw only 15 or 25 trials.

J. RICHARDS (*University of South Carolina, Columbia, SC*): It is hard to say that you get the same results because what he is reporting is how long it takes to reach a criterion of 13 out of 18.

W. OVERMAN (University of North Carolina, Wilmington, NC): A very stringent criterion. Yours is a criterion of 5 out of 5, mine is 87%.

DIAMOND: But even with my weaker criterion, Bill, those who passed at the 5-sec delay generally passed at the 30- and 60-sec delays, where there were more trials and the criterion was 90%.

That is, those who passed 5 out of 5 trials at 5 sec, generally went on to succeed on most of the following trials, even though much longer delays were used. So it would seem our criterion was sufficient in this case. All I am saying is that the difference Bill finds over age in how hard or easy it is for infants at a given age to pass the criterion and how they perform at different delays are in exact agreement with our results.

Fox: I don't see how you can say that; I really don't understand. Can you just pursue that for a second?

DIAMOND: I'm not talking about absolute number of trials. I am talking about the decrease over age in the number of trials needed to reach criterion. I'm saying that there is an age difference here in how easy or difficult it is for infants to learn the rule, and in how long it takes them to learn the rule. The age trends that Bill [Overman] found on this are comparable to the age trends I found.

R. NAKAMURA (National Institute of Mental Health): Basically, you are saying that they are fruit, and he is saying that they are apples and oranges. One person is talking about the tremendous difference in number of trials taken to attain apparent criterion or very good performance. You are just talking about different aspects of the same situation.

Fox: Adele, you have a decrease there for at least 2½ to 5 years . . . Your 3-. 4-,

and 5-year-olds are performing at 90%, and as I remember from Bill's data, he still had at least ...

DIAMOND: He didn't have any 4- or 5-year-olds. I believe that by 3 years they were performing well in Bill's study. The oldest he tests is 3 years, and they do superbly on his task by that age, just as I found on my task.

Bill started testing children months before they could succeed on the task. Because he tested them every day, they had been tested for thousands of trials before they reached the age at which they could succeed. I tested the children crosssectionally, only once. My results show the children succeeding at roughly the same age, on roughly the same delays, as do Bill's results. This suggests, I think, that the months of training Bill gave the children had little effect. When they are able to master the task, a few trials will suffice to train them.

S. ROSE (Albert Einstein College of Medicine, Bronx, NY): Adele, if I understand what is going on in the procedure you were talking about with the infants on this "direct" delayed non-matching to sample task, they were reaching directly for the object as opposed to having to find a reward underneath the object.

We did a study a number of years ago, just a small study, when I first started working with preschoolers." We were using a learning task modeled after the WGTA, and we found that we halved the number of trials it took a child to learn by just giving him or her the reward as opposed to having the child displace the object and find the reward underneath. I never made too much of that, but the reason I did it to begin with was that it appeared to me the reason it was taking the children so long to learn was that you are disrupting what you're trying to get them to learn; you are re-focusing them on the reward, on the action. He covers the object with his hand while he is moving it off, and so forth.

DIAMOND: Right. That's fascinating, Sue. Would you then say that the procedure I have tried to show with the jack-in-the-box, that we want to use with the infants, would get at that?

Rose: Oh, yes.

J. FAGAN (Case Western Reserve University, Cleveland, OH): On the visual paired comparison test you did, you departed from what is typically done in a couple of ways. One is you moved the stimuli. Two, you weren't getting percent of fixation to a particular target; you were getting some sort of a choice measure. I'm not quite sure what your measure was.

DIAMOND: No. We looked at the time they looked at the novel, at the time they looked at the familiar, and the percent of that total that they looked at the novel. Then we also looked at the percent of children who fixated the novel object 67% of the time or more, just so we could get some measure comparable to the dependent measure used on delayed non-matching to sample. In delayed non-matching to sample, the basic dependent measure is what percent of the subjects chose the novel object. So we had to find some way to get something comparable to that on the visual paired comparison task. What we came up with was percent of infants fixating the novel object at least twice as much as they fixated the familiar object, at least 67% of the time. Sue [Rose], I think, and others have used the criterion that if percent of fixation is 67% or more to the novel, then you conclude that they have shown a preference for the novel.

FAGAN: I think with your 4-month-olds you used straight percentage.

DIAMOND: RATE OF MATURATION OF HIPPOCAMPUS

DIAMOND: Nope. We used about 10 different dependent measures and got the same results on all measures for the 4-month-olds. And other studies, regardless of the dependent measures they have used, have found essentially the same results for 4-month-olds. Some say 4-month-olds show a novelty preference after as long as 15 sec; others find it is after 10 sec, but not after 15 sec. We found 4-month-olds show a novelty preference after 10 sec, but not after 15 sec. The results are pretty comparable, I think, especially since by 6 months they show this preference after substantially longer delays (i.e., 1-3 min).

FAGAN: I have never seen any movement of the stimuli, though.

DIAMOND: Well, the moving stimulus may be different. You and others often use two slides for the sample, where the sample stimulus is shown in both the left and right positions. We didn't want to have to build yet another identical copy of all of our different objects, so we presented one stimulus during the sample presentation, rather than identical objects to the infant's right and left. To keep the infants looking at the sample as long as we could, we moved the stimulus to the left and right.

P. TALLAL (Rutgers University, Newark, NJ): I wanted to go back to one of the points you raised at the beginning, and that was the interaction potential in all kinds of memory experiments (with amnesics, with monkeys, or with babies) pertaining to the amount of exposure time, and the role that plays with the subsequent "memory performance." We did a study, I think I did it for my Ph.D. dissertation in 1971, in which we looked directly at the effect of amount of exposure time on the memory span of children aged 3, 4, 5, 6, 7, and 8 years old. We found very clearly that the exposure time specifically related to the number of items a child could remember, so we found that 3-year-old children could only remember 2 items. let's say, if you gave them a 75-msec exposure time. But they could remember 4 items if you just gave them a 200-msec exposure time. I have always been very concerned about memory studies that seemed to leave this variable floating. How do you know you are studying memory if you are not sure the individual perceived, or integrated, what they were supposed to remember to begin with?

DIAMOND: Right. That is a good point. Although, considering a coarse measure of exposure time, on the standard "indirect" delayed non-matching to sample task the exposure is brief, whereas on the "direct" delayed non-matching to sample task and on the visual paired comparison task the exposure time was always long.

TALLAL: I am talking about a millisecond difference between 75, 125, and 250 msec, and an enormous difference in memory in terms of number of items that could be recalled at 0 delay, much less any other delay, and I do not think that with the procedures that are being used you could possibly be controlling for those sorts of things. It is different for each individual and I am sure it is being controlled at some level by the individual, in terms of how fast a research assistant can in fact put the screen down and so forth.

ROSE: Even at a grosser level, I am going to reiterate that I am sort of astonished it takes monkeys so long to learn the delayed non-matching to sample task. I'm also astonished that it takes humans so long. When I first came to the cross-modal literature, I went to the monkey literature, they go on for 100s and 1000s of trials.

BLANK, M. & S. A. Rose. 1975. Some effects of testing methodology on children's cross-modal performance. Developmental Psychology 11: 120.

Now one of the things I don't think is ever controlled is how much looking time. On this delayed non-matching to sample task, is the monkey getting a *good look* at the stimulus before he is asked to choose?

J. BACHEVALIER (National Institute of Mental Health, Bethesda, MD): Yes, because he has to touch it and has to move his eyes toward it in order to move it and get the reward. He has at least 2–5 sec to really glance at the object, and, in fact, the reason the task was designed with the reward under the object was so that we could be sure that if the monkey obtained the reward he had seen the object.

ROSE: I understand that you are getting some of that, but what I am really saying is the amount that the monkey will look at the stimulus may very much determine how quickly he learns these kinds of tasks.

BACHEVALIER: Right. For example, in the preferential looking task (visual paired comparison) if you give infant monkeys a familiarization time of 30 sec and then calculate the amount of time they look at the object during those 30 sec, there is not a big difference between the young infant and the adult monkey. They require approximately 5–6 sec. Infant monkeys only look at the sample about 5–6 sec during the entire 30-sec period.

DIAMOND: That is quite different from human infants.

TALLAL: Some monkeys must be fast at going for touching that object, and other ones might be slower. Is there a difference in the performance on the delayed non-matching to sample task depending on the individual difference of the monkeys, how fast they initially touch the object?

BACHEVALIER: No, because they go very fast.

TALLAL: They are stupid. They should leave the object on longer.

BACHEVALIER: That does not differ from preferential looking. The time that they glance before they reach the object is something around 2–5 sec, which is the length of time they look on my preferential looking task. I don't get long looking times.

DIAMOND: Oh, that's good. I didn't know that. That's good.

BACHEVALIER: I am starting to make comparisons because some look for 3 sec and others look for 6 sec. So I'm looking to see if there is a difference in performance just by this small amount of difference in initial looking time. I don't think there is a difference in performance.

DIAMOND: That is a very important point. Jocelyne just said that when she does the visual paired comparison task, she gives them as long to look at the stimulus as they take to reach for the stimulus in the delayed non-matching to sample task, so that suggests that the dramatic difference in performance on visual paired comparison and delayed non-matching to sample is not due to differences in familiarization time between the two tasks, at least in the monkey.

J. COHEN (Carnegie-Mellon University, Pittsburgh, PA): But if there are different rates of processing, then it may not be comparable. The times may not be comparable. There might be different speeds of encoding the visual stimulus than there are for encoding which is novel or familiar and generating a reach.

DIAMOND: But in both cases you are encoding it visually. Either you encode it because you have displaced it, or you encode it because you have looked at it. You get a visual presentation for choice in either experiment.

A. MELTZOFF (University of Washington, Seattle, WA): Did you have an inference

that you wanted to draw about memory in 4-month-olds given that you had 4-month-olds failing visual paired comparison after a 10-sec delay? Were you thinking, therefore, that they cannot remember longer than 10 sec?

DIAMOND: Yes and no. There are different kinds of memory. I think 4-montholds may not be able to remember something they saw only once, briefly, for more than about 10 sec, but if Daddy were gone a week I am sure they would still remember him, and if Carolyn [Rovee-Collier] came back with her mobile a week after the 4-month-old had learned to kick to make the mobile move, I am sure the infant would still remember that stimulus—response association.

There is another fundamental difference between 4-month-olds and 6-month-olds. One of the things you find with 4-month-olds, with my procedure anyway (using our habituation criterion [rather than a set familiarization time]), is that 4-month-olds were clearly bored way before they reached habituation criterion. Phenomenonologically they were habituated way before they met our habituation criterion. What seemed to be happening was that they could not keep themselves looking away from the object for 3 sec, they kept being drawn back to the object.

J. WERKER (University of British Columbia, Vancouver, B.C.): That's right.

DIAMOND: So, they got many more "look aways," many more glances away from the sample and then back before they met the habituation criterion of three 3-sec "look aways." You get this incredible number of "look aways" with the 4-month-olds, and many fewer for infants 6 months and older. It was as if the 4-month-olds could not control their attention. They kept going back to the object, when you could see that the poor kids were *sick* of the object, but they hadn't met our habituation criterion yet.

S. Zola-Morgan (University of California, San Diego Medical School, La Jolla, CA): I want to respond to Paula [Tallal's] question again, concerning time looking at the sample. It is a fundamental question, and I don't think we have looked at it in a formal way. The key question would be, Do animals take a different amount of time on the trials where they are correct, for instance, than on the trials on which they are not correct? It is a basic empirical question, and I think we don't know the answer to that yet. It's an important question.

Fox: Many people have shown that infants are inhibited in reaching to novel objects. Yet you find infants reaching preferentially to novel objects. Those two sets of findings would seem to be contradictory. Could you comment on that?

DIAMOND: You are right that it appears at first to be contradictory, but I think the findings are quite compatible. Schaffer and Parry (1969)^s and Rothbart (1988)^t presented one object at a time and measured the infants' latency to reach for that object. I haven't been studying latency to reach. I present infants with a choice of two objects, and look at which one they select. The objects are visible for a few seconds

³For example. Schaffer, H. R. & M. H. Parry. 1969. Perceptual motor behavior in infancy as a function of age and stimulus familiarity. British Journal of Psychology 60: 1–9.

SCHAFFER, H. R., A. GREENWOOD & M. H. PARRY. 1972. The onset of wariness. Child Development 43: 165-175.

¹ROTHBART, M. K. 1988. Temperament and the development of inhibited approach. Child Development **59**: 1241–1250.

before the infant is allowed to reach because we want to make sure the infant has seen both objects before he or she reaches.

C. KOPP (*University of California*, *Los Angeles*, *CA*): I have a naive question. What's the bottom line? What developmental implications does this have?

DIAMOND: Good question. The first implication is that this questions an assumption that has been fairly widely held, the assumption derived primarily from studies with rats, that the hippocampus, and the type of memory for which it appears to be critical, are late maturing. It is true that success on delayed non-matching to sample requires a properly functioning hippocampal formation, and it is true that success on this task does not appear until quite late in development for both children and monkeys. However, (1) success (i.e., consistent choice of the non-matching stimulus) occurs quite early in development for visual paired comparison, and (2) not only does this task appear to pose memory requirements similar to those for delayed non-matching to sample, but Jocelyne [Bachevalier] has demonstrated that combined lesions of the hippocampus + amygdala produce deficits on the visual paired comparison task in adult monkeys and in infant monkeys, even in the first week or two of life. This suggests that the reason for the late appearance of success on delayed non-matching to sample is something other than its dependence on the type of memory function subserved by the hippocampus.

Well, if a late-developing memory system dependent on the hippocampus is not the explanation, what is? Another related question is why can infants of only 4-5 months show that they know, and remember, that a hidden object is still there in Renee Baillargeon's visual habituation studies, while they act as if they do not know, or remember, a hidden object is still there when required to reach for, or uncover, that object? It seemed to me there were two possible answers to each of these questions, and I tried to generate competing predictions based on those two answers and to test those predictions. On the one hand, the critical difference could be looking versus reaching (success appears early on visual paired comparison and visual habituation, which require only looking, but relatively late on delayed nonmatching to sample and uncovering a hidden object, both of which require reaching). Perhaps abilities become integrated earlier with the visual system than they do with the reaching system. On the other hand, delayed non-matching to sample and uncovering a hidden object require displacing one object in order to retrieve another (i.e., they require a 2-part action sequence; an indirect, circuitous response), whereas visual paired comparison and visual habituation require only that subjects look at what interests them (a simple, direct response). Perhaps the indirect, means-end requirement of delayed non-matching to sample and uncovering a hidden object accounts for why success appears later there.

To test this, I administered a version of delayed non-matching to sample where instead of displacing the object to retrieve the reward, the object itself was the reward. Thus, this task still required reaching, but only a simple, direct response was needed. We found that success on this task appears very early, and that from the earliest age infants can be tested they can tolerate delays every bit as long on this version of delayed non-matching to sample as they can on visual paired comparison.

This work eliminated the possibility that the critical difference between the tasks was reaching versus looking. It may be that the critical difference is an indirect, 2-part response versus a simple, direct one, or it may be length of presentation time

(in visual paired comparison, visual habituation, and delayed non-matching to sample, "direct," the stimulus is presented for a long time [e.g. 30 sec], whereas in delayed non-matching to sample, "indirect," and uncovering a hidden object the stimulus is presented only briefly [e.g., 2–5 sec]). Or, the critical difference may be whether the visible stimulus stands for the reward, indicates where the reward is (as in delayed non-matching to sample "indirect" and uncovering a hidden object), or whether the visible stimulus is the reward itself (as in visual paired comparison and delayed non-matching to sample "direct"). Further investigation is needed to distinguish among these hypotheses, and we are currently in the process of doing exactly that. Why the developmental timetables should be so different for such seemingly similar tasks as (a) Baillargeon's visual habituation task and Piaget's uncovering a hidden object task and (b) delayed non-matching to sample "direct" and delayed non-matching to sample "indirect" is a fascinating question. As we attempt to unravel this puzzle, I think we will learn much about the nature of development.

M. STANTON (Environmental Protection Agency, Research Triangle Park, NC): Is there a difference between the visual paired comparison task and delayed non-matching to sample using the standard "indirect" procedure in terms of how impaired subjects are, or how disrupted their performance is, by hippocampal damage? Is there any difference between those two tasks in terms of how easily performance can recover following hippocampal damage?

BACHEVALIER: This has not been studied yet. The same animals have not been tested on both tasks, although we hope to do that. It is hard to compare performance in two different groups of monkeys, on two different tasks with different dependent measures, but it is my impression from our results and from those of Saunders that the impairment in the monkeys with hippocampal-amygdala lesions is comparable on both tasks. Monkeys with lesions excluding the amygdala have not yet been tested on the visual paired comparison task.