Knowing Where Things Are in the Second Year of Life: Implications for Hippocampal Development

Julia Sluzenski, Nora S. Newcombe, and Eric Satlow

Abstract

■ Prior data have revealed striking contrasts between 18- and 24-month-old children in place learning, an ability known to depend on the hippocampus (Newcombe, Huttenlocher, Drummey, & Wiley, 1998). The current research examined the development of three other basic abilities of mature spatial competence: the representation of multiple locations, the learning of relations among objects, and the recall of a single location after a substantial filled delay. Results indicated a transition from 18 to 24 months in all three abilities. This evidence supports a general transition in spatial representation that occurs towards the end of infancy. Existing neurobehavioral data suggest that a corresponding change in hippocampal functioning underlies this development. ■

INTRODUCTION

What features of infant spatial memory distinguish it from that of adults? At a minimum, mature spatial competence includes the ability to remember the locations of several objects simultaneously, to find objects based on the visible locations of other objects, and to remember locations across time. Only after such basic abilities are in place is spatial functioning at a level that allows for success in the spatial demands of everyday life. It is now evident that even young infants demonstrate knowledge of an object's location in continuous space (Newcombe, Huttenlocher, & Learmonth, 1999), that toddlers can retrieve objects using information about distance (Huttenlocher, Newcombe, & Sandberg, 1994) and geometric relations (Hermer & Spelke, 1994, 1996), and that toddlers can use landmarks to reduce uncertainty about geometric relations (Learmonth, Nadel, & Newcombe, 2002; Learmonth, Newcombe, & Huttenlocher, 2001).

Despite these competencies, some marked limitations on early spatial competence have been found. For instance, Newcombe et al. (1998) examined the development of the use of distal landmarks (those not touching or near some target). Children ages 16–36 months observed a toy being hidden in a rectangular sandbox, moved to the opposite side, and then searched for the toy. Half of the children performed this search with visible landmarks in the room and half without visible landmarks. Children 22 months and older performed better when the landmarks were visible, while younger children did not. In other words, children younger than 22 months did not seem to use the relations among surrounding objects to reorient after movement. These results are consistent with earlier work (Bushnell, McKenzie, Lawrence, & Connell, 1995; DeLoache & Brown, 1983) and suggest that spatial memory in late infancy involves a deficit in learning and/or using relations among distal landmarks.

The ability to navigate through the environment using knowledge of spatial relations among objects involves an externally based kind of spatial memory called "place learning." This important spatial ability is believed to depend on the hippocampus based on animal studies using single cell recordings (Ono, Nakamura, Nishijo, & Eifuku, 1993; Muller, Kubie, & Ranck, 1987; O'Keefe & Speakman, 1987; O'Keefe, 1976; O'Keefe & Dostrovsky, 1971) and lesions (Jarrard, 1993; Morris, Garrud, Rawlins, & O'Keefe, 1982), as well as on studies involving both brain-injured and normal human adults (Holdstock et al., 2000; Bohbot et al., 1998; Maguire, et al., 1998; Maguire, Frackowiak, & Frith, 1996; Maguire, Frackowiak, & Frith, 1997). Thus, the marked improvement in place learning at the end of infancy is possibly an indication of a corresponding change in hippocampal functioning, an idea raised previously by Nadel and Zola-Morgan (1984).

The first goal of the present research was to examine the development of three basic spatial abilities that are a fundamental part of adult spatial competence: remembering more than one location at a time, using one location to find another location, and remembering a single location after a delay of more than a few seconds. Of interest was whether these abilities undergo a transition at the end of infancy similar to that observed with place learning or whether they undergo more gradual improvement. In examining each of these abilities, we

Temple University

© 2004 Massachusetts Institute of Technology

included 18-, 24-, 30-, 36-, and 42-month-olds and used as the measure of interest the amount of error when searching for an object in a long rectangular sandbox.

In the ''two-location task,'' children watched an experimenter hide two identical objects one at a time in the sandbox. Immediately after a brief break in eye gaze toward the hiding locations (e.g., by turning around to hug or kiss the parent), children were encouraged to retrieve the objects from the sand. Successful performance on this task requires simultaneous representation of the two locations as well as durability of the second representation during retrieval of the first chosen object.

In the ''relational task,'' we investigated the ability to use known relations among locations during search. Children first received a fixed amount of training on the following spatial relation: that two different objects varied locations in a sandbox but were always a fixed distance apart and each was always on the same side relative to the other. After the training, an experimenter surreptitiously hid the two objects in the sandbox, then revealed one of the objects and asked the children to find the other object.

In the ''retention task,'' we examined the ability to search for a single object after a substantial filled delay between hiding and search. Children observed as an experimenter hid an object in the sandbox; together they left the room for 2 min and then went back into the room to find the object. This task was of interest not only because it involved a basic component of mature spatial competence (i.e., the ability to remember where things are at a later point in time), but also because of its relevance to the existing infant memory literature. For instance, even children as young as 9 months can recall complex events that occurred as much as a month prior (e.g., Carver & Bauer, 1999). We were interested in whether recall is still robust when the learned information is spatial in nature.

The second goal of this research was to consider the neural development that would support improvement on such tasks. Each of the three tasks used has been linked by neurobehavioral evidence to the hippocampus. For instance, monkeys with hippocampal resections show impairments in remembering two locations but not one after only a very brief delay (Angeli, Murray, & Mishkin, 1993; Parkinson, Murray, & Mishkin, 1988) and adults with damage to the hippocampus are impaired in memory for the distance between two objects (Kesner & Hopkins, 2001); such findings suggest that the ability to represent multiple objects requires intact hippocampus. In addition, the requirements of our relational task closely resemble those in learning a conditional spatial discrimination, a task that has been used to study complex associative learning. During such a task, the subject learns to make a left or a right response depending on which of two cues is present. Similarly in the present work, after learning a constant spatial relation between two objects, children had to search to the left or right depending on which of two objects the experimenter revealed. Lesions to the hippocampus impair performance on conditional spatial discrimination tasks both in animals (Marston, Everitt, & Robbins, 1993; Kimble, 1963) and humans (Myers, Hopkins, Kesner, Monti, & Gluck, 2000; Daum, Shugens, Channon, Polkey, & Gray, 1991), with impairment apparently reflecting the need for increased training rather than a complete inability to learn the task. Finally, there is evidence that hippocampal lesions lead to impairment in the memory for a single location with delays as brief as 10–20 sec when egocentric responding cannot be used to solve the task (Bohbot et al., 1998; Long & Kesner, 1998). Recently, Lee and Kesner (2003) have suggested that the hippocampus may play a special role in spatial information that is trial-unique (i.e., episodic) and that must be remembered across a delay of just a few minutes. Thus, if infants have difficulty remembering locations across delays, this would suggest that the hippocampus may still need to undergo relevant development. In sum, if these abilities do have a developmental time course similar to that of place learning, this would provide further support both for marked improvement at the end of infancy and for hippocampal involvement in the improvement.

RESULTS

For all three tasks, initial analyses were performed to check for gender differences in search accuracy. In no case was such a main effect found, nor did this factor interact with the factor of age group. Therefore, all analyses reported are collapsed across gender.

Two-Location Task

Each child participated in four trials during which the experimenter hid two identical objects in a rectangular sandbox and then asked the child to retrieve them. Mean errors were calculated across these four trials and separately for the first-object and second-object searches (see Table 1). Analyses were performed to determine whether there was improvement with age in search accuracy. As expected, t tests with a Bonferroni correction did not reveal reliable age differences in accuracy of first-object searches (p's $> .10$).[1] This finding is consistent with earlier work showing that 16-month-olds are as accurate as older children in an immediate search for one object (Huttenlocher et al., 1994). In sharp contrast, the results for the second-object searches revealed improvement from 18 to 24 months ($p < .001$), but no reliable age differences among the older groups (p's $> .10$) (see Figure 1).

Of additional interest was movement in the correct direction for the second object, defined as movement at least 15 cm toward the second object. Comparisons again revealed a transition from 18 to 24 months of

Table 1. Descriptive Statistics[a] and Hiding–Search Correlations in the Two-Object Task

	First Error (cm)		Second Error (cm)		Correct Direction		Return To First Location	
Age (months)	*n*	*M (SD)*	*n*	*M (SD)*	*n*	*M (SD)*	*n*	*M (SD)*
18	23	11.37 (2.91)	21	37.36 (7.55)	21	.28 (.26)	21	.71 (.25)
24	29	11.91 (4.35)	29	24.82 (11.91)	28	.76 (.24)	29	.23 (.25)
30	25	11.56 (4.87)	25	23.33 (12.17)	24	.83 (.18)	23	.12 (.18)
36	21	10.50 (2.87)	20	20.96 (10.92)	21	.79 (.23)	22	.15 (.20)
42	18	9.03 (1.89)	19	16.87 (6.51)	18	.94 (.11)	18	.06 (.11)

	First Search Correlations		Second Search Correlations	
Age (months)	*Pearson's r*	*Comparison to 18 months (p)*	*Pearson's r*	*Comparison to 18 months (p)*
18	.85	–	.21	–
24	.82	.48	.64	<.001
30	.77	.11	.70	<.001
36	.87	.62	.66	<.001
42	.95	<.001	.83	<.001

[a]In this and in subsequent tables, values for *n* represent sample size after removal of outliers (defined as children with mean search errors that were 2 or more standard deviations from the group mean). In this table and in Table 2, means for ''correct side'' were computed from the proportion of trials that each child searched in the correct direction for the second object. Means for ''return to first location'' were computed from the proportion of trials that each child exhibited that behavior.

age ($p < .001$), but older groups all performed comparably to each other, with the possible exception of the comparison between the 24- and 42-month-olds ($p = .063$). On average, the 18-month-olds searched in the correct direction on 28% of the trials, in contrast with 82% for the older children. We also examined the frequency with which children searched within 15 cm of the first location. The youngest children showed a strong tendency to do so (on an average of 71% of the trials) compared to older children (15%), who did not differ reliably from each other. (Although, again, the comparison between the 24- and 42-month-olds approached significance, $p = .08$).

A final set of analyses was conducted in order to examine whether the children's searches systematically varied with hiding location. A Pearson's r was computed for the first- and second-object searches for each age group and for each of the four trials separately. First searches were highly correlated with hiding location (p's $< .001$). However, for the 18-month-olds only, second searches were *not* correlated with hiding locations (p's $> .10$). Of the 16 correlations for the older groups, there were only 2 exceptions: the correlations for trial 4 for the 24-month-olds and trial 3 for the 36-month-olds (p's $> .10$). Correlations were then combined across trials for the first and second searches in order to simplify age comparisons.[2] The18-month-olds differed only from 42-month-olds in first-object searches, but differed from each group in second-object searches. These results indicate a transition from 18 to 24 months from random to nonrandom searching for a second object.

The relatively poor performance of the 18-month-olds in the search for multiple objects could have been due to several factors. First, these children may have been unable to represent two locations simultaneously. Another possibility is that memory for the second location may have decayed during the first search. In fact, the delay before the children returned for the second object was somewhat longer for the 18-month-olds than for the 24-month-olds. However, the magnitude of the differ-

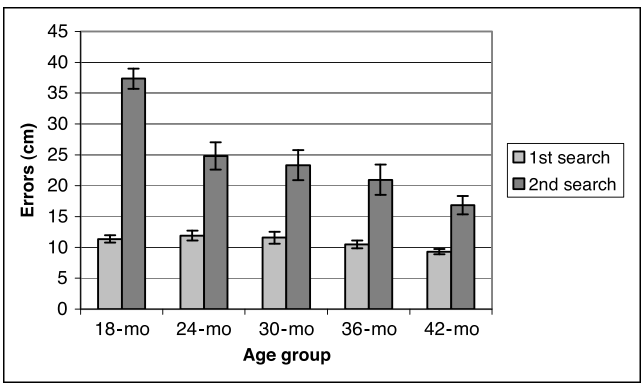

Figure 1. Two-location task: first and second search errors.

ence was small (the mean delays for each age group differed by less than 10 sec), and 18-month-olds' second searches were unrelated to the length of this delay. Yet another possibility is that the act of retrieving the first object from the sand altered memory for the second location. This latter possibility is supported by the fact that the children often searched near the first location when searching for the second object. The three explanations are not mutually exclusive, however, and all three suggest weak or absent memory for the second location. Consistent with this argument is recent evidence that continuing to search in a previous location is related to cognitive demands (in this case, demands on memory) rather than to age and is a behavior elicited even in older children in certain contexts (Zelazo, Reznik, & Spinazzola, 1998).

Relational Task

After training on the spatial relation, each child participated in eight trials during which the experimenter hid the two different objects (while the child was not looking) in the sandbox, then revealed one and asked the child to search for the other.

The primary data of interest were the percentages of children at various ages that were able to master the task. Notably, there was an unusually high percentage (61%) of 18-month-olds who were unable to do so. To "master the task," children had to complete the fixed amount of training and then provide data on at least four of the eight test trials. This percentage contrasts with 15% of the 24-month-olds and 8% of the oldest three groups in the same task and with 29% of the 18-month olds in the two-location task. Because children as young as 16 months have willingly performed searches in the same experimental setting (Huttenlocher et al., 1994), shyness or reluctance seems an unlikely explanation. Rather, the comparatively high exclusion rate in the relational study was likely due to the lack of knowledge about the location of the requested object.

The 18-month-olds who did provide useable data did not differ from older children in either mean search errors or in the proportion of times that they searched on the correct side of the visible object (see Table 2). Examination of correlations between hiding and search locations revealed that, for each age group, searching was significantly correlated with hiding location on about half of the trials, and age groups did not differ in correlations that were combined across trials. It is doubtful, however, that these results indicate no development after 18 months, given that many of the youngest children appeared unable to learn the relation during the training. Furthermore, it is doubtful that the minority of 18-month-olds who did learn the relation used it consistently, because these children completed on average significantly fewer of the eight trials than did any older group. This difference was due to the 18-month-olds' failure to search on some of the trials rather than an inability to complete all eight trials, indicating an inconsistent use of the spatial relation rather than fatigue with the task. Clearly, the ability to learn the spatial relation and/or to use that relation in effective searching was more difficult for the youngest children. Like amnesic patients, 18-month-olds may need more training to acquire useable knowledge of the relation between a cue and a spatial response.

Retention Task

This task involved one trial during which the experimenter hid an object in the sandbox, took the child out of the room for two minutes, and then brought the child back into the room to find the object. With the hypothesis that the 18-month-olds would differ from the older children, we performed a contrast analysis using four orthogonal contrasts[3]: one contrast that compared the 18-month-olds to the older children (the primary contrast of interest); one that compared the 42-month-olds to the 36-, 30-, and 24-month-olds; one that compared the 36-month-olds to the 30- and 24-month-olds; and

Table 2. Descriptive Statistics and Hiding–Search Correlations in the Relational Task

	Error (cm)		*Correct Direction*		*Search Correlations*	
Age (months)	*n*	*M (SD)*	*n*	*M (SD)*	*Pearson's r*	*Comparison to 18 months*[a] (*p*)
18	20[b]	22.08 (7.37)	20	0.87 (0.16)	.38	–
24	25	23.57 (6.12)	26	0.91 (0.10)	.42	.80
30	25	22.34 (8.20)	25	0.89 (0.14)	.48	.30
36	22	21.05 (7.45)	21	0.90 (0.10)	.45	.48
42	21	21.99 (7.62)	20	0.89 (0.09)	.34	.70

[a]These values are difficult to interpret because the reasons for dropout in the youngest group were likely related to the dependent variable of search location.

[b]Because there was such a high dropout rate for the 18-month-olds, it was necessary to run approximately twice as many 18-month-olds as older children in order to obtain a comparable sample size.

one that compared the 30-month-olds to the 24-month-olds. Only the first contrast (pitting the 18-month-olds against the older groups) approached significance [$t(33.08) = -1.53$, $p = .063$, one-tailed; for the remaining contrasts, p's $> .10$]. Furthermore, the correlation between hiding and search locations was highly reliable for all age groups (p's $< .01$) except the 18-month-olds ($p = .12$). A contrast analysis performed on these effect sizes again revealed that the youngest group differed from the older groups ($z = 1.89$, $p = .029$, one-tailed) (see Table 3 for the results on this task).

DISCUSSION

The present data involved examination of development between 18 and 24 months of age in three spatial tasks that each involved a crucial component of mature spatial competence. Additionally, a present consideration is what the behavioral data may indicate about underlying brain functioning.

In the two-location task, children observed as two objects were hidden simultaneously in a sandbox. When asked to retrieve the objects, there was no improvement in accuracy in the retrieval of the first chosen object but marked improvement from 18 to 24 months in retrieval of the remaining object. Importantly, this finding cannot be accounted for by preference for one object over the other, because the objects on each trial were identical. Another alternative explanation for the age differences is that the youngest children's performance was somehow adversely affected by removal of the first toy by the experimenter (see Methods section). In support of this possibility, Overman, Bachevalier, Sewell, and Drew (1993) found that children younger than 22 months spent significantly more time visually exploring an object than did older children. However, it is unlikely that frustration over removal of the first toy hindered performance of the 18-month-olds in the present work, because these children willingly conducted searches for the second object. Therefore, worse performance regarding retrieval of the second object was most likely due to the memory demands of the task (i.e., the simultaneous spatial representation of and search for two objects).

Table 3. Descriptive Statistics and Hiding–Search Correlations in the Retention Task

		Error (cm)	*Search Correlations*	
Age (months)	*n*	*M (SD)*	*Pearson's r*	*Comparison to 18-mo*[a] *(p)*
18	26	30.96 (22.51)	.31	–
24	25	25.40 (15.79)	.64	.072
30	23	24.08 (19.79)	.52	.20
36	22	26.54 (15.91)	.57	.15
42	19	18.85 (13.56)	.80	.0084

[a]Due to the hypothesis that there would be improvement after 18 months, and due to the reduction of power in this single-trial task, reported p values are one-tailed.

In contrast to the two-location task, in which development was illustrated by improvement in search accuracy, in the relational task a developmental trend was revealed by age differences in the ability to perform the task at all. In this task, children were given a fixed amount of training to learn a spatial relation between two objects and then were asked to search for an object when the experimenter revealed one of the objects. The large proportion of the 18-month-olds who did not provide data, in combination with the sporadic performance of the remaining children in this age group, suggests that the training was not sufficient for these children to learn the relation and to use it effectively. Future work might use as the dependent variable the number of training trials necessary to reach some criterion of performance.

In the retention task, children were asked to search for a single object after a delay, during which children were removed from the hiding context. Again, 18-month-olds performed significantly worse than older children, with less dramatic differences among children 24 months and older. As noted in the Methods section, this task involved a single-trial due to the practical difficulties of taking very young children in and out of a potentially very interesting playroom. Yet, even with a single trial there was still clear improvement from 18 to 24 months of age in search accuracy, as indicated by the correlations between hiding and search locations (which were .31 and .64 for 18- and 24-month-olds, respectively). These data are of particular interest, given earlier abilities to remember information across delays much longer than the 2-min delay used here, such as in visual paired comparison (e.g., Fagan, 1990) and elicited imitation (e.g., Mandler & McDonough, 1995). The present data suggest that an important limitation of early memory may be long-term memory of location.

In summary, there was clear improvement from 18 to 24 months of age in these three tasks, with only gradual improvement in later years. Combined with evidence that place learning undergoes dramatic improvement during this time (Newcombe et al., 1998), these findings point to a time in development when spatial functioning is changing rather dramatically. Additionally, due to the preliminary evidence that these tasks rely on hippocampus and the wealth of evidence that place learning is dependent on hippocampus (discussed in the Introduction), this brain substrate is a viable candidate for underlying neural change.

One should consider whether changes in hippocampal functioning are part of medial temporal lobe development more generally. For instance, Bohbot et al. (1998) found that the right parahippocampus also seems to play a critical role in location memory. Other possibilities for development include entorhinal and perirhinal cortical areas. In fact, recent data from Nemanic, Alvarado, and Bachevalier (2004) indicate that perirhinal cortex, but not the hippocampus itself, is critically involved in performance on the delayed-non-matching-to-sample (DNMS) task[4] (see also, Pascalis & Bachevalier, 1999), a task in which human infants show marked improvement around 20–22 months of age (Diamond, Towle, & Boyer, 1994; Diamond, 1990; Overman, 1990).[5] Although the data on the development of DNMS performance are at present inconclusive in terms of what they reveal about brain development, it is very possible that infants' eventual success is related to changes in cortical structures that surround the hippocampus. Further investigation of the neural correlates of nonspatial tasks (such as DNMS) and spatial tasks (such as those employed here) is needed to understand of the nature of behavioral age trends and the extent of development in the medial temporal area. Additionally, a deeper understanding of the neural substrates of these tasks is needed to improve the inferences we can make about individual differences in performance. Such research will be critical to furthering our knowledge of the biological mechanisms involved in the vast cognitive changes that occur early in life.

METHODS

All tasks were completed under the following conditions. The parent and child entered a room where curtains hung from the ceiling, creating an enclosure approximately 2 m by 2 m and devoid of landmarks. Centrally located in the enclosed space was a sandbox measuring 41 × 152 × 36 cm. Each parent and child remained on one side of the sandbox while the experimenter hid objects from the other side. There were decorative markings on one side of the sandbox that divided it into sections of 15 cm, marking nine possible hiding locations across its length axis. These intervals were further divided into six equal intervals in order to aid in the coding of searches (see Figure 2).

We used a video camera to record the parent, child, and experimenter. The video camera protruded through the curtain approximately 1.5 m off the floor and from the side opposite to the child's location. Before the trials began, the child experienced a period of familiarization with the sandbox during which the experimenter hid single objects and immediately asked the child to retrieve them. During both the familiarization and subsequent test trials, the experimenter smoothed the sand over completely to remove any indications of the hidden objects' locations. Blind observers could not determine the placement of the objects.

During test trials, after asking the child to search, the experimenter moved out of the way of the video camera so that the child's behavior could be recorded in its entirety. Observers later scored the child's searches from the videotape, with a "search" defined as the location of the child's first touch of the sand (judged by one of the markings on the sandbox). An error score was defined as the distance (along the length axis) between the correct location and the child's search location.

Figure 2. Picture taken during the training portion of the relational task. Parent and child sat on one side of the sandbox, while the experimenter sat on the other side that had the demarcation lines and a strip of paper noting the hiding locations for each trial. Here the experimenter has hidden the two objects in front of the child, revealed one, and then asked the child to dig the other object out of the sand.

In order to expedite the tasks and, thus, avoid fatigue in the children, once a child had touched the sand and searched unsuccessfully for a few seconds (but never longer than 10 sec), the experimenter intervened and revealed the target object. However, the experimenter allowed the child to pull the object out of the sand.

In all tasks, 20% of the children were scored by two independent observers; reliabilities were high (all Pearson's r's > .95).

Two-Location Task

Participants

Children were drawn from suburban regions of Philadelphia. There were five age groups who participated in each task: 18-, 24-, 30-, 36-, and 42-month-olds. The range for each group included children up to 2 months older than the specified age. For the two-object task there were 18-month-olds (n = 23, 13 males and 10 females, range = 18.16 to 20.55 months, M = 19.38), 24-month-olds (n = 30, 15 males and 15 females, range = 24.16 to 26.77 months, M = 25.22), 30-month-olds (n = 25, 14 males and 11 females, range = 29.90 to 33.27 months, M = 31.74), 36-month-olds (n = 22, 9 males and 13 females, range = 35.45 to 39.19 months, M = 37.31), and 42-month-olds (n = 20, 10 males and 10 females, range = 41.80 to 45.13 months, M = 43.23).

Design and Procedures

The child watched as two identical small toys (that were roughly 5 × 5 × 5 cm in dimensions for all tasks) were hidden one at a time 45 cm apart in the sandbox. Each child participated in four trials, with hiding locations changing across trials. The objects changed across trials but were always identical within a trial. After turning around to break eye gaze toward the locations, the child was immediately allowed to search for the objects without any direction by the experimenter other than a request of "can you find the toys." After the child retrieved one object from the sand, the experimenter took the object from the child and then continued with "can you find the other one." Each child received a mean error score, calculated from the errors on all completed trials.

Relational Task

Participants

The following groups of children participated in the relational task: 18-month-olds (n = 20, 9 males and 11 females, range = 18.45 to 20.52 months, M = 19.50), 24-month-olds (n = 27, 13 males and 14 females, range = 24.10 to 26.77 months, M = 25.24), 30-month-olds (n = 26, 15 males and 11 females, range = 29.71 to 33.27 months, M = 31.66), 36-month-olds (n = 22, 10 males and 12 females, range = 35.15 to 39.19 months, M = 37.31), and 42-month-olds (n = 21, 11 males and 10 females, range = 41.70 to 45.39 months, M = 43.33).

Design and Procedures

All children in the relational task were given the same amount of training on the following spatial relation: that two different objects would always be hidden in the sand 45 cm apart on the same side relative to each other even in changing locations across the sandbox. To teach the relation, the experimenter hid both objects in front of the child and revealed each object one at a time. Using the same locations, the experimenter repeated the procedure but revealed the objects in the opposite order. The experimenter then hid the objects two more times in the same locations, but after revealing an object encouraged the child to find the other object (see Figure 2). The whole procedure was then repeated in the same manner but at the other end of the sandbox. In total, the child had observed the objects being hidden and revealed eight times, actively participating in revealing the objects four times. No child was given extra training.

During the test trials that followed the training, the child was no longer allowed to watch the experimenter hide the objects. On each of eight test trials, the experimenter hid the objects (in all possible location pairs except the two used during training) while the child was not watching, and then revealed one object (which object varied randomly) and asked the child to retrieve the other object. Each child received a mean error score, calculated from the errors on all completed trials.

Retention Task

Participants

The following groups of children were included in this task: 18-month-olds (n = 27, 15 boys and 12 girls, range = 18.02 to 20.55 months, M = 19.16), 24-month-olds (n = 27, 14 boys and 13 girls, range = 24.16 to 26.77 months, M = 25.28), 30-month-olds (n = 24, 13 boys and 11 girls, range = 29.90 to 33.27 months, M = 31.71), 36-month-olds (n = 22, 9 boys and 13 girls, range = 35.45 to 39.19 months, M = 37.33), and 42-month-olds (n = 20, 10 boys and 10 girls, range = 41.80 to 45.13 months, M = 43.23).

Design and Procedures

After a familiarization period with the sandbox, the child performed the following single-trial task: He or she observed an experimenter hide an object in the sandbox, was taken by the experimenter into a playroom for 120 sec to hear a story, and then was brought back to find the object. A single trial was used due to the difficulty of repeatedly removing the children from the playroom in order to return to the experimental room.

Acknowledgments

This research was funded by the National Science Foundation (grant # BCS-9905098). We thank Carly Slutzky and Meredith Meyer for their help with data collection, as well as all of the participating families from the Temple University Infant Laboratory.

Reprint requests should be sent to Julia Sluzenski or Nora S. Newcombe, Temple University, or via e-mail: julia.sluzenski@temple.edu, newcombe@temple.edu.

Notes

1. Unless otherwise specified, all p values reported in this article are two-tailed.
2. Here and in the relational task, combination of correlations across trials involved transforming the Pearson's r values to Fisher's z values, finding the mean of the Fisher's z values, then transforming this mean into a Pearson's r, with degrees of freedom calculated from the sum of the sample sizes for the original r values.
3. A more focused test was used not only because of the specific hypothesis that 18-month-olds would perform worse than older groups, but also because of the single-trial nature of the task (i.e., a powerful test was necessary to detect differences).
4. In this task, a subject displaces an object and retrieves a hidden food reward. The object is removed, and after a brief delay of 5 to 10 sec, the same object is shown together with a novel object. The subject must choose the novel object to

receive another reward. After the subject demonstrates proficiency on the task, indicated by having reached some learning criterion, it is possible to test the response using longer delays.

5. Success on DNMS can be reached much earlier by human infants when certain cognitive demands are removed (Diamond, Churchland, Cruess, & Kirkham, 1999; Diamond et al., 1994; Diamond, Lee, & Hayden, 2003).

REFERENCES

Angeli, S. J., Murray, E. A., & Mishkin, M. (1993). Hippocampectomized monkeys can remember one place but not two. *Neuropsychologia, 31,* 1021–1030.

Bohbot, V. D., Kalina, M., Stepankova, K., Spackova, N., Petrides, M., & Nadel, L. (1998). Spatial memory deficits in patients with lesions to the right hippocampus and to the right parahippocampal cortex. *Neuropsychologia, 36,* 1217–1238.

Bushnell, E. W., McKenzie, B. E., Lawrence, D. A., & Connell, S. (1995). The spatial coding strategies of one-year-old infants in a locomotor search task. *Child Development, 66,* 937–958.

Carver, L. J., & Bauer, P. J. (1999). When the event is more than the sum of its parts: 9-month-olds' long-term ordered recall. *Memory, 7,* 147–174.

Daum, I., Schugens, M. M., Channon, S., Polkey, C. E., Gray, J. A. (1991). T-maze discrimination and reversal learning after unilateral temporal or frontal lobe lesions in man. *Cortex, 27,* 613–622.

DeLoache, J. D., & Brown, A. L. (1983). Very young children's memory for the location of objects in a large-scale environment. *Child Development, 54,* 888–897.

Diamond, A. (1990). Rate of maturation of the hippocampus and the developmental progression of children's performance on the delayed nonmatching-to-sample and visual paired comparison tasks. *Annals of the New York Academy of Sciences, 608,* 394–426.

Diamond, A., Churchland, A., Cruess, L., & Kirkham, N. Z. (1999). Early developments in the ability to understand the relation between stimulus and reward. *Developmental Psychology, 35,* 1507–1517.

Diamond, A., Lee, E. Y., & Hayden, M. (2003). Early success in using the relation between stimuli and rewards to deduce an abstract rule: Perceived physical connection is key. *Developmental Psychology, 39,* 825–847.

Diamond, A., Towle, C., & Boyer, K. (1994). Young children's performance on a task sensitive to the memory functions of the medial temporal lobe in adults—the delayed nonmatching-to-sample task—reveals problems that are due to nonmemory-related demands. *Behavioral Neuroscience, 108,* 659–680.

Fagan, J. F., III (1990). The paired-comparison paradigm and infant intelligence. In A. Diamond (Ed.), *Annals of the New York Academy of Sciences: Vol. 608. The development and neural bases of higher cognitive functions* (pp. 337–364). New York: New York Academy of Sciences.

Hermer, L., & Spelke, E. (1996). Modularity and development: The case of spatial reorientation. *Cognition, 61,* 195–232.

Hermer, L., & Spelke, E. S. (1994). A geometric process for spatial reorientation in young children. *Nature, 370,* 57–59.

Holdstock, J. S. (2000). A comparison of egocentric and allocentric spatial memory in a patient with selective hippocampal damage. *Neuropsychologia, 38,* 410–425.

Huttenlocher, J., Newcombe, N., & Sandberg, E. H. (1994). The coding of spatial location in young children. *Cognitive Psychology, 27,* 115–147.

Jarrard, L. E. (1993). On the role of the hippocampus in learning and memory in the rat. *Behavioral and Neural Biology, 60,* 9–26.

Kesner, R. P., & Hopkins, R. O. (2001). Short-term memory for duration and distance in humans: Role of the hippocampus. *Neuropsychology, 15,* 58–68.

Kimble, D. P. (1963). The effects of bilateral hippocampal lesions in rats. *Journal of Comparative and Physiological Psychology, 56,* 273–283.

Learmonth, A. E., Nadel, L., & Newcombe, N. S. (2002). Children's use of landmarks: Implications for modularity theory. *Psychological Science, 13,* 337–341.

Learmonth, A. E., Newcombe, N. S., & Huttenlocher, J. (2001). Toddlers' use of metric information and landmarks to reorient. *Journal of Experimental Child Psychology, 80,* 225–244.

Lee, I., & Kesner, R. P. (2003). Differential roles of dorsal hippocampal subregions in spatial working memory with short versus intermediate delay. *Behavioral Neuroscience, 117,* 1044–1053.

Long, J. M., & Kesner, R. P. (1998). Effects of hippocampal and parietal cortex lesions on memory for egocentric distance and spatial location information in rats. *Behavioral Neuroscience, 112,* 480–495.

Maguire, E. A., Burgess, N., Donnett, J. G., Frith, C. D., Frackowiak, R., O'Keefe, J. (1998). Knowing where and getting there: A human navigation network. *Science, 280,* 921–924.

Maguire, E. A., Frackowiak, R. S., & Frith, C. D. (1996). Learning to find your way: A role for the human hippocampal formation. *Proceedings of the Royal Society of London—Series B: Biological Sciences, 263,* 1745–1750.

Maguire, E. A., Frackowiak, R. S. J., & Frith, C. D. (1997). Recalling routes around London: Activation of the right hippocampus in taxi drivers. *Journal of Neuroscience, 17,* 7103–7110.

Mandler, J. M., & McDonough, L. (1995). Long-term recall of event sequences in infancy. *Journal of Experimental Child Psychology, 59,* 457–474.

Marston, H. M., Everitt, B. J., & Robbins, T. W. (1993). Comparative effects of excitotoxic lesions of the hippocampus and septum/diagonal band on conditional visual discrimination and spatial learning. *Neuropsychologia, 31,* 1099–1118.

Morris, R. G., Garrud, P., Rawlins, J. N., & O'Keefe, J. (1982). Place navigation impaired in rats with hippocampal lesions. *Nature, 297,* 681–683.

Muller, R. U., Kubie, J. L., & Ranck, J. B., Jr. (1987). Spatial firing patterns of hippocampal complex-spike cells in a fixed environment. *Journal of Neuroscience, 7,* 1935–1950.

Myers, C. E., Hopkins, R. O., Kesner, R. P., Monti, L., & Gluck, M. A. (2000). Conditional spatial discrimination in humans with hypoxic brain injury. *Psychobiology, 28,* 275–282.

Nadel, L., & Zola-Morgan, S. (1984). Infantile amnesia: A neurobiological perspective. In M. Moscovitch (Ed.), *Infant memory: Its relation to normal and pathological memory in humans and other animals* (pp. 145–172). New York: Plenum Press.

Nemanic, S., Alvarado, M. C., & Bachevalier, J. (2004). The hippocampal/parahippocampal regions and recognition memory: Insights from visual paired comparison versus object-delayed nonmatching in monkeys. *Journal of Neuroscience, 24,* 2013–2026.

Newcombe, N., Huttenlocher, J., Drummey, A. B., & Wiley, J. G. (1998). The development of spatial location coding: Place learning and dead reckoning in the second and third years. *Cognitive Development, 13,* 185–200.

Newcombe, N., Huttenlocher, J., & Learmonth, A. (1999). Infants' coding of location in continuous space. *Infant Behavior and Development, 22,* 483–510.

O'Keefe, J. (1976). Place units in the hippocampus of the freely moving rat. *Experimental Neurology, 51,* 78–109.

O'Keefe, J., & Dostrovsky, J. (1971). The hippocampus as a spatial map: Preliminary evidence from unit activity in the freely moving rat. *Brain Research, 34,* 171–175.

O'Keefe, J., & Speakman, A. (1987). Single unit activity in the rat hippocampus during a spatial memory task. *Experimental Brain Research, 68,* 1–27.

Ono, T., Nakamura, K., Nishijo, H., & Eifuku, S. (1993). Monkey hippocampal neurons related to spatial and nonspatial functions. *Journal of Neurophysiology, 70,* 1516–1529.

Overman, W. H. (1990). Performance on traditional matching-to-sample, nonmatching-to-sample, and object discrimination tasks by 12- to 32-month-ols children: A developmental progression. *Annals of the New York Academy of Sciences, 608,* 365–393.

Overman, W. H., Bachevalier, J., Sewell, F., & Drew, J. (1993). A comparison of children's performance on two recognition memory tasks: Delayed nonmatch-to-sample versus visual paired-comparison. *Developmental Psychobiology, 26,* 345–357.

Parkinson, J. K., Murray, E. A., & Mishkin, M. (1988). A selective mnemonic role for the hippocampus in monkeys: Memory for the location of objects. *Journal of Neuroscience, 8,* 4159–4167.

Pascalis, O., & Bachevalier, J. (1999). Neonatal aspiration lesions of the hippocampal formation impair visual recognition memory when assessed by paired-comparison task but not by delayed nonmatching-to-sample task. *Hippocampus, 9,* 609–616.

Zelazo, P. D., Reznik, J. S., Spinazzola, J. (1998). Representational flexibility and response control in a multistep multilocation search task. *Developmental Psychology, 34,* 203–214.