



PAPER

Relational memory during infancy: evidence from eye tracking

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Abstract

Here we report evidence from a new eye-tracking measure of relational memory that suggests that 9-month-old infants can encode memories in terms of the relations among items, a function putatively subserved by the hippocampus. Infants learned about the association between faces that were superimposed on unique scenic backgrounds. During test trials, infants were shown three faces presented on a familiar scene. All three faces were equally familiar; however, one had been presented with the test background earlier. Visual behavior was recorded continuously using a TOBII eye tracker. Infants looked preferentially at the face that matched the test background very early in the trial; however, the time course of this preferential looking effect varied as a function of delay. These results suggest that by 9 months of age infants can form memories that represent the relations among items and maintain them over short delays.

Introduction

Memory systems are designed to do far more than simply allow us to remember the events that we experience. Humans learn from experience, but perhaps more critically, we also use the knowledge gained to guide future adaptive behavior. A fundamental characteristic of memory in the adult is the ability to generalize knowledge to new situations and to use memories to make inferences about the world in which we live (Eichenbaum, 2002).

Human infants also acquire knowledge from experience; however, memories of their experiences are extremely specific, and retrieval will only occur if the cues present at the time of encoding are identical to those present at the time of the test. The ability to retrieve memories despite changes in the cues available at testing has been termed 'representational flexibility' (Eichenbaum, 1997). Age-related changes in flexibility are evident in studies using the mobile conjugate reinforcement task with 3- to 6-month-olds (Borovsky & Rovee-Collier, 1990; Butler & Rovee-Collier, 1989; Gerhardstein, Adler & Rovee-Collier, 1999; Hayne, Greco, Earley, Griesler & Rovee-Collier, 1986; Rovee-Collier, Griesler & Earley, 1985), the deferred imitation task with 6- to 24-month-olds (Hanna & Meltzoff, 1993; Hayne, Boniface & Barr, 2000; Hayne, MacDonald & Barr, 1997; Learmonth, Lamberth & Rovee-Collier, 2004), and visual paired-comparison task with 6- to 24-month-olds (Robinson & Pascalis, 2004). Infants' memories are specific to the context in which they occurred until at least 12 months of age (Hayne *et al.*, 2000; Learmonth *et al.*, 2004; Robinson & Pascalis, 2004), and changes in stimulus cues disrupt infants' memory until at least 18

months of age (Hayne *et al.*, 1997). How can we account for age-related changes in memory flexibility during infancy?

Eichenbaum (1999) has suggested that it is the ability to encode events in relational representations that allows us to use memories flexibly. According to this view, the hippocampus is critical in forming memories that are relational in nature; memory events are encoded in networks of representations that link parts of an event to each other and to existing knowledge. The major advantage of this type of this relational coding is that it permits us to make inferences about items that are only indirectly connected, and allows for flexible memory expression (Eichenbaum, 1999). In contrast, parahippocampal regions are able to form representations for individual items; however, these are 'hyperspecific' and cannot be used flexibly.

How does relational memory develop? Behavioral studies with older infants and children suggest that the ability to represent memories in relational networks develops gradually across infancy and early childhood. Sluzenski, Newcombe and Satlow (2004) have shown that the ability to learn about the spatial relation between two locations improves significantly between 18 and 24 months of age. In this task, infants were asked to find an object that was buried in a sandbox based on the location of another hidden object. During training, the child watched the experimenter hide and uncover the objects and then was given the opportunity to help find the second object based on the revealed location of the first object. The two objects were hidden in the sand in different locations from trial to trial in the same relative position to each other. During the eight test trials, the

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experimenter hid the two objects while the child looked away. Children then watched the experimenter reveal the location of one of the objects and were encouraged to search for the second object. Using this spatial relations task, Sluzenski *et al.* (2004) showed that while 24- to 36-month-olds were able to learn the consistent relation between the hidden objects and use that knowledge to search for objects in novel locations, 18-month-olds performed very poorly on the task and seemingly were unable to learn the spatial relation.

Studies with older children have shown that the ability to bind memory items together in relational representations continues to improve throughout early childhood. Sluzenski, Newcombe and Kovacs (2006) have reported age-related changes in relational memory in 4- and 6-year-old children using a picture recognition task. Children learned about the relation between pictures of animals that were associated with different backgrounds. Four- and 6-year-old children performed equally well on the recognition task when asked to remember individual items (i.e. either animals or places). In contrast, 4-year-olds performed more poorly than 6-year-olds when asked to recognize the animal/background combinations; 6-year-olds did not differ from adults in their performance on the relational task.

In summary, it seems that the ability to form relational representations develops gradually during infancy and early childhood. Given that relational representation is essential for flexible memory expression, the protracted development of relational representation may, at least in part, account for age-related changes in memory flexibility during infancy (Jones & Herbert, 2006; Richmond & Nelson, 2007). Of course, in order to form relational memories, infants must first separate their visual world into meaningful elements, segregate figure and ground, and differentiate between features to be related. Considerable research has demonstrated that these necessary perceptual processes develop rapidly during the first months of life, as infants accumulate visual experience (for review, see Johnson, 2001). Little is understood about the emergence of early relational memory abilities, however, as preverbal infants do not have the motor or language skills to perform spatial search tasks or picture recognition tasks that can be used with older infants and children. Here we have adapted eye-tracking measures of relational memory that were designed for use with adult amnesics to study relational memory during the first year of life. Eye-tracking measures are particularly well suited for studies of development because the dependent measure (i.e. the proportion of time spent looking at a particular area of interest) does not require complex motor or language ability, allowing memory to be measured in infants and children varying widely in age, independent of changes in motor skill.

Studies using eye tracking with adults have shown that relational memory for arbitrarily paired scenes and faces is evident in non-conscious changes in adults' eye movements (Hannula, Ryan, Tranel & Cohen, 2007). In

this paradigm, participants are presented with a scenic background for 3000 ms after which time a face is superimposed on the scene for a further 5000 ms. Participants are asked to remember each scene/face pair for a later recognition test. During the test phase, the scenic backgrounds are again presented for 3000 ms, after which time three faces are simultaneously superimposed on the scene. Each face in the triad is equally familiar, but only one of the faces was presented with that particular background during the study phase. Participants demonstrate memory for the relations between faces and scenes both in their ability to explicitly identify the matching face and in disproportionate looking at the face that matches the test scene; preferential looking at 'match' faces typically develops very early in the test trial (approximately 500–700 ms after the faces are presented), and occurs independently of behavioral responding. Critically, Hannula *et al.* (2007) have shown that eye-movement measures of relational memory are dependent on the hippocampus; patients who have damage to the hippocampus are unable to form memory for the relations between scenes and faces, and perform poorly when asked to identify which face matches the background during probe trials. Unlike healthy controls, patients with amnesia also fail to look preferentially at a matching face during the probe trial, suggesting that the preferential looking may index hippocampally dependent relational memory processing.

In the current study, we use the scene/face paradigm to assess the nature of memory representations during infancy. If it is the case that memories are susceptible to changes in retrieval conditions because infants do not encode events relationally, then infants should fail to look preferentially at the matching face during probe trials. If in fact infants are able to encode components of an event in a relational network, we should see a preferential looking effect similar to that of adults. Given that significant changes in infants' ability to remember across changes in retrieval conditions occur late in the first year of life, in this study we tested 9-month-old infants on the scene/face eye-movement paradigm.

Method

Participants

Forty-three healthy, full-term 9-month-old infants (18 boys and 25 girls) participated. Families were recruited from a database of parents who had expressed an interest in participating in research by sending back a postcard in response to an information letter. Infants were tested within 10 days of the infants' 9-month-old birthday (M age = 276.33 days; SD = 5.63). Infants received a small toy for their participation. Nine infants were excluded from final analyses for insufficient looking; four were excluded for exhibiting position biases; five were excluded for poor calibration accuracy.

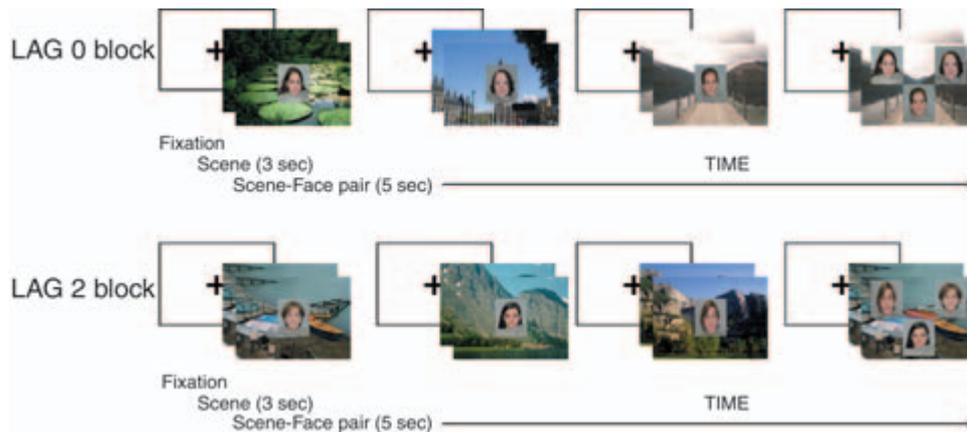


Figure 1 Examples of Lag 0 and Lag 2 match blocks. Each block consisted of three study trials and one probe trial. The position of the match face was counterbalanced across trials.

Apparatus and stimuli

A TOBII 1750 eye tracker was used to measure infants' fixation. The eye tracker consisted of infra-red light sources and cameras that are integrated into a 17" thin film transistor technology (TFT) monitor. Using corneal reflection techniques, the TOBII eye tracker records the X and Y coordinates of infants' eye position at 60 Hz. Calibration procedures were run using Clearview software (TOBII Technology, Sweden) which allows an optimal accuracy of 0.5 degrees. Stimulus presentation and data output were accomplished using Eprime software (Psychology Software Tools, Pittsburgh, PA).

Infants were presented with pictures of scenes and faces. The scenes (650 × 500 px) were obtained from vacation pictures along with commercially available stimulus sets (MasterClips: Premium Image Collection by IMSI, San Rafael, CA). The face stimuli (180 × 230 pixels) were obtained from the NimStim Face Stimulus Set (Tottenham, Tanaka, Leon, McCarry, Nurse, Hare, Marcus, Westerlund, Casey & Nelson, in press), and other face stimuli that were taken under similar conditions. Half the faces were male and half were female; all face photographs were taken in front of a grey cloth, subjects wore a grey cloth to cover clothing, and the subject in each picture had a neutral expression.

Procedure

Calibration

Infants were seated on their parent's lap 60 cm in front of the TOBII monitor, which was mounted on an Ergotron HD45 extension arm. The experimenter manipulated the monitor until the cameras detected the infant's corneal reflection. Infants were then shown a series of looming balls that appeared in 5-point calibration sequence. Calibration accuracy was checked and repeated if necessary.

Match blocks

Infants were shown blocks of scene/face trials (see Figure 1). Each block was made up of three study trials and one probe trial. During study trials, a background scene was presented for 3000 ms after which time a single face was presented on top of the scene for an additional 5000 ms. A fixation cross appeared during the inter-trial interval and remained on until the experimenter had confirmed that the infant was looking at the screen and that the cameras were tracking. During probe trials, a familiar scene was presented for 3000 ms before three faces were presented on top of it for an additional 5000 ms. The three faces were equally familiar, but only one had been presented with the probe scene (i.e. matched). The position of the matching face (left, right, bottom) was counterbalanced. Because both normal adults' and amnesics' performance on relational memory tasks is affected by delay (Hannula, Tranel & Cohen, 2006), we chose to include both immediate and delayed probe trials. Probe trials were presented either after a Lag of 0 (i.e. the scene/face match appeared on the immediately previous study trial) or a Lag of 2 (i.e. the scene/face match appeared two trials back). Lag 0 blocks and Lag 2 blocks were presented in a random order, and represented an immediate vs. a 20–30 s delay. A fixation cross followed each probe trial; the experimenter confirmed that the infant was looking and that the cameras were tracking before initiating the next block.

Non-match blocks

Non-match blocks were administered to assess the pattern of infants' looking behavior in the absence of a match between the scene and any of the probe faces and to determine whether infants exhibited a preference for any of the stimulus positions (left, right, or bottom). In previous studies using the scene/face paradigm, Hannula *et al.* (2007) used two different types of non-match trials.

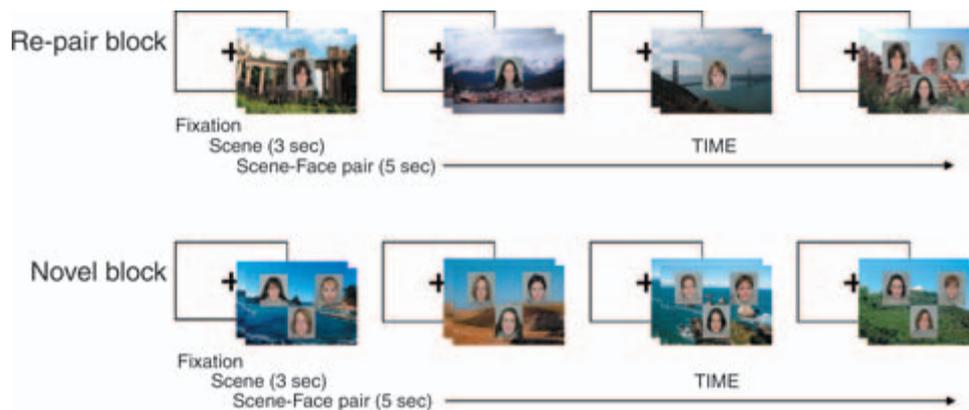


Figure 2 Examples of Re-pair and Novel non-match blocks. For infants in the re-pair group, non-match blocks consisted of three study trials followed by a test probe in which the three familiar faces were presented on a novel scene. Re-pair blocks were evenly distributed among Lag 0 and Lag 2 blocks. For infants in the novel group, non-match trials consisted of three novel faces that were presented on a novel scene. A series of four novel non-match trials were presented at the beginning of the session.

Adults were tested with ‘re-pair’ trials in which three familiar faces were presented on a novel scene, along with ‘novel’ trials in which three novel faces were presented on a novel scene. Given infants’ short attention span, infants in the current study were tested with either ‘re-pair’ or ‘novel’ non-match trials (see Figure 2). For half of the infants, re-pair blocks occurred among Lag 0 and Lag 2 trials. The procedure for these blocks was identical to the Lag 0 and Lag 2 blocks (i.e. there were three study trials followed by a test trial); however, the background scene that was used for the probe test was novel, rather than familiar. Thus all three faces were familiar but there was no relation between the scene and one of the faces, as the scene was novel. For the remaining half of the infants, four ‘novel’ trials occurred during a baseline period at the beginning of the experimental session. For novel non-match trials, there was no study phase; a novel background was presented for 3000 ms after which time three novel faces were superimposed on it for an additional 5000 ms. In all cases, non-match probes consisted of a 3000 ms scene presentation followed by a 5000 ms period in which three faces were superimposed on the scene.

There were 12 match blocks (six Lag 0 and six Lag 2) in total; however, testing was discontinued after 9.3 blocks on average, due to inattention or fussiness. Breaks were taken between blocks when necessary. Fixation data were recorded continuously throughout and processed offline.

Results

A fixation filter¹ was applied to the raw eye-tracking data to determine the length of each fixation. Given the

¹ A fixation was defined as a period of looking in which the position of the eyes did not shift more than 50 pixels for at least 200 ms.

sparseness of infant eye-tracking data, we set stringent criteria for the minimum amount of looking time that infants had to exhibit in order for probe trials to be included. Probe trials in which the track was lost, where the infant spent less than half of the test trial (i.e. less than 2500 ms) fixating the faces, or did not allocate at least one fixation to each face position (left, right, and bottom) were excluded from analysis. On average, infants contributed data from 2.4 Lag 0 probes, 1.9 Lag 2 probes, and 2.1 non-match probes for analysis; this constituted 55% of trials watched.

Eye-movement measures

Match analyses

Previous studies using this task with adults have taken preferential looking at the matching face (i.e. significantly greater than would be expected if looking behavior was equally distributed between the three faces in test displays) as evidence of memory for the relation between the test scene and match face (Hannula *et al.*, 2007). Here, fixation data from match trials were also analyzed using one-sample *t*-tests to determine whether infants devoted a greater proportion of time and a greater number of fixations to the match face during each probe than would be expected by chance. Preferential looking scores were tested against chance performance of 0.33, which would be expected if looking behavior were equally distributed between the three probe faces.

Across the 5000 ms probe, the proportion of time that infants directed toward the matching face on Lag 0 probes did not differ significantly from chance, $t(24) = 0.77$, $p > .05$. On Lag 2 trials, however, infants exhibited a significant preference for the matching face, $t(24) = 2.04$, $p < .05$. Similarly, the proportion of fixations that were directed at the matching face was significantly greater than would be expected by chance on Lag 2 trials, but not Lag 0

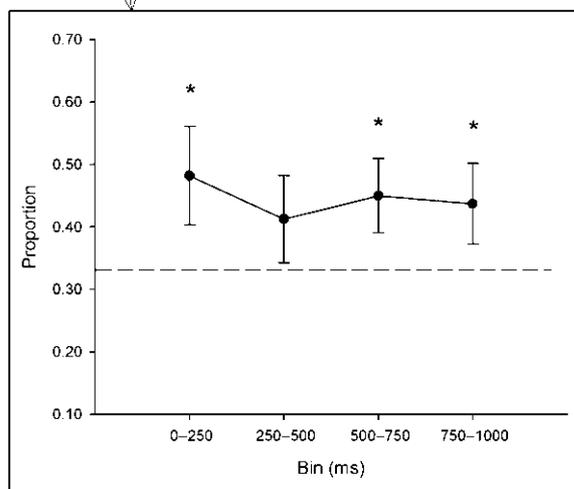
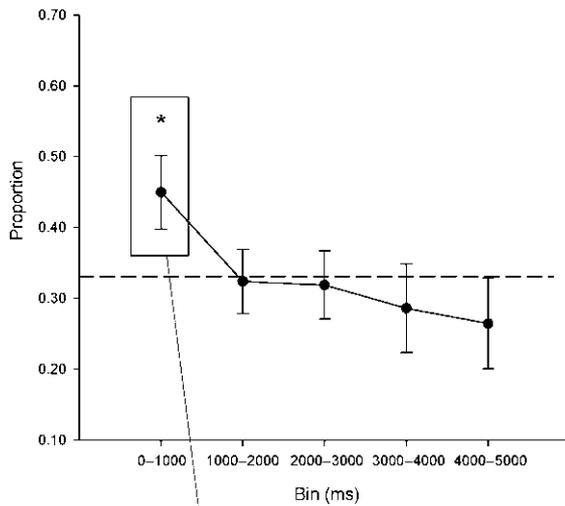


Figure 3 Mean proportion of time spent fixating the matching face during Lag 0 trials presented in 1000 ms time bins. Panel B. Mean proportion of time spent fixating the matching face during Lag 0 trials presented in 250 ms time bins. Preferences that are significantly above chance values of 0.33 are marked with an asterisk. Error bars indicate the standard error of the mean.

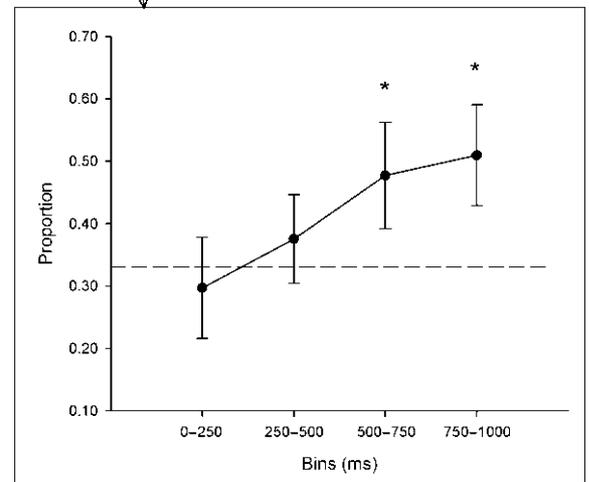
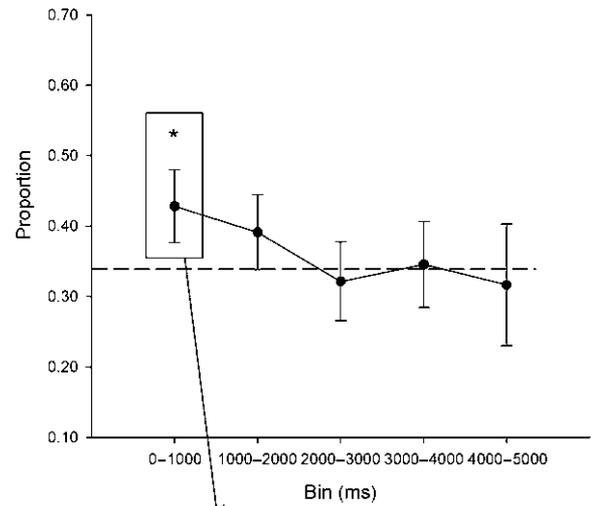


Figure 4 Mean proportion of time spent fixating the matching face during Lag 2 trials presented in 1000 ms time bins. Panel B. Mean proportion of time spent fixating the matching face during Lag 2 trials presented in 250 ms time bins. Preferences that are significantly above chance values of 0.33 are marked with an asterisk. Error bars indicate the standard error of the mean.

trials, $t(24) = 3.68$, $p < .05$ and $t(24) = 1.61$, $p > .05$, respectively.

In adults, relational memory effects occur very early in the trial, and time course analysis has been used to describe the temporal emergence of preferential looking (Hannula *et al.*, 2007). Here we analyzed the proportion of time that infants spent looking at the matching face separately in 1000 ms time bins. For each trial, the proportion of each 1000 ms time bin that was devoted to the matching face was determined by summing the length of fixations to the match face within a given time period (i.e. between 0 and 1000 ms) and dividing by the total time spent looking at all three faces during that time bin. Because of the continuous nature of visual behavior, it was possible for a single fixation to contribute data to adjacent time bins. As is illustrated in Figures 3 and 4, the proportion of time that infants spent fixating the

matching face was significantly greater than would be expected by chance between 0 and 1000 ms following stimulus onset. This preferential looking effect occurred for both Lag 0 and Lag 2 trials, $t_s(24) = 2.29$ and 1.90, $p_s < .05$, and did not differ in magnitude as a function of delay, $F(1, 24) = .09$, $p > .05$.

To define further the time course of infants' preferential looking during the first 1000 ms of the test, looking behavior was analyzed separately in 250 ms time bins. Again, for each trial the proportion of each 250 ms time bin that was devoted to the matching face was determined by summing the length of fixations to the match face within a given time period (i.e. between 0 and 250 ms) and dividing by the total time spent looking at all three faces during that time bin. This analysis revealed differences in the temporal emergence of preferential looking in Lag 0 and Lag 2 trials. As is illustrated in

Figure 3B, for Lag 0 trials, the proportion of time spent looking at the matching face was significantly above chance during the first 250 ms of the probe trial, $t(24) = 1.93$, $p < .05$, and remained high throughout the first 1000 ms. In contrast, for Lag 2 trials, preferential looking did not emerge until 500–750 ms following stimulus onset, $t(24) = 1.73$, $p < .05$ (see Figure 4B). The magnitude of the preferential looking effect did not differ between Lag 0 and Lag 2 trials in the first time bin in which it occurred, $t(24) = .05$, $p > .05$.

Non-match analyses

In the absence of a relation between the scene and faces, we expected that participants would distribute visual behavior equally between faces in the left, right and bottom positions. To test this, infants were tested on one of two types of non-match blocks; infants saw either trials in which three novel faces were presented on a novel scene (novel group) or trials in which three familiar faces were presented on a novel scene (re-pair group). Four infants did not give sufficient looking data during any non-match block; a total of 21 infants contributed data to the non-match analyses.

Infants in the novel group on average contributed a greater number of non-match trials than did infants in the re-pair group ($M = 3.18$ and 1.70 , respectively, $t(19) = 2.91$, $p < .05$). A repeated-measures ANOVA with group (novel and re-pair) and position (left, right, bottom) as factors revealed no main effect of group or position on infants' looking behavior during non-match trials, $F(1, 19) = 0.95$, $p > .05$ and $F(2, 38) = 3.08$, $p > .05$, respectively.² In the absence of a match between the background scene and the faces, infants looked equally at faces in the left, right, and bottom positions, irrespective of whether the non-match trial consisted of three familiar faces presented on a novel scene (i.e. re-pair) or three novel faces presented on a novel scene (i.e. novel). Given that infants showed no preference for a particular stimulus position during non-match probes (see Figure 5), we can confidently interpret preferential looking effects that occur during match probes as evidence of relational memory, rather than evidence for position biases.

In summary, infants exhibited evidence of memory for the arbitrarily paired scenes and faces as reflected in preferential looking at the matching face. Preferential looking occurred after a Lag 0 and Lag 2; however, the effect emerged later in the trial when a delay was imposed between the study and the test. Critically, in the absence of a match between the scene and faces, infants looked equally at the faces in the left, right and bottom positions,

² The main effect of position approached significance and was driven by a tendency for infants to spend a greater proportion of time during non-match trials fixating faces in the bottom position than faces in the right position, $t(21) = 3.26$, $p < .05$. During match trials, the matching face appeared equally often in the left, right, and bottom positions, and subsequent analyses of looking behavior revealed no effect of match position on the magnitude of the preferential looking effect.

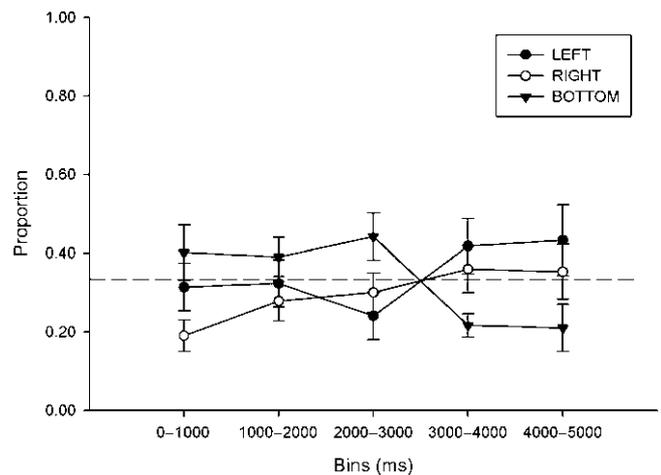


Figure 5 Mean proportion of time spent fixating faces in the left, right and bottom positions during non-match trials presented in 1000 ms time bins. Error bars indicate the standard error of the mean.

supporting the notion that preferential looking in the match trials occurred because of memory for relations, and not because of position biases in visual fixation.

General discussion

Previous accounts of infant memory flexibility have suggested that in the absence of functionally mature hippocampal circuitry, infants may fail to encode events in a relational manner, which precludes flexible memory expression (Jones & Herbert, 2006). Here we tested infants on an eye-movement paradigm that has been shown to require relational representations in studies of normal adults and human adult amnesics. This approach provides a unique opportunity to inform the nature of infant memory representations and to test the hypothesis that memory inflexibility during infancy can be attributed to infants' failure to encode memories relationally.

Nine-month-old infants exhibited evidence of memory for the relations between arbitrarily associated scenes and faces. Infants exhibited preferential looking effects that were similar in magnitude and time course to those seen in previous studies of adults, despite significant differences in stimulus exposure. Adults in the Hannula *et al.* (2007) study spent approximately 45% of the first 1000 ms fixating the matching face, when they were not required to make an explicit response. This effect emerged between 500 and 750 ms following stimulus onset. Infants in the current study also spent on average 44% of the first 1000 ms fixating the matching face; however, there was a significant effect of lag on the time course of this preferential looking effect. As with adults, when there was a short delay imposed between the critical scene/face match and the probe trial, the preferential looking effect emerged between 500 and 750 ms after stimulus onset. In contrast, for trials in which the critical scene/face

match had occurred in the immediately previous study trial, infants showed a significant preference for the matching face within the first 250 ms time bin.

It seems that the time course of preferential looking in this scene/face task may index retrieval-related processing. This idea is consistent with data from the Hannula *et al.* (2007) study in which adults were tested with probe trials that did not have a scene preview (i.e. the three faces appeared at the same time as the background). Under these conditions, the preferential looking did not emerge until 1500–1750 ms following stimulus onset. This delayed effect, along with data from infants showing rapid emergence of preferential looking in the absence of a delay, converge to suggest that retrieval of relational representations is automatic and that the time course of preferential looking may reflect the accessibility of the relational memory.

The current study has shown that 9-month-olds can form relational representations and maintain them over short delays. As discussed earlier, infants' ability to retrieve memories across changes in context does not emerge until 12 months of age, and the ability to use memories flexibly when the stimulus cues are changed continues to develop throughout the second year of life (Hayne *et al.*, 2000; Hayne *et al.*, 1997). In addition, behavioral studies with older infants and children have shown that changes in relational memory are seen at different points in development, depending on the demands of the task (Sluzenski *et al.*, 2006; Sluzenski *et al.*, 2004). How do we reconcile infants' ability to form relational representations, as measured by eye-tracking tasks, with their inability to use memories flexibly when tested in other situations? Graded representations may be at play here (Munakata, 2001). It is possible that within the first year of life the hippocampus forms relational representations that are weak, but sufficient to support automatic, possibly non-conscious shifts in visual attention that are seen in paradigms like the scene/face task. With further hippocampal maturation during the second year of life (Seress, 2001; Seress & Abraham, in press), infants and children are capable of forming stronger relational representations that can be used to guide spatial search behavior and support flexible memory retrieval (Hayne *et al.*, 2000; Robinson & Pascalis, 2004; Sluzenski *et al.*, 2004; Hayne *et al.*, 1997). Finally, adult-like relational representations are required to support performance on a task requiring intentional encoding and explicit recognition of stimulus relations (Sluzenski *et al.*, 2006).

There is now much evidence to suggest that certain experiences can also influence memory flexibility (Hayne, Barr & Herbert, 2003; Herbert, Gross & Hayne, 2007; Herbert & Hayne, 2000). For example, Herbert *et al.* (2007) have shown that 9-month-olds who are crawling are better able to imitate a target action when the retrieval conditions are changed than are their non-crawling peers. Eichenbaum (2002) suggests that relational memory networks allow new memories to be linked to each other

and to prior knowledge. Infants' knowledge networks are initially sparse; however, they increase in complexity with experience. Perhaps the onset of independent locomotion allows infants to seek experiences which contribute to the richness of the networks into which new memories can be related.

This study highlights the potential of eye-movement measures in understanding the development of relational memory. Unlike other measures of infant memory, the dependent measure in eye-tracking tasks is not confounded by age-related changes in motor skill. Thus, eye-movement paradigms allow us to take a truly developmental approach, testing participants on the same paradigm across the lifespan. In addition, eye-tracking measures of relational memory are well characterized in terms of the neural basis of performance (Hannula *et al.*, 2007). Future studies using paradigms like the scene/face task may highlight the relative contribution of brain development and experience in age-related changes in infant memory flexibility.

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