

Working Memory in Infancy: Six-Month-Olds' Performance on Two Versions of the Oculomotor Delayed Response Task

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The capacity of 6-month-old infants to maintain information in working memory for several seconds was studied using two versions of an oculomotor delayed response task. Infants were presented with either a cue stimulus in a target location (Experiment 1), or an abstract, central stimulus (Experiment 2) which could be used to predict the peripheral location in which an attractive target stimulus subsequently appeared. Eye movements during delay periods from 600 to 5000 ms were recorded. The results indicated that infants maintained information about stimulus locations in working memory for 3-5 s. These results imply maturity of regions of the prefrontal cortex closely associated with a similar task used in neurophysiological and neuroimaging studies. © 1995 Academic Press, Inc.

Responding adaptively in a dynamic environment demands that organisms have the ability to store and use information to guide action over time scales ranging from seconds to months or years. Despite the central importance of memory capacities in accounting for performance in complex cognitive tasks in adults (Baddeley, 1986; Just & Carpenter, 1992), an adequate understanding of the emergence of memory in infancy and its relationship to adult capacities has proved elusive. Since improvements in

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memory may underlie central features of cognitive change in early infancy (Diamond, 1990; Goldman-Rakic, 1987; Piaget, 1954), the study of basic memory capacities in infants is of considerable interest.

While most developmentalists agree that the durability of infants' memory over time improves with age, specific estimates of its persistence at a given age vary widely. Rovee-Collier and colleagues have carried out some of the most systematic explorations of infants' memory for simple associations (see Rovee-Collier, 1993, for a review) using variations of the mobile conjugate reinforcement task. These studies have shown that the length of time that infants can retain simple associations increases from 6 to 8 days at 2 months of age (Enright, Rovee-Collier, Fagan, & Caniglia, 1983), to 3 weeks by 6 months of age (Rovee-Collier, 1993). Other experiments (Colombo, Mitchell, Coldren, & Atwater, 1990) indicate that young infants' mental representations may have much shorter periods of activation. When fixation of a visual target was paired with a simultaneous auditory reward, 3-month-olds could remember either a specific pattern independent of its location or a specific location independent of the pattern over short inter-trial delays, but they failed to remember either association after a 5-min interval. Older infants had no difficulty remembering the association after the delay (Colombo et al., 1990). Similarly, Diamond and colleagues (1985, 1990; Diamond & Doar, 1989) have found that infants younger than $7\frac{1}{2}$ months fail to retrieve hidden objects if there is any delay between hiding and retrieval. However, infants older than $7\frac{1}{2}$ months begin to succeed in the task with delays of 2 to 3 s, and the length of delay that infants can withstand increases over the next several months. By 12 months, infants can retrieve hidden objects after delays of 10 s or more.

These varying estimates of infants' capacities to represent information over time stem, in part, from differences in the demands of the tasks and may reflect the influence of different memory processes. The conjugate reinforcement task appears to tap simple associative memory: Infants learn an association between foot kicking and the simultaneous movement of a particular mobile which serves as the reward. In contrast, the object search paradigm has several critical features that distinguish its memory demands from other tasks which involve either simple short-term or associative memory: Infants must maintain information about the toy's location in an active form over short delays in order to receive a reward, the specific hiding location frequently changes, and success requires the infant to inhibit responses to competing locations (see Diamond, 1990, for a discussion). These features—active representation for subsequent action, trial-to-trial updating of information, and inhibition—make the object search task similar to those which tap working memory capacities (Baddeley, 1986) in adults. In fact, Diamond (1985, 1990) has argued that developmental changes in infants' object search performance from $7\frac{1}{2}$ to 12 months reflect, in part, gradual improvements in working memory and response inhibition capacities.

While object search performance may index the emergence of working memory and response inhibition abilities late in the first year of life, other evidence (e.g., Canfield & Haith, 1991; Colombo et al., 1990; Haith, 1993; Haith, Hazan & Goodman, 1988) suggests that rudimentary capacities to represent dynamic spatiotemporal information may emerge even earlier. Haith and colleagues (see Haith, 1993, for a review) have shown that infants as young as $3\frac{1}{2}$ months of age can learn to anticipate shifts in the position of stimuli which appear in regular sequences in the visual field. The information which infants use to make predictive eye movements may consist of abstract stimulus characteristics, such as the number of patterns viewed independent of their shape, and successful anticipation requires infants to note regularities in the sequence of pattern presentation that span delays of several seconds (Canfield & Haith, 1991). While the specific processes which permit infants to perform Haith's visual expectation tasks are not fully understood, one interpretation of these results is that memory for representing and maintaining information about future events over short delays emerges early in life. Clearly, more sensitive measures of infants' memory capacities would help to determine more precisely when these abilities emerge and how they change with time.

Understanding the neural basis of infants' memory capacities may help to answer these behavioral questions. Since the brain undergoes dramatic change in the first several months of life (see Johnson, 1993, for a review), development in neural structure or connectivity may have a direct impact on what infants can remember. For example, developmental changes in infants' object search performance from $7\frac{1}{2}$ to 12 months have been argued to reflect maturation of the prefrontal regions of the cortex thought to be crucial for working memory and response inhibition (Diamond, 1985, 1990). Similarly, theorizing about the functional components of adult memory continues to be influenced by the types of dissociations produced by injury to different parts of the brain (see Squire, 1992). Consequently, a better understanding of the neural basis of infants' memory capacities and their patterns of development may ultimately shed light on issues concerning the nature and mechanisms that underlie memory abilities in the adult.

Goldman-Rakic and colleagues have used a visuospatial memory task, the oculomotor delayed response (ODR) task, to study the neural basis of working memory in monkeys (Funahashi, Bruce, & Goldman-Rakic, 1989, 1990; Funahashi, Chafee, & Goldman-Rakic, 1993; Wilson, Scalaidhe, & Goldman-Rakic, 1993) and which others have used with human adults (Jonides, Smith, Koeppe, Awh, & Minoshima, 1993; Luciana, Depue, Arbisi, & Leon, 1989). In the basic ODR task, the subject is exposed to a brief visual cue stimulus in one of several positions in the periphery while viewing a fixation stimulus in a central location. The subject is trained not to respond to this cue, but rather to wait with eyes fixated at center until the fixation stimulus goes off. At this point, the subject is supposed to make a

saccade to the location that was cued several seconds earlier. The error rates of subjects can be measured in relation to the length of the delay between cue and fixation offset (Luciana et al., 1989). The task requires the active representation of the cued location during short delays, involves trial-to-trial changes in the location to be remembered, and requires that reflexive responses to the cue be inhibited during the delay, making its memory demands similar to the object search task and others thought to tap working memory. The ODR task does not require verbal instructions or responses, however, making it suitable for studies with monkeys who have been suitably trained or, as we demonstrate in this paper, human infants.

Single cell recordings from regions of the prefrontal cortex and frontal eye fields in rhesus monkeys performing this task have demonstrated the existence of populations of cells which appear to maintain information about cued spatial locations (Funahashi et al., 1989, 1990) and specific object characteristics (Wilson et al., 1993) during delays of up to 6 s. These results have been confirmed in a PET study on human subjects (Jonides et al., 1993). Further evidence (Funahashi et al., 1993) suggests not only that neurons in the prefrontal cortex maintain a representation of the spatial location where the saccade is to be made, but that some of them also specifically inhibit eye movements to the cued location during the delay period.

Since the ODR task was devised to assess working memory in nonverbal subjects, the present experiments were conducted to see if variants of the same procedure could be applied to human infants. If infants prove successful in these tasks, then the ODR paradigm offers the opportunity to study the ontogeny of working memory in the first few months of life. In addition, the substantial body of evidence relating the oculomotor delayed response task to the activity of specific parts of the prefrontal cortex suggests that it might serve as a "marker task" (Johnson & Gilmore, in press) to assess the functional maturity of this region of the brain.

In the first experiment reported, we presented infants with a brief stimulus in one of two possible spatial locations which indicated the spatial location for a subsequent saccade. In the second experiment, we presented an abstract stimulus in the central location which could be used to predict the appropriate peripheral location for a target that appeared after a delay. Unlike studies with monkeys, where liquid rewards were used to reinforce the delayed saccades, the current experiments presented dynamic and colorful target stimuli as a reward at the end of each trial.

EXPERIMENT 1

Method

Subjects

Fifteen healthy, full-term 6-month-old infants (nine female and six male) of varied ethnic backgrounds were recruited for the study via newspaper announcements and word of mouth referrals. Infants ranged in age from 182

to 197 days ($M = 187.6$). Five additional infants were tested but excluded from these analyses because they showed a highly significant bias to look toward one particular side ($p < .01$) regardless of trial type.

Design and Procedure

Testing was conducted in a single session in the laboratory. Infants were placed in an infant seat 55 cm from the center of three 12-inch color computer monitors which were controlled by a Macintosh IIfx computer. Each infant was presented with 36 trials in a fixed pseudorandom presentation sequence; all trial types were presented in a balanced fashion within each of three blocks of 12 trials. Each trial began with the presentation of an attractor/fixation display on the central screen. The display consisted of one of three repeating sequences of multicolored, abstract geometric shapes which subtended a maximum of 5° of visual angle. Each display was accompanied by a randomly generated sequence of auditory tones. The stimulus served to attract the infant's attention to the central screen and to keep the infant's attention focused at that location until the subject made a saccade away from the screen some time later. The experimenter could observe the infant by means of a video camera mounted above the display screens. When the experimenter had determined that the infant was looking at the attractor pattern, the experimenter pressed a key to begin the trial. The key press initiated the presentation of a cue stimulus on one of the two side screens (29° to the left or right of the center of the attractor stimulus). The cue was a blue equilateral triangle, 3° in width, which appeared for 150 ms. The attractor stimulus remained on during the presentation of the cue.

600-ms trials. Fifty milliseconds following the offset of the cue, the attractor stimulus was extinguished and a 400-ms interstimulus interval began before the presentation of identical target stimuli on both the left and right screens (29° to the right and left of the center of the attractor stimulus). The stimulus onset asynchrony (SOA) between cue onset and target onset was 600 ms. The target stimulus consisted of a dynamic, multicolored, rotating, cogwheel shape, which previous studies had shown to be highly attractive to infants of this age. When the infant shifted gaze from the central screen toward one of the two side screens, the experimenter pressed a key to terminate the trial. The computer began the next trial with the presentation of the central attractor. Figure 1 shows a schematic of the typical presentation sequence.

3000- and 5000-ms trials. These trials were identical to the 600-ms trials except that the SOA between cue onset and target onset was 3000 or 5000 ms. The attractor stimulus remained on throughout the SOA until 400 ms prior to target onset. If infants broke fixation prior to target onset, the trial was kept running until after the targets had appeared.

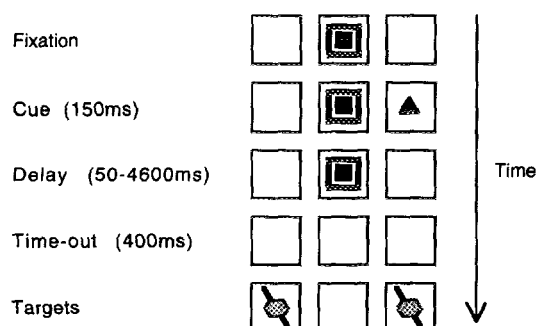


FIG. 1. Schematic showing typical stimulus presentation sequence during the spatial ODR study (Experiment 1). Each box represents one of the three computer screens.

Data Scoring

Video tapes were analyzed on a frame by frame basis by trained coders for whom intercoder reliability was high ($\kappa = 0.85$). Coders recorded the time (in frames) of the first eye movement away from the central fixation point and the direction of the eye movement. Valid trials were those in which infants were fixated centrally throughout the cue presentation and made an eye movement in the direction of either the left- or the right-hand computer screen, as judged by the coder. Valid eye movements were further sorted into one of three categories:

Cue-driven responses. Saccades that began prior to 800 ms following cue onset were classified as cue-driven. Eye movements at a latency of less than 800 ms are within two standard deviations of the mean reaction time of 529 ms ($SE = 37$) observed in 6-month-old subjects who were presented with an attractive target stimulus at the same eccentricity as used in the current experiment (Johnson, 1994) while maintaining fixation at a central location. Evidence from Johnson, Posner, and Rothbart (1991) provides support for this classification. Johnson et al. (1991) showed that by 4 months of age, infants are reliably able to move their eyes away from an attractive central stimulus to foveate a peripheral target with minimal delay. Thus, we assumed that 6-month-old subjects in the current experiment were capable of disengaging gaze from the central attractor stimulus without difficulty.

Anticipatory responses. Saccades that began between 800 ms following cue onset and 200 ms following target onset were classified as anticipatory responses. Looks occurring prior to 200 ms following the onset of one stimulus are commonly considered (e.g., Haith et al., 1988; Johnson et al., 1991) to be responses to a previous stimulus since the mean reaction time for eye movement responses in infants of this age is much larger. Anticipatory responses to the cued location in the absence of any stimulus at that location were considered analogous to the eye movements made by monkeys in the ODR task. In both cases, subjects broke central fixation to make

an eye movement to a previously cued location where no stimulus was currently present.

Target-driven responses. Eye movements that began more than 200 ms following target onset were classified as target-driven.

Invalid trials. Trials for an individual infant were classified as invalid if the infant was not fixated centrally during the cue stimulus or looked away from the experimental apparatus during the delay period. Twenty-four percent ($n = 132$) of the total trials pooled across infants ($n = 540$) were classified as invalid. The percentage of discarded trials was lower in the 600-ms delay (14%) condition but nearly identical in the 3000-ms (29.4%) and 5000-ms (30%) delay conditions.

Pooling of responses. The data from individual subjects were pooled in order to increase the size of the sample in each of the time periods of interest and to increase the sensitivity of the analysis. The number of anticipatory eye movements generated by a single subject in any given time period was too small for accurate estimation of individual subject preferences over time. Moreover, analytical methods for categorical responses are far less reliable with small sample sizes. Without pooling, the relatively small number of data points for any given subject in a particular time period would have resulted in less sensitive estimates of cue preference for the sample as a whole. Finally, as the results indicate, every subject but one contributed data to each type of eye movement. The net effect of response pooling was to bias the sample toward subjects who responded more frequently.

Results

The total valid eye movements across subjects were pooled, and the proportion of valid eye movements that were directed toward the cued location vs the opposite location computed. Table 1 summarizes the proportion of total valid eye movements which were directed toward the cued location pooled across all subjects in the experiment.

Cue-Driven Responses

All 15 subjects contributed cue-driven responses, and when their data were pooled, 29% ($n = 121$) of the total valid trials ($n = 408$) were classified as cue-driven. Strong preferences for the cued location relative to the uncued location were observed at every SOA: 600 ms ($\chi^2(1, n = 68) = 54.72, p < .01$),¹ 3000 ms ($\chi^2(1, n = 31) = 21.81, p < .01$), and 5000 ms ($\chi^2(1, n = 22) = 13.14, p < .01$). The proportion of responses in the direction of the cue when cue-driven eye movements from all delays are pooled was also significant ($\chi^2(1, n = 121) = 92.86, p < .01$).

¹ All reported χ^2 values used the Yates-corrected Pearson statistic to compensate for the single degree of freedom.

TABLE 1
Proportion of Valid Eye Movements to Cued Location for Experiment 1

Cue/Target SOA (ms)	Response type		
	Cue-driven	Anticipatory	Target-driven
600	0.96**	^a	0.44
3000	0.94**	0.61	0.52
5000	0.91**	0.79**	0.36*
Pooled	0.94**	0.71**	0.4

Note. Pooled responses combine data from all SOAs.

^aCoding criteria precluded anticipatory responses from being recorded at the shortest SOA.

* $p < .05$.

** $p < .01$.

Anticipatory Responses

Fourteen of 15 subjects made anticipatory responses. For subjects who made two or more anticipatory responses ($n = 12$), an individual cue preference score was computed. The number of anticipatory looks each subject made toward the cued location was divided by the subject's total number of anticipatory responses to determine the cue preference score. The mean individual cue preference score of 0.71 ($SE = .08$) exceeded chance levels, $t(11) = 2.56$, $p < .03$.

When subjects' responses were pooled, 17% ($n = 68$) of the total valid trials were classified as anticipatory. No eye movements at the short SOA met the criteria for an anticipatory response since the time between cue and target onset was less than 800 ms.

Subjects had no information that indicated how long the delay period would last at the start of a given trial; consequently, anticipatory looks for both the 3000- and the 5000-ms delays should reflect the same underlying processes of memory and eye movement generation. When responses from the two delay conditions were grouped by time from cue onset, the proportion of looks to the cued location in each time period was found to be largely consistent. Therefore, data from both delay conditions were pooled in order to increase the power of the analysis. This analysis revealed a strong overall cue preference ($\chi^2(1, n = 68) = 10.72$, $p < .01$). Most of this effect was due to eye movements from the 5000-ms ($\chi^2(1, n = 43) = 13.4$, $p < .01$), not the 3000-ms ($\chi^2(1, n = 23) = 0.70$, ns), delay conditions.

In order to estimate the persistence of cue information over time, cue-driven and anticipatory eye movements were grouped into bins according to the time in seconds from cue onset associated with the start of the saccade. This analysis (see Fig. 2) showed that the proportion of looks to the cued location exceeded 0.5 in every time period prior to the target and was significantly above chance ($\chi^2(1, n = 16) = 5.06$, $p < .05$) for as long as 4–5.2 s following the cue presentation.

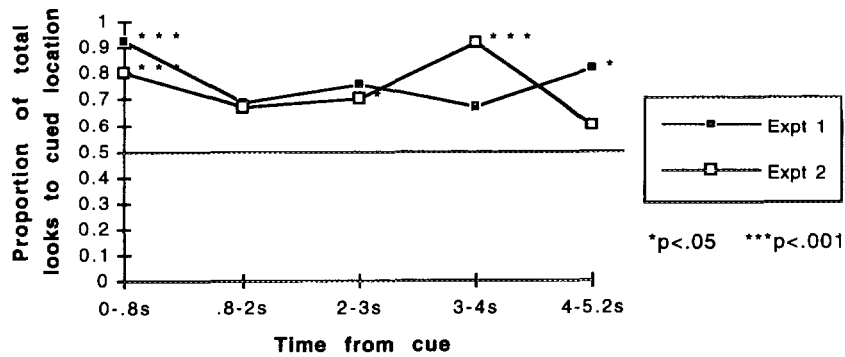


FIG. 2. Cue preferences plotted as a function of time from the cue for both the spatial (Experiment 1) and the pattern (Experiment 2) ODR studies.

Target-Driven Responses

All fifteen subjects made target-driven responses. Fifty-four percent of the total valid trials pooled across subjects ($n = 221$) were categorized as target-driven. No significant preferences were observed at the 600-ms SOA ($\chi^2(1, n = 87) = 1.15, ns$) or 3000-ms delay conditions ($\chi^2(1, n = 73) = 0.22, ns$). A marginally significant preference for the opposite (uncued) side was shown in the 5000-ms condition ($\chi^2(1, n = 61) = 4.20, p < .10$). Only 44% of responses pooled across the three delay conditions were directed toward the cued location, but the result was not significant ($\chi^2(1, n = 221) = 2.61, ns$).

Discussion

Subjects showed strong preferences to look to the cued location on those trials when they broke fixation between the cue presentation and the targets' appearance. While strong preferences to look toward the cue shortly after its presentation probably reflect the effects of the cue driving a saccade directly, the tendency to break fixation and look toward the cued location in the absence of a stimulus in that position persisted even at the longest delays preceding the onset of the targets. These responses appear to reflect the influence of a sustained internal representation of the cued location that persists for several seconds following the cue.

This sustained internal representation of the cued location during the delay period appears to be similar to the spatial working memory capacities thought to underlie monkeys' performance on the ODR task (Funahashi et al., 1989, 1990, 1993). Like monkeys in the ODR task, infants observed a peripheral cue stimulus which changed location from trial to trial, while maintaining fixation on a central display. Trained monkeys inhibited an eye movement toward the stimulus for periods of several seconds before making a saccade to the cued location in the absence of a specific target. Infants

frequently delayed making eye movements for several seconds, and on those trials when infants broke fixation prior to target onset, they showed a significant preference to look first toward the cued location, despite the fact that no target stimulus was present. The finding that infants showed a preference to look toward the cued location during the delay period suggests that they formed a representation of that spatial location. The fact that infants continued to look more often to the cued location despite delays of several seconds implies that infants have the capacity to maintain the representation of the cued location in an active form that can be used to plan eye movements several seconds later. While it is difficult to make comparisons between tasks, especially ones that involve different species, the similarity in memory demands between the infant and monkey versions of the ODR task suggests that similar memory processes may be involved in both.

There are several differences in the tasks that complicate the comparison, however. One is the motivation that subjects have to perform and the training they receive prior to the task. Monkeys are trained over lengthy periods to perform the task and receive a specific liquid reward when they look in the cued direction (Funahashi et al., 1989); adult human subjects receive verbal instructions to withhold their saccade until the central fixation point disappears (Jonides et al., 1993; Luciana et al., 1989). This contrasts with infant subjects who received no specific training in the task and whose motivation to perform may have been simply the interest derived from observing the attractive sequence of stimuli. Previous studies had shown that similar target stimuli were highly attractive to infants of this age (see Johnson et al., 1991), but the targets' appearance in the present experiment was contingent neither on infants inhibiting saccades to the cue nor on their looking toward the cued location during the delay. It is possible that the absence of training or instruction changed the way that infants performed the task in a way that makes comparison between infants and adult humans or monkeys *inadvisable*. Alternatively, one might argue that the particular instantiation of the ODR task used in Experiment 1 relies on similar memory processes, but the infant version underestimates subjects' abilities since there were no task instructions and no contingent rewards. Experiment 2 helps to resolve this point since in this study infants were specifically trained to associate a centrally presented cue with a specific target location.

A further difference between the tasks is that infants were presented with only two possible cue/target locations while monkeys and human adults have performed the task with eight or more target locations. In this sense, the infant task requires less absolute memory capacity than the adult version and might, therefore, tap different neural mechanisms. The use of only two target locations does not eliminate the involvement of DPFC in monkeys performing the ODR task (Wilson et al., 1993), but the effect of this manipulation in infants is unknown.

If we assume that working memory processes governed infants' anticipatory eye movements to the cue, why did the strong preferences for the cue dissipate once the targets appear? Experiment 1 presented targets in both locations in order to test whether memory for the cued location would bias the infants to look toward the cued side even when identical targets appear in both locations. Instead, it appears that the targets' appearance interfered with infants' memory for the cued location. The targets were larger, more colorful and dynamic than the simple cue stimulus, but the differences in visual salience do not explain why subjects tended to look to the side opposite the cue after target onset since the targets were identical in appearance.

One explanation of this result is that infants did not in fact make any inferences about the relationship between cue and target since they were not rewarded for doing so. When infants broke fixation prior to target onset, their internal representation of the cue guided the response. When identical bilateral targets appeared, they looked at either location randomly.

The alternative explanation concerns the effect of inhibition on subsequent eye movements. On more than half of the valid trials, infants withheld eye movements until the targets had appeared, a finding consistent with the interpretation that infants were able to actively inhibit eye movements to the cue. The argument that infants have difficulty in disengaging from the central attractor stimulus is unlikely since in previous studies involving similar stimuli and testing conditions, infants as young as 4 months of age readily disengaged from a central stimulus to orient toward a peripheral target (Johnson et al., 1991). If infants did, in fact, inhibit eye movements to the cued location during the delay period, then on trials where infants withheld eye movements until the targets appeared, the level of inhibition for that location was likely to be especially strong. This direction-specific inhibition might have suppressed gaze to the specific cued location. Thus, when targets appeared in both the cued and the uncued locations, the side where the cue appeared previously would have been more strongly inhibited than any other specific location. The stronger level of inhibition in the direction of the cue may have biased subjects to look to the opposite target, as the results from the 5000-ms delay condition suggest.

This interpretation is supported by the finding that on trials when subjects delayed responding until the targets appeared, subjects were slower to look toward the target that appeared in the cued location ($M = 481$ ms, $SE = 1.1$) than to the opposite, uncued target ($M = 451$, $SE = .58$), $t(213) = 14.12$, $p < .0001$. Further, neural evidence consistent with this interpretation comes from the finding that half of the neurons in the dorsolateral prefrontal cortex (DLPC) recorded by Funahashi et al. (1993) in monkeys performing the spatial ODR task showed selective inhibitory responses to specific target directions. This explanation implies that if the monkey version of the ODR task were modified to include target stimuli in both the cued and a competing location, subjects would look toward the

cued location less frequently and more slowly than to the uncued location. To our knowledge, this prediction remains to be tested.

We have argued that sustained cue preferences reveal the existence of working memory capacities, but an alternative explanation might take the more modest position that cue preferences during the delay period are the result of some sensory representation of the cued location that has a long time course of activation and decay. On such an account, anticipatory eye movements to the cue do not involve working memory per se, since subjects see the identical target stimulus whichever direction they look, and therefore have no particular motivation to look to the cued side. Rather, the observed cue preferences reflect a form of sensory priming for the cued location that persists during the delay period. Habituation to the central fixation, or a weakening of inhibition, causes this sensory bias to be expressed in eye movements to the cue. This argument holds that anticipatory looks to the cue do not tap working memory processes or involve the volitional control of eye movements, but instead reflect the effect of a sustained sensory response to the cue stimulus. The sensory response need not engage working memory capacities, nor, by extension, the parts of frontal cortex that sustain these capacities, in the same way as other, more demanding memory tasks.

The sensory priming hypothesis would predict that when bilateral targets are presented infants should look more frequently at the cued target since that spatial location has been primed. However, as discussed earlier, infants' preferences for the cued location dissipated once the targets appeared. In fact, there were more looks to the uncued location than the cued location, suggesting that some inhibition of the cued location was taking place. A second line of evidence that suggests ODR task performance in monkeys involves more than sensory priming comes from a recent variant of the task that presented animals with centrally appearing patterns in addition to spatial cues.

Wilson et al. (1993) trained monkeys on two tasks: a spatial delayed response task where a stimulus in one of two peripheral spatial locations was a cue to look to that location after a delay period (similar to Experiment 1), and a pattern delayed response task in which one centrally presented visual pattern was a cue to look to the left and a different pattern a cue to look to the right. Single cell responses during delay periods were recorded from two adjacent regions of the prefrontal cortex, the DPFC and the orbitofrontal cortex. Cells in the DPFC were found which fired during the delay period of the spatial task, but not during the pattern task; cells in the orbitofrontal cortex appeared to fire during the pattern, but not the spatial task. Both tasks required working memory for the cued location and an identical eye movement response, but the modality of the cues differed. The authors argue that the similar pattern of cell firing found in these tasks and the anatomical proximity of the two frontal areas recorded from suggest that both tasks

tapped related, but possibly anatomically separate, forms of working memory. In particular, the pattern task is immune to alternative explanations in terms of sensory priming since there were no peripheral cues.

The second experiment that we report is an infant version of the Wilson et al. (1993) pattern ODR task. If 6-month-olds are able to learn to use a central stimulus to predict the spatial location where a target will appear after a delay, then this strengthens the view that sensory priming was not the basis of performance in Experiment 1. In addition, in Experiment 2 we attempted to train infants to respond to the cue after the delay period to make the procedure more similar to that used in the monkey and adult studies.

EXPERIMENT 2

Method

Subjects

Thirteen healthy, full-term, 6-month-old-infants (six female and seven male) of varied ethnic backgrounds were recruited for the study via newspaper announcements and word of mouth referrals. Infants ranged in age from 183 to 196 days ($M = 189$). An additional four infants were tested but did not complete the procedure due to fussiness. Their data were excluded from these analyses.

Design and Procedure

The apparatus was identical to that used in Experiment 1. Each trial began with the presentation of an attractor/fixation display as described in the previous experiment, but which was presented without sound. When the experimenter had determined that the infant was looking at the attractor pattern, the experimenter pressed a key to begin the trial. There were eight training trials in which single targets were presented, followed by 36 test trials in which targets were presented on one of the two side screens (24 trials) or both side screens (12 trials). Each infant viewed the same set of trials in a balanced, fixed pseudorandom presentation sequence.

Training trials. In these trials, the key press initiated the presentation of one of two distinctive, dynamic, graphic cue stimulus sequences on the central computer screen, each of which lasted for 1500 ms. One sequence consisted of four large light and dark blue circles arrayed in a square pattern. The circles shifted positions rapidly. The other sequence consisted of two small red and yellow squares which orbited one another in an inward spiral pattern toward the center of the computer monitor. Both patterns subtended a maximum of 5° of visual angle. Each visual stimulus was accompanied by a distinctive pattern of tones which was randomly generated by the computer for each subject. The pattern of tones was used to assist the infants in distinguishing the cue stimuli from the fixation and the cues from one another. Following the offset of the cue, the attractor stimulus returned to the central screen for the duration of a variable delay period, which

increased successively from 850 ms on the first trial to 2300 ms on the eighth trial. At the end of the delay period, the central attractor was extinguished and no stimuli were presented for a period of 400 ms. Then, a target stimulus appeared on one of the two side computer screens, 29° from the central fixation. The side of presentation was determined by which of the cues had been presented previously. The side of target presentation associated with each of the cues was randomized for each subject, but was consistent within a given experimental run. The target stimulus consisted of a short animated sequence (duration 1500 ms) of a colorful animal-like face which moved about the computer screen in a fixed pattern. The target sequence subtended 5° of visual angle.

Following target onset, the experimenter pressed a key to terminate the trial. The computer began the next trial with the presentation of the central attractor.

Testing trials. These trials were identical to the training trials with two exceptions. Delays were randomly alternated between 2600 and 4600 ms (total ISI including 400 ms time-out period of 3000 and 5000 ms), and the targets appeared on either a single side monitor or both monitors. In the 24 *single-target trials*, the target stimulus appeared on either the far left or the far right screens; the side of presentation was determined by which of the cues had been presented previously. In the 12 *double-target trials*, the target stimulus was presented on both the left and the right screens, the one associated with the earlier cue and the opposite side. A short time afterward (500 ms), the target on the side opposite the cue was extinguished while the target in the cued location remained illuminated for an additional 1000 ms before the trial ended and all stimuli were extinguished. Figure 3 is a schematic of the typical presentation sequence.

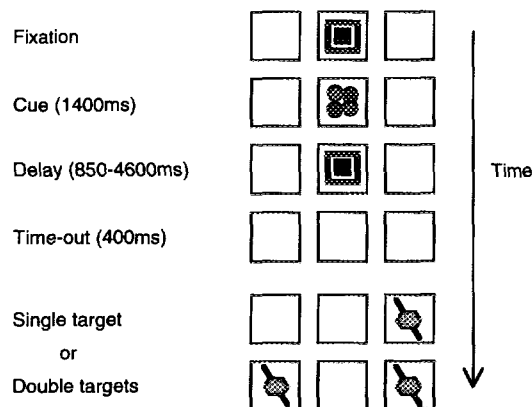


FIG. 3. Schematic showing typical presentation sequence for single- and double-target trials in the pattern ODR study (Experiment 2).

Data Scoring

Eye movements were scored in a manner similar to that described in Experiment 1. There was no peripheral cue stimulus to elicit eye movements to the side screens or to serve as a target for eye movement planning, so the cue-driven category was eliminated. Instead, responses were categorized into one of two groups. Eye movements that began after cue onset and prior to 200 ms following target onset were classified as anticipatory, following the procedure described in Experiment 1. Saccades that began more than 200 ms after target onset were classified as target-driven.

Invalid trials. As in Experiment 1, trials for an individual infant were coded as invalid if the infant was not fixated centrally during the cue stimulus or looked away from the experimental apparatus during the delay period. When trials across infants were pooled, 37% ($n = 211$) of the total trials ($n = 572$) were classified in this manner. The percentage of invalid trials was very low among training trials (6%), but these trials were smaller in overall number and were presented first in the session. Forty-five percent of total trials in the 3000-ms condition and 54% of trials in the 5000-ms condition were invalid.

As in Experiment 1, data across subjects were pooled to increase sample sizes within each of the sampling periods.

Results

Valid eye movements were pooled across subjects and the proportion of total anticipatory and cue driven responses that were directed toward the cued location computed (see Table 2).

Anticipatory Responses

All 13 subjects made anticipatory responses. Following the procedure described for Experiment 1, individual cue preference scores were computed for those subjects ($n = 13$) who made two or more anticipatory eye

TABLE 2
Proportion of Valid Eye Movements to Cued Location for Experiment 2

Cue/Target SOA (ms)	Response type		
	Anticipatory	Target-driven	
		Single targets	Double targets
3000	0.77**	0.96**	0.39
5000	0.69**	1.00**	0.44
Pooled	0.72**	0.98**	0.41

Note. Pooled responses combine data from all SOAs.

** $p < .01$.

movements. The mean cue preference of 0.67 exceeded chance, $t(12) = 2.46, p < .03$.

When data were pooled across subjects, 39% ($n = 140$) of the total valid responses ($n = 361$) were categorized as anticipatory. Only a small number of anticipatory responses ($n = 6$) were observed during the initial training trials.

Since subjects do not have any information that indicates whether a trial will contain single or double targets, nor about the length of the delay in a given trial, the processes that initiate anticipatory responses should be similar across both target and delay conditions. Consequently, anticipatory responses for the testing trials were pooled across the single and bilateral target conditions and across SOAs in order to improve power.

This analysis revealed a strong overall preference for the cued location ($\chi^2(1, n = 134) = 25.98, p < .001$). Further, when the pooled data were analyzed by time from cue offset in order to determine the persistence of representations over time (see Fig. 2), we found that proportion of looks to the cued location exceeded the chance level of 0.5 in every period preceding target onset, and was significant from 2–3 s ($\chi^2(1, n = 46) = 6.28, p < .05$) and 3–4 s following cue offset ($\chi^2(1, n = 24) = 15.04, p < .001$).

These strong cue preferences for the pooled results were similar to those found in the single-target testing trials at both the 3000-ms ($\chi^2(1, n = 42) = 6.88, p < .02$) and 5000-ms ($\chi^2(1, n = 43) = 9.30, p < .01$) delays. In the double-target trials, a significant cue preference was also found at the 3000-ms delay ($\chi^2(1, n = 22) = 10.23, p < .01$) but not at the 5000-ms delay ($\chi^2(1, n = 27) = 0.59, ns$).

Target-Driven Responses

All subjects contributed target-driven responses. Further, 61% ($n = 221$) of the total valid responses pooled across subjects were classified as target-driven. In single target trials, subjects showed extremely strong preferences to look toward the cued side both in the initial training trials ($\chi^2(1, n = 92) = 86.1, p < .01$) and in the subsequent 3000-ms ($\chi^2(1, n = 54) = 44.5, p < .001$) and 5000-ms trials ($\chi^2(1, n = 34) = 28.3, p < .001$).

In the double target trials, subjects showed no preference for either side although the proportion of eye movements to the cued side was below chance levels in the pooled sample (0.41) and both the 3000-ms (0.39) and the 5000-ms conditions (0.44) considered separately.

Discussion

Experiment 2 sought to determine whether infants could associate an abstract visual pattern with the location of a subsequent target stimulus, then use that information to plan a predictive eye movement after delays of several seconds. The experiment specifically included a training phase in or-

der to familiarize infants with the stimuli and provide them an opportunity to learn the predictive relationship between cue stimulus and target location at gradually increasing delays. Only one-third of the trials during the testing phase of the experiment presented a target on both side screens. Accordingly, unlike Experiment 1, where the cue did not uniquely specify the target location, the cue in the current study predicted the location of the target stimulus on 72.7% of the total trials in the experiment.

Infants responded to this association between cue and target location by showing strong preferences to look to the cued location when they broke fixation prior to target onset. The strength of the preference indicates that subjects were readily able to learn the association between the two different, abstract cues and the target locations that they predicted. Further, the tendency to prefer the cued location over the opposite location persisted even when infants delayed making an eye movement for as long as 3–4 s following the cue. Taken together, these findings argue strongly against the claim that anticipatory responses in this version of the ODR task stem from some form of sustained sensory trace of the cue since both cue stimuli were presented in the same, central spatial location. The findings are consistent with those from Haith's visual expectation paradigm which have shown that infants as young as 3½ months are capable of using a regular sequence of patterns to make predictive eye movements toward the location of the next stimulus (Canfield & Haith, 1991; Haith, 1993; Haith, Hazan, & Goodman, 1988). In short, the ODR experiments provide further support for the argument that rudimentary working memory capacities have emerged by 6 months of age.

We should stress, however, that 6-month-olds' working memories do not appear to be particularly robust; infants continue to make some anticipatory errors, and more than one-third of the time they look away from the experimental apparatus entirely at some point during the delay period. The proportion of trials classified as invalid for this reason and infant fussiness increases at longer delays, a pattern similar to that observed in Experiment 1. This suggests both that subjects grew increasingly restless at long delays and that some of the invalid trials may have represented failures of memory. At this point, we are unable to say whether the high rate of invalid trials stemmed from a lack of motivation to complete a trial or whether they resulted from failures to remember the cued location during the delay.

Finally, we note that responses to the onset of bilateral targets in this study are consistent with those from Experiment 1. Cue preferences that were strong during the delay period diminish following target onset. Indeed, on nearly 60% of double target trials, subjects looked to the side opposite the cue, a pattern consistent with the inhibition account outlined earlier.

GENERAL DISCUSSION

These experiments demonstrate that 6-month-old infants are capable of using both spatial and abstract cue information to plan anticipatory eye

movements to locations in the visual periphery. In both experiments, infants reliably disengaged attention from an attractive central stimulus to look toward a predicted location at latencies that exceeded 3 s from the presentation of either type of cue. The similarity of cue preferences over time in both experiments (see Fig. 3) suggests that related memory processes may be involved in both forms of the task.

Infants' success in anticipating the target's spatial location raises the question of what information they retain over the delay. One possible explanation for the findings from Experiment 2 is that infants store information about the cue pattern. However, the similarity between the results obtained in Experiment 1, where the spatial location was indicated directly by the cue, and those in Experiment 2, where the pattern of the cue contained no information relevant to target location, makes this unlikely to constitute a complete explanation. Two remaining possibilities are that (i) the infants plan their saccade to a specific location shortly after cue presentation but withhold it for several seconds or (ii) that infants compute the spatial location indicated by the cue and retain that over the delay. At present there are no data from infants which would allow us to dissociate these possibilities. However, evidence from monkeys in the pattern and spatial delayed response tasks (Wilson et al., 1993) suggests that different sets of cells have memory-related activities depending on whether pattern or spatial information must be remembered. If indeed memory for different forms of visual information is maintained separately in prefrontal cortex, then the fact that both types of information can drive similar oculomotor responses suggests that this part of the brain may be part of a network—including the frontal eye fields, basal ganglia (Hikosaka & Wurtz, 1983), posterior parietal (Gnadt & Andersen, 1988), and temporal cortex (Fuster & Jervey, 1982)—that forms dynamic bindings between stimulus information and responses that are appropriate in the current behavioral context (Fuster, 1986).

The results from the infant ODR experiments suggest that the variability in previous attempts to estimate the persistence of infants' working memory may stem from differences in the modality of the responses which were measured. Brody (1981) studied 8-, 12-, and 16-month-old infants' abilities to reach toward a remembered spatial location over delays ranging from 250 ms to 9 s and found that 12- and 16- but not 8-month-olds responded correctly after delays longer than 250 ms. Similarly, the average delay infants $7\frac{1}{2}$ to 8 months of age could withstand in object search tasks has been estimated at 2 s (Diamond, 1990). The current experiments suggest that when eye movements are the dependent measure, 6-month-olds may both inhibit reflexive responses to the cue and maintain spatial representations over delay periods significantly longer than older infants can withstand in tasks which require reaching toward or retrieving objects. Recent evidence (Bihun, Lanthier, & Haith, 1994) using Haith's visual ex-

pection paradigm supports this claim, indicating that infants as young as 3½ months of age have memory spans that persist over periods of several seconds but degrade when delays exceed 5–7 s.

Infant performance on the ODR tasks is also relevant to claims about the relationship between prefrontal cortex maturation and behavior. One explanation of infants' improved performance on object retrieval tasks is that prefrontal cortex undergoes significant maturation during the last half of the first year of life (Diamond, 1990; Goldman-Rakic, 1987). Infant monkeys whose frontal regions are presumably immature and adult monkeys with lesions in the frontal cortex (Diamond & Goldman-Rakic, 1986, 1989) show a pattern of performance in object permanence tasks similar to young human infants—they seem unable to either remember the location of the object they have just seen hidden or inhibit the tendency to reach toward the last location where they successfully retrieved the target object. Similarly, human adults with disorders affecting the prefrontal cortex show deficits in perceptual tasks which require the inhibition of reflexive eye movements (Guitton et al., 1985) and in cognitive tasks such as the Wisconsin Card Sort (e.g., Milner, 1963), which require forms of working memory and response inhibition.

Consistent with this evidence, Johnson (1990) argued that areas of the frontal cortex, e.g., the frontal eye fields, begin to influence shifts of eye gaze between 3 and 4 months of age. The effect of this influence is one of increasing control over both the initiation and inhibition of eye movements. For example, 4-month-olds show more anticipatory looks to stimuli that have been associated with spatial locations in a training task (Johnson et al., 1991), and 5-month-old infants can learn to reduce the number of eye movements that they make toward a stimulus appearing on one side of a display and redirect their eye movement toward the appearance of another stimulus which appears slightly later on the opposite side (Johnson, 1994). These findings suggest that infants between the ages of 3 and 6 months gain increasing control over eye movements, including the capacity to inhibit saccades to peripheral locations and to direct their gaze to specific locations based on predictive visual patterns (Haith, Hazan, & Goodman, 1988; Haith, 1993). These abilities would seem to be essential precursors for successful performance on the ODR tasks.

The relationship between the memory demands and brain mechanisms required by the ODR task and those of other, more extensively studied memory tasks, such as those involving the medial temporal or hippocampal system (Squire, 1992), have not been fully explored, however. At present, the neurophysiological and neuroanatomical evidence linking the infant version of the ODR task to the maturation and activation of the DPFC and FEF regions of the prefrontal cortex is indirect, based on the findings from related studies in monkeys (Funahashi et al., 1989, 1990, 1993; Wilson et al., 1993) and human adults (Jonides et al., 1993; Luciana et al., 1992). More-

over, while evidence concerning the maturation of prefrontal cortex is extremely limited, previous estimates have described this region as having a slower, and longer developmental time course than other parts of the brain such as primary sensory cortex (Huttenlocher, 1990). Chugani and colleagues (Chugani, Phelps, & Mazziotta, 1987) reported that glucose metabolism in frontal cortex begins to increase by 6 months of age and continues to do so over the next several months, but significant increases in activity were not observed until 8 months of age. Accordingly, the current experiments cannot rule out the possibility that infants' performance on the ODR tasks was mediated largely by other, earlier maturing parts of the brain, whose involvement in adult or monkey versions of the task may have been overlooked. The current experiments do demonstrate that infant versions of the ODR task can be useful indicators for the maturation of the mechanisms involved in working memory (Johnson & Gilmore, *in press*), wherever their neural substrate may lie.

Furthermore, the findings are consistent with evidence that orienting behavior may be a more sensitive measure of infants' knowledge than more demanding behavioral measures such as object retrieval. The suggestion that looking measures may tap infant's capacities at earlier ages is not new (see Baillargeon, 1987), but the ODR task may help to shed light on a puzzling dissociation that has been observed between looking and reaching measures of object permanence. If young infants performing the object search task are permitted to stare at the hiding location during the delay, they are able to retrieve the object after the delay period (Cornell, 1979; Diamond, 1985; Fox, Kagan, & Weiskopf, 1979). If their fixation is interrupted, they fail. On rare occasions, an infant will reach to the incorrect location while looking to the correct location. These results imply that spatial information derived from the visual domain plays a crucial role in driving reaching responses in object search tasks. The current experiments suggest that when the infant's response involves eye movements alone, spatial information can be maintained for several seconds without the subject fixating the target location. Why information about locations in space can be maintained for several seconds to drive eye movements but not reaching responses is unclear, but at least two possible explanations have been suggested. One is that memory for location may be closely tied to the form of response and is not easily transferable to other domains until later in development. Another possibility is that looking to locations in space may be easier than reaching toward them, so a unified spatial working memory system would require stronger representations to guide reaching than are necessary to guide looking (Munakata, 1994). Further information about the development of infants' visual memory capacities and the specificity and strength of the representations they sustain will enrich our understanding of age-related improvements in infants' performance on object permanence tasks in particular and about cognitive development in general.

The current experiments investigated whether young infants could demonstrate spatial working memory capacities when measured using an oculomotor delayed response task that is similar to one used previously with human adults and rhesus monkeys. The results indicate that some capacities to maintain spatial information over delays of several seconds exist at 6 months of age. When these capacities emerge, how they change over time, and how individual infants differ remain questions for future research.

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