Episodic Retention in Early Childhood and Hippocampal Contributions

By

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General Abstract

When babies are born into the world, they have no concept of how much there is to learn and know about the world. As they age and grow, infants make and retain memories with rapid improvements in recollection for the unique spatio-temporal circumstance. Three studies investigate episodic memory in toddlers, emphasizing the role of the hippocampus in encoding and retrieving spatio-temporal and context-specific memories. Through innovative research methods including behavioral experiments, neuroimaging during natural sleep, and eye-tracking techniques, it was found that hippocampal activation correlates with the ability to retain episodic details and distinguish between similar events. Key findings across the chapters highlight that while spatial associative memory capacities are more robust earlier in development, the abilities to process temporal sequences and perform context discrimination are also evident in the second and third year of life and are linked to hippocampal function. These insights contribute to our understanding of the foundational aspects of memory development and its implications for cognitive development in early life.

Introduction

Episodic memory development, particularly its reliance on the maturation of the hippocampus, represents a fundamental aspect of cognitive development in early life. The ability to remember past events within their spatial and temporal contexts is crucial for learning and adaptation. However, understanding how these abilities emerge and evolve during the critical early years remains relatively under-explored. This dissertation presents three interrelated studies focusing on how toddlers encode, retrieve, and differentiate memories within varying episodic contexts.

Chapter 1 establishes that toddlers retain information about spatio-temporal details and that memory for these details, especially temporal aspects of the memory, is associated with hippocampal reactivation during sleep triggered by an auditory stimulus encountered during the target episodes.

Chapter 2 delves deeper into how toddlers differentiate between aspects of associative memory, showing that they are able to form memory representations of both spatial and temporal details, an ability that improves with age. Those associative abilities are not equally robust however, with children performing better on spatial aspects of the tasks compared to temporal aspects of the tasks. Furthermore, spatial memory experienced less decay and benefited more from relearning compared to temporal memory. The study employed a novel task integrating a new tablet matching behavioral task with previously validated imitation puzzle task.

Finally, Chapter 3 explores the development of context discrimination capabilities in the second year of life and within the hippocampus, focusing on memory discrimination between similar events in different contexts. To date, findings indicate that toddlers show hippocampal activation in response to familiar stimuli, which helps in distinguishing contexts. They are also

more likely to direct their visual attention to an auditorily matched stimulus when presented alongside a visual stimulus from a distinctly unique context compared to the same context.

Taken together, these findings begin to elucidate the understanding that the development of episodic memory in toddlers is intricately tied to the maturation of the hippocampus. Results contribute to our understanding of memory development but also challenges existing models by demonstrating that complex memory functions begin to develop earlier than previously believed. Each chapter builds upon the previous, illustrating a nuanced understanding of the specific behavioral and neurocognitive abilities of 18- to 33-month-olds, building on decades of work to assert that temporal memory lags behind spatial memory older children – while the hippocampus supports all aspects of memory development.

Chapter 1

Memory-Related Hippocampal Activation during Sleep and Temporal Memory in Toddlers

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Abstract

Nonhuman research has implicated developmental processes within the hippocampus in the emergence and early development of episodic memory, but research in humans has been constrained by the difficulty of examining hippocampal function during early development. In the present study, we assessed 48 2-year-olds with a novel paradigm in which participants completed two games on a tablet that required remembering associations between unique characters, the places they visited, and the temporal order with which they did so. At game completion, a novel song played. Toddlers remembered spatial locations better than temporal locations during an immediate test, after a 20-minute delay, and after a week delay. After the last behavioral session, toddlers underwent an fMRI task during natural nocturnal sleep evaluating hippocampal activation in response to learned and novel songs. We found that the extent of hippocampal activation for learned songs compared to novel songs during sleep was correlated with memory for the order in which the characters were moved across all time delays, but not their spatial locations. The results confirm that that the functional contribution of the hippocampus to early memory can be assessed during sleep and suggest that assessment of temporal aspects of memory in the current task best capture this contribution.

Keywords: hippocampal development, songs, episodic memory, fMRI, spatial, temporal

Highlights

- During a tablet game associated with novel songs, 2-year-olds remembered the locations visited by characters better than the order with which they visited them.
- Song-related hippocampal activation during sleep is associated with memory for temporal order in 2-year-olds

1.0 Introduction

Episodic memory, or the ability to remember past events in rich detail, requires that individuals retain information about the spatio-temporal context in which those events occur (Tulving, 2002). This ability first emerges in infancy, but undergoes substantial improvement throughout the second and third years of life (Bauer, 2005; Bauer et al., 2000).

The hippocampus is critical for forming and retrieving episodic memories (Eichenbaum et al., 2007; Eichenbaum & Cohen, 2001), and developmental processes within this structure have been hypothesized to be responsible for behavioral changes in memory functioning during infancy and early childhood (Bauer, 2008; Gomez & Edgin, 2016; Lavenex & Banta Lavenex, 2013; Mullally & Maguire, 2014). For example, it has been argued based on non-human evidence that the full integration of the dentate gyrus and CA3 subfields within the hippocampal circuitry may promote the ability to form distinct memory representations that can be distinguished from those related to similar events (Keresztes et al., 2018) and reinstated flexibly (Newcombe et al., 2014). The timing of these developmental processes might coincide with sizeable volumetric increases in the hippocampus observed during the first few years of human life (Gilmore et al., 2012). To date, however, the examination of functional changes in young children has largely eluded research.

The function of the hippocampus has been primarily investigated with task-related functional Magnetic Resonance Imaging (fMRI), which is notoriously difficult to use with infants and toddlers. A previous study attempted to overcome these challenges by collecting task-related fMRI data during natural nocturnal sleep (Prabhakar et al., 2018). Specifically, Prabhakar and colleagues tagged a laboratory experience with a song, a stimulus that could be delivered through headphones during sleep. Presentation of auditory stimuli associated with past

experiences during sleep has been shown to activate the network of brain regions involved in episodic memories (van Dongen et al., 2012) and studies of sleeping infants have confirmed processing of sensory properties of auditory stimuli during sleep (Dehaene-Lambertz et al., 2002), suggesting that memory-related activation would be observable in toddlers.

Consistent with this possibility, Prabhakar et al. (2018) found that hippocampal activation for a previously heard song was correlated with memory for the room in which the song had been heard; the association was even stronger when the memory measure additionally reflected whether toddlers remembered which of two puppets they experienced with the song and the room. These results indicate that the hippocampus can be reactivated in toddlers during sleep, that this activation may capture aspects of past episodic experiences and, for this reason, is associated with behavioral measures of recall. Several questions remain unanswered, however. First, in Prabhakar et al. (2018), songs were presented as background music in laboratory rooms, likely tagging overall contextual representations and not discrete aspects of the experience. Second, memory was assessed only with two questions at the end of a learning experience lasting 3 weeks and after an interval of several minutes from the last exposure. Therefore, it was difficult to fully evaluate memory retention and its associations with hippocampal function. The present study begins to address these limitations by promoting memory associations between songs and specific events including spatio-temporal information, and includes multiple assessment occasions, including immediate memory, 20-minute delay, and a 1-week delay.

1.1 Memory for Spatio-Temporal Information in Toddlers

Infants demonstrate remarkable memory abilities, including memory for the spatial and temporal context of past events. Memory for the association between events and their spatial context has been examined primarily with paradigms in which toddlers' memory is inferred from

their searches for hidden objects. For example, Newcombe and colleagues (2014) asked toddlers to find two toys, each hidden in one of four boxes in two separate rooms. The same boxes were used in the two rooms, and the task required toddlers to recall the correct toy-box-room association. The authors found that 21- and 26-month-old toddlers could remember the correct box that was used to hide a toy in each of the two rooms, but only when the experimenters cued their memory for the box with a part of the hidden toy. Younger toddlers (15- to 20-month-olds) could remember which boxes were used in either room, but not the association with room context, and older toddlers (34-months and older) could recall the entire toy-box-room association correctly. Prior work has shown that retrieval support in the form of context clues or unique physical markings helps young children engage spatial search abilities. Further evidence comes from Prabhakar et al.'s (2018) study wherein toddlers' hippocampal activation in response to a learned song was correlated with their memory for the specific testing room in which they had previously heard the song. Beginning around 25 months, toddlers develop the ability to recall objects or events with increasing specificity and without support (Ribordy et al., 2013). Overall, these studies suggest that the ability to recall spatial features can be observed early in the second year of life but continues to improve throughout the third year. Based on Prabhakar et al. (2018) and other analyses of non-human animals (Lavenex & Banta Lavenex, 2013), these improvements may be supported by hippocampal development.

An episodic representation also includes retention of temporal information. A wealth of work using imitation paradigms demonstrates that infants retain temporal aspects of their experiences (e.g., Bauer & Leventon, 2013). However, the sequences of actions used with young infants were typically functionally enabling, such that an early step was required for the next step to be possible, which may have provided strong retrieval cues. Clear evidence of long-term

retention of arbitrarily ordered, non-enabling actions was found in 28-month-olds who reproduced the sequences after a month delay (Bauer et al., 1998).

Overall, these results suggest that the ability to retain arbitrary relations between events and their spatio-temporal context is reliable during the third year of life. However, very few studies have examined retention of spatio-temporal information within the same paradigm, limiting our ability to directly compare memory for these types of information in early childhood. Studies conducted with preschoolers (Ribordy Lambert et al., 2017) and older children (Lee et al., 2016; Picard et al., 2012) have suggested that memory for temporal order may lag behind that of memory for spatial location, despite the development of both being linked to hippocampal change (e.g., Lee et al., 2020). We examined memory for spatial and temporal features within the same paradigm and predict that toddlers might retain memory for the former better than the latter.

1.2 Memory Retention

Infants and toddlers forget event details at a faster rate than their older counterparts (e.g., Bauer, 2005). For example, Bauer (2005) matched groups of 16- and 20-month-olds for immediate memory and showed that 16-month-olds forgot more information than 20-month-olds after 1-month and 6-month delays. Moreover, 22-month-olds could imitate sequences of arbitrary actions immediately, but not after a delay; only at 28-months could infants do so both immediately and after a two-week delay (Bauer et al., 1998). Overall, time delays result in significant information loss in infants and young children. In this study, we asked whether the predicted difference between retention of spatial and temporal features persisted across delays or whether memory for temporal information is lost at a faster rate.

1.3 Study Overview

The goal of the present study was to examine the association between hippocampal function and memory for specific events, including spatio-temporal information, and whether this association differed as a function of type of information and persisted across multiple testing intervals. We taught a sample of 2-year-olds to play games which required them to remember where and in what order to place 3 characters. The completion of the game activated a novel song. Toddlers' memory for the game was tested immediately after learning, after a 20-minute delay, and after 1-week delay.

We expected that toddlers would remember better the unique locations visited by each character compared to the order with which the characters were moved. In addition, we predicted that memory would decline as a function of time delay. However, we also considered the alternative hypothesis that memory declines would be limited due to repeated opportunities to learn the game prior to the delay; this procedural choice was motivated by our interest in ensuring that there would be sufficient retention by the time toddlers participated in the fMRI session.

Our fMRI paradigm took place during natural nocturnal sleep after the completion of the behavioral sessions. It included one of the learned songs, one reversed song (which was either the same learned song played backward, or the other learned song played backward). The reversed song was included so as to examine whether associations between memory performance and hippocampal activation depended on the presentation of the exact song or whether pitch, tone, timber, tempo, of the song without the exact melody were sufficient to reactivate the memory. We expected that behavioral performance would be generally associated with hippocampal activation in response to the learned songs, especially the songs played as they

were learned (i.e., forward). Based on Prabhakar et al. (2018), associations were expected to be stronger in the right hippocampus compared to the left hippocampus.

Although the current study focuses on hippocampal activation because the literature has largely focused on changes in this structure to explain early development of memory (e.g. Bauer, 2008; Gomez & Edgin, 2016; Lavenex & Banta Lavenex, 2013; Mullally & Maguire, 2014), we recognize that episodic memory emerges from the additional contribution of a network of cortical regions, including the parahippocampal and angular gyri (e.g., Moscovitch et al., 2016; Ranganath & Ritchey, 2012). Thus, we explored whether the predicted associations between memory and activation extended to these cortical regions associated with episodic retrieval.

2.0 Methods

2.1 Participants. A total sample of 87 2-year-old toddlers participated. Neuroimaging data were collected from 48 of them (*Mean* = 28.36 months; SD = 2.02 months, *range* = 25.22–32.15 months; 20 males), although two of the 48 failed to provide any behavioral measures of memory. The other 39 toddlers provided behavioral data but did not provide neuroimaging data because they were either unable to fall asleep (n = 32), stay asleep (n = 6) during fMRI data collection, or there was error in fMRI acquisition (n = 1).

2.2. Procedure. Our procedure included three laboratory visits which were, on average, one week apart (M = 5.92 days, SD = 3.03 days). In addition, there was a nighttime visit to the Imaging Research Center, which occurred as soon as possible after the second session.

2.2.1 Preparatory Session. An initial session was held to acquaint the participant with the experimenters, obtain consent, and prepare families for the neuroimaging aspect of the study. After consent, parents or guardians completed questionnaires about their child's demographics, verbal ability via the MacArthur-Bates Communicative Development Inventories (Fenson et al.,

2007), temperament via the Early Child Behavior Questionnaire (ECBQ; Putnam et al., 2006), and an in house questionnaire designed to assess toddlers' sleep habits for use during collection of neuroimaging data. Sleep habits included whether children primarily slept on their backs, were sensitive to noise while sleeping, and slept through the night; each of these questions was scored as either 0 for no, 1 for yes, 0.5 for sometimes. While parents completed these assessments, experimenters played with their toddlers. In preparation for the neuroimaging session, parents were sent home with a practice kit that consisted of earplugs and headphones, as well as information about the online location of audio files of sample scanner sounds. Parents were instructed to insert the earplugs and have children wear headphones while listening to the scanner sounds for approximately 1 hour at the beginning of each night for at least 1 week before the scanning session. This allowed parents and toddlers to become familiar with the MR environment. Experimenters were in frequent contact with parents during this time to assess their child's comfort and preparation for the actual scanning procedure.

2.2.2 Behavioral Session 1. During Session 1, participants were exposed to two songs. Three songs were created for use in this study and were counterbalanced across participants and conditions. We used 20-second clips that included unique rhythms, tempos, and keys with vocalizations consistent with English phonotactics (e.g., Bodu). Two of the songs were each uniquely associated with the completion of one of two versions of the ***Tablet Song Game.*** The third song was used as novel song in the fMRI paradigm. Each game version was played in a consistent laboratory room for all sessions. Characters, locations and order were always the same in each of the games across time intervals. A unique puppet animal accompanied the toddler and experimenter throughout the room in order to keep the toddler engaged. Thus, toddlers met a total of two puppets (e.g., an elephant and a lion), which were identified by name. Game versions

and room order were counterbalanced across participants but were consistent across sessions for each individual participant.

The ***Tablet Song Game*** (adapted from Prabhakar & Ghetti, 2020) involved turning on a song by inputting a sequence of actions on a touchscreen tablet by placing characters in locations where they belonged. The game started with a screen showing 3 characters (e.g. Astronaut, Doctor, etc.) and 3 arbitrary locations (e.g., School, Slide, etc.; Figure 1a). Toddlers were shown that each of the three characters ought to be placed in one of the three locations in a certain order (Figure 1b), resulting in the final display (Figure 1c). Although characters and locations were meaningful, the verbal labels for the locations were not used, and they were indicated to the participants in vague terms (e.g., "First, she goes there, then he goes there, last she goes there") to reduce the possibility of facilitating toddlers with better vocabulary skills. Once the sequence was completed accurately, a novel song played, and a new character appeared to dance on the screen (see Figure 1d). During the first demonstration, toddlers were instructed to "help turn on "Puppet's name" song." The experimenter then performed the matching procedure slowly, indicating the characters' chosen order using order signifiers (i.e., first, next, last) and verbally acknowledging their locations (e.g., here, there, etc.). When the song began to play, experimenters said "And that's how you turn on the song! Now it's your turn." Accuracy for spatial location was calculated as the number of correctly placed characters out of three. More than one character could be placed in the same location, which toddlers did occasionally (26% of total trials in across all participants and testing times). Thus, chance performance for the spatial details was 0.33 (i.e., calculated as the average of 0.33 chance of being correct in 3 trials, each associated with the same chance level). Accuracy for temporal order was calculated as the number of characters chosen in the correct order. For temporal order, chance performance levels

also amounted to 0.33, but for different reasons. Determination of chance accounts for dependency in temporal order trials and the fact that chance levels depend on which choice toddlers make. If toddlers select the first character correctly, then chance for them was 0.415 (i.e., the mean of 1/3 and 1/2). If toddlers first wrongly selected the second character, then their second choice could never be correct and chance can be calculated as 0.167 (i.e., the mean of 1/3 and 0). Finally, if toddlers wrongly select the third character at start, then the second choice can still be correct and chance corresponds to 0.415 (i.e., the mean of 1/3 and 1/2). Overall the average chance level across participants is the average of 0.415, 0.167, and 0.415, which corresponds to the average excepted value (i.e., 0.33).

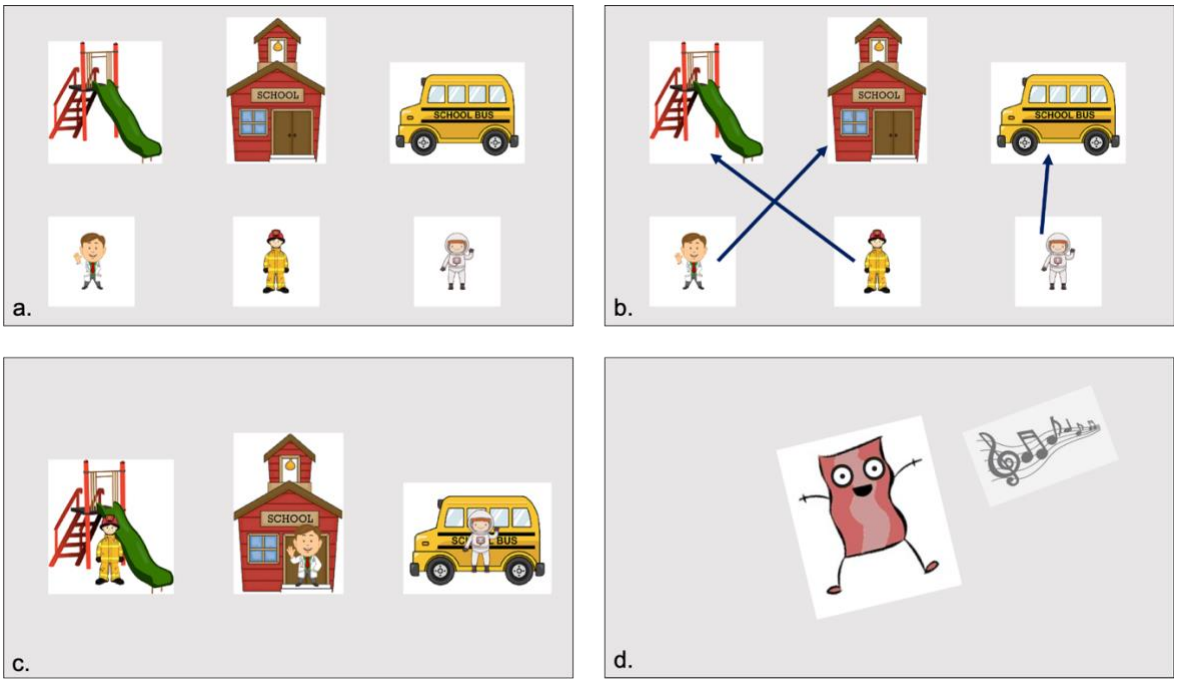


Figure 1: Character-location matching tablet game. In each of the two rooms at both sessions, the Tablet Song Game began with two rows of arbitrary characters and locations. Toddlers were shown that the characters on the bottom row moved to specific locations (a-c) in the top row in a specific temporal order. If the characters were properly matched to their spatial locations (regardless of temporal order) a unique character (d)

appeared to dance to a novel song.

In each room, toddlers were first shown the procedure of the ***Tablet Song Game.*** As soon as the experimenter completed the sequence, the song specific to that room played for 30 seconds. Then, toddlers were asked to imitate the experimenter and recreate the sequence to play the song (practice trial). Regardless of the toddlers' success reproducing the correct sequence, the experimenter showed the sequence again resulting in the song playing. At this point, toddlers' initial memory was tested (Immediate Test) to assess whether they could correctly position the characters in their location and whether they moved them in the correct temporal order.

Based on extensive piloting that suggested difficulty with retention of temporal order, we decided that placing the characters in the correct location was sufficient to trigger the song to play in an attempt to increase the probability that toddlers would cause the song to play on their own and maintain motivation. In other words, if toddlers made incorrect spatial placements, but selected the characters in the correct order, the song would not play. However, this happened in only 5.4% of trials over the total number of trials across time interval and room. We elected not to give corrective feedback following mistakes so as to not discourage toddlers and make the task more demanding. Instead, we gave multiple opportunities to learn through the experimenter's demonstrations. We elected not to let the song play regardless of performance level, because we told the toddlers that the song would be triggered by performing well.

Participants and experimenters completed the game together before ending the task, in order to strengthen their memory for the game. The song continued to play throughout the remainder of the session in a given room, while toddlers engaged in other activities, and then

toddlers reengaged with the song when they were asked to play the ***Tablet Song Game*** again (20-Minute Delay). After attempting to recall, all toddlers were shown how to play the game again regardless of their success to ensure equal exposure to the song.

Each time the song started playing, the experimenter demonstrated a simple dance action (e.g., shake your head; reach for the sky). We reasoned that this procedure would facilitate further attention to the song. Immediately after finishing the games in the first room, toddlers moved to the second room, where the other version of the game was played with a different song.

2.2.3 *Behavioral Session 2*. During this session approximately one week after *Behavioral Session 1*, the toddlers returned to the lab and were asked to demonstrate how to play the ***Tablet Song Game*** (One –Week Delay). Although entering the same room where the sequence was previously learned may have cued toddlers' memories, no reminder demonstration or practice sequence was given to toddlers before completing the one-week delay test. After completing the one-week delay test, participants viewed the experimenter playing the game correctly once and, finally, participants and experimenters completed the game together again to ensure exposure to the song regardless of performance and to promote retention prior to the nighttime neuroimaging session.

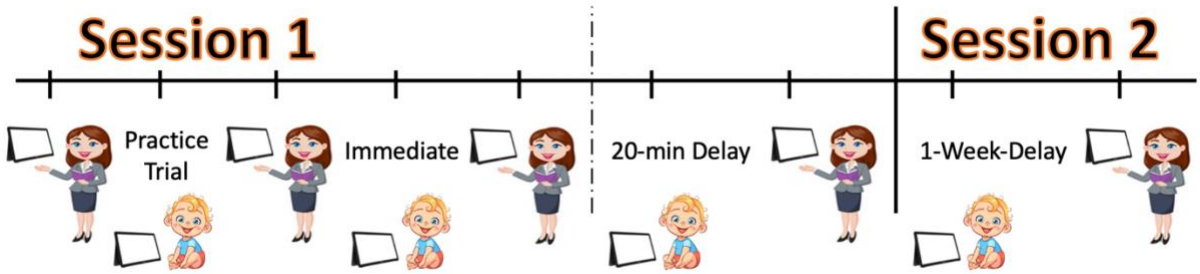


Figure 2: Sequence of Events in Tablet Matching Game. Toddlers' memory was assessed across two sessions with an Immediate test, a 20-Minute-Delay test, and One – Week-Delay Test.

2.3 ***Nocturnal Neuroimaging Session.*** Toddlers underwent their neuroimaging session during natural nocturnal sleep within 3 days after the second laboratory visit (*M* = 1.80 days, *SD* = 2.88 days). During the night visit, families arrived between 7 PM and 10 PM depending on their toddler's typical sleeping schedule and the session lasted approximately 2 hours. The scanner bed was outfitted with a memory foam mattress pad and pillows, as well as several blankets and stuffed animals for the child's comfort. Parents could bring comfort items for their child, which were properly screened for safety ahead of time. Earplugs and headphones were placed on the toddlers for sound protection and auditory stimulus delivery, approximately 10–15 min after they had fallen asleep on the scanner bed. We confirmed children were asleep if they had been lying on their back with earplugs and headphones on the scanner bed and had not moved for 10 min. At this point, the parent and experimenter attempted to move the child's arm to determine whether they would wake up with the movement. If the child continued to sleep through this disruption, the scan proceeded. Using this procedure, the scan generally began at least 30 min after sleep onset and was completed within the first 50 minutes after sleep onset (1 typical infant sleep cycle) to increase the chances that children were in slow-wave sleep during the functional scans (e.g., Anders & Taylor, 1994; Mitra et al., 2017). Although the examination of the effects of slow-wave sleep falls beyond the scope of the current research, we sought to maximize our chances of observing reliable hippocampal activation, given previous studies identifying memory reactivation during slow-wave sleep (Rudoy et al., 2009; van Dongen et al., 2012). A parent and a researcher were present inside the scanner room within arm's reach of the

child for the duration of the scan. Lights in the back of the scanner allowed the parent and experimenter to have full view of the child's face and body, and monitor for signs of waking up (e.g., any body, face, or eye movements). When the child showed such signs, it was determined that the child was waking, and the experimenter stopped the scan.

2.4 ***FMRI Acquisition and Design.*** Images were acquired via a 3T Siemens TIM Trio MRI System at the University of California, Davis, Imaging Research Center using a 32-channel coil. Functional images were acquired using a gradient echo-planar imaging pulse sequence [repetition time (TR), 1,500 ms; echo time (TE), 24 ms; field of view (FOV), 216 mm; number of slices, 46; voxel size, 3 mm isotropic; 250 volumes acquired]. During the functional scan, children heard three 20-second blocks of three different stimuli: one of the songs heard during the laboratory visits (Target), a song novel to the child (Novel), and either the target song or the other song presented in the laboratory sessions played in reverse (Reverse). Approximately half of the participants were exposed to the reversed version of the target song (R_T) while the other half were exposed to the reversed version of the non-target song (R_{NT}). Twenty-second blocks of silence separated the song blocks. In total, there were nine song blocks, three blocks of Target, Reverse, and Novel respectively, interspersed by silence, with each 20-second song block modeled as a distinct Target, Reverse, or Novel event block. We used a randomized sequence to present the order of Target, Reverse, and Novel blocks for the remaining eight blocks for each participant. This functional protocol lasted 6:23 minutes. A T1- weighted high-resolution magnetization-prepared rapid-acquisition gradient echo (MPRAGE) scan in the sagittal plane was also obtained (TR, 2,500 ms; TE, 3.23 ms; FOV, 226 mm; voxel size, 0.70 mm isotropic) prior to the functional scan (7:08 minutes) Overall, with the localizers (00:22 minutes), the complete scanning protocol took 13:53 minutes to complete.

2.5 *fMRI Data Processing and Analysis.* Data were preprocessed and analyzed using FEAT in FSL5.0.8. (https://fsl.fmrib.ox.ac.uk/fsl/fslwiki/). Preprocessing included slice timing and motion correction. FSL's motion outliers function (https://fsl.fmrib.ox.ac.uk/fsl/fslwiki/FSLMotionOutliers) identified motion outliers greater than 0.9mm by measuring relative intensity differences and defining outliers using the upper threshold for creating boxplots. We excluded scans with more than 20% of the volumes with motion outliers as defined by this function. This resulted in 2 scans being excluded for excessive motion because of an average of 30% volumes affected in these participants. A total of 227 volumes were rejected across 23 participants (average = 9.87 volumes per participant, range = 1-41 volumes) and they were corrected by including a confound matrix of outliers in the general linear model. The sample included in these analyses showed an average relative framewise displacement of 0.16mm (*SD* = 0.12mm, range = 0.04-0.64mm) and an average absolute displacement of 0.39 mm (*SD* = 0.70mm, range = 0.07-1.48mm).

Functional and structural data were all registered to a standard toddler template created by the University of North Carolina (26) from a sample of 95 toddlers (*M* = 33.65 months) (bric.unc.edu/ideagroup/free-softwares/). Each registration was visually inspected by investigators to ensure it was successful. We confirmed visually that all were successfully registered to the template.

General linear models were conducted using FEAT in FSL to model Target, Novel, and Reverse song types during the time series and were convolved with a double-gamma hemodynamic response function to yield two main contrasts of interests (e.g., Target > Novel and Reversed > Novel) to examine whether increased activation for the exact reproduction of the song or a changed representation via reversing was associated with memory. Our hypotheses

centered on hippocampal function, and thus we focused our analyses to the right and left hippocampal masks, which were obtained from parcellation maps provided by the University of North Carolina 2-year-old template (right: 5538 voxels, 50% probability; left: 5785 voxels, 50% probability; see Figure 3a). Parameter estimates were extracted from these structurally defined hippocampal masks. We also investigated activation in the left and right parahippocampal gyrus (right: 8542 voxels, 50% probability; left: 7585 voxels, 50% probability; see Figure 3b) and angular gyrus (right: 17988 voxels, 50% probability; left: 12992 voxels, 50% probability; see Figure 3c) obtained via parcellation maps from the University of North Carolina 2-year-old template.

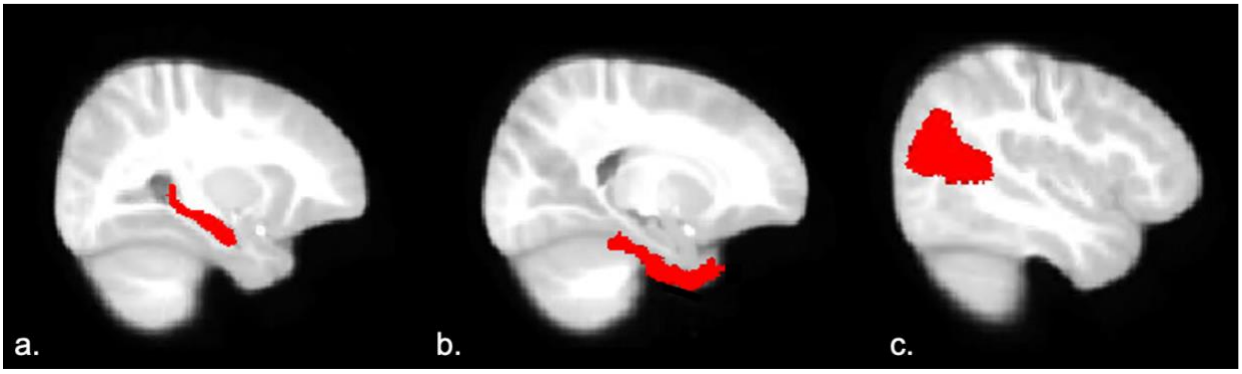


Figure 3. Masks Utilized for Structurally defined Regions-of-Interest Analysis. a. Right and Left Hippocampal Masks. Group analyses were constrained to the right (5538 voxels, 50% probability) and left (5785 voxels, 50% probability) hippocampal masks using age-appropriate hippocampal templates from the University of North Carolina 2-year template. Shown at X = 25, Y = -11, Z = -12. **b. Right and Left Parahippocampal Gyrus Masks.** Right (8542 voxels, 50% probability) and left (7585 voxels, 50% probability) parahippocampal gyrus masks taken from University of North Carolina 2-year template. Shown at X = 18, Y = -9, Z = -31. **c. Right and Left Angular Gyrus Masks.** Right (17988 voxels, 50% probability) and left (12992 voxels, 50%

probability) angular gyrus masks taken from University of North Carolina 2-year template. Shown at X = 38, Y = -55, Z = 15.

3.0 Results

3.1 Behavioral Results. We first conducted preliminary analyses to examine whether there were any differences between toddlers who successfully completed the neuroimaging sessions and those who did not in terms of background variables (e.g., age, language, temperament, etc.) and memory performance. Results showed that there were no significant differences between those scanned and not scanned in age, inhibition, attention shifting, attention focusing, vocabulary, sleep behavior, temporal memory, or spatial memory (see Table 1).

	Scanned	Non Scanned	
	n = 48	*n* = 39	
Age	*M* = 28.42; *SD* = 1.99	*M* = 28.02; *SD* = 2.25	*t*(83) = -0.70, *p* = .49
Sex	21 male; 27 female	16 male; 23 female	
ECBQ Inhibition	*M* = 3.06; *SD* = 0.66	*M* = 2.82; *SD* = 0.82	*t*(74) = -1.42, *p* = .16
ECBQ Attention Shifting	*M* = 5.31; *SD* = 0.65	*M* = 5.28; *SD* = 0.67	*t*(74) = -0.20, *p* = .84
ECBQ Attention Focusing	*M* = 4.72; *SD* = 0.85	*M* = 4.84; *SD* = 0.54	*t*(75) = 0.68, *p* = .50
MacArthur Words Known	*M* = 32.9%; *SD* = 20.6%	*M* = 33.0%; *SD* = 22.2%	*t*(78) = 0.04, *p* = .97
Back Sleeping *	*M* = 0.94; *SD* = 0.29	*M* = 0.97; *SD* = 0.12	*t*(68.07) = 0.70, *p* = .49
Sleeping Through Night ±	*M* = 0.85; *SD* = 0.34	*M* = 0.86; *SD* = 0.34	*t*(69.51) = 0.12, *p* = .90
Noise Sensitivity **	*M* = 0.25; *SD* = 0.41	*M* = 0.17; *SD* = 0.37	*t*(73.72) = -0.95, *p* = .34
Temporal Memory	*M* = 0.46; *SD* = 0.23	*M* = 0.44; *SD* = 0.27	*t*(74) = 0.03, *p* = .97
Spatial Memory	*M* = 0.52; *SD* = 0.23	*M* = 0.56; *SD* = 0.31	*t*(74) = 0.82, *p* = .42

* Do toddlers sleep primarily on their back? 0-1 score for no/yes responses

± Do toddlers sleep through the night? 0-1 score for no/yes responses

** Are toddlers sensitive to noise while sleeping? 0-1 score for no/yes responses

Table 1. Comparison of toddlers who completed the fMRI session and toddlers who, for various reasons, did not complete the fMRI session.

We then conducted a 2 (Information type: Spatial or Temporal) X 3 (Test occasion: Immediate, 20-minutes, 1-week) within-subjects ANOVA investigating memory accuracy. This ANOVA revealed a significant effect of information type ($F(1, 40) = 5.33$, $p = .03$, $\eta_p^2 = .02$), such that memory for the spatial location the characters visited was significantly higher ($M = 0.53$, $SD = 0.28$) than memory for the temporal order with which characters were moved ($M = 0.46$, $SD = 0.31$). There was no significant main effect of test occasion (immediate, M = 0.48, $SD = 0.32$; 20-minute interval, $M = 0.50$, $SD = 0.29$, 1-week interval, $M = 0.51$, $SD = 0.29$; $F(1, 80) = 0.42$, $p = .66$) or trial by type interaction ($F(1, 80) = 0.08$, $p = .92$; Figure 4).

Participants were significantly above chance (0.33) on all spatial ($ts(42) \leq 5.07$, $p < .001$) and temporal trials ($ts(42) \leq 3.01$, $p \leq .002$). There were no differences between first and second room performance for either spatial memory ($ts(41) \leq -0.72$, $p = .47$) or temporal memory ($ts(41) \leq 0.68$, $p = .50$) in any of the intervals.

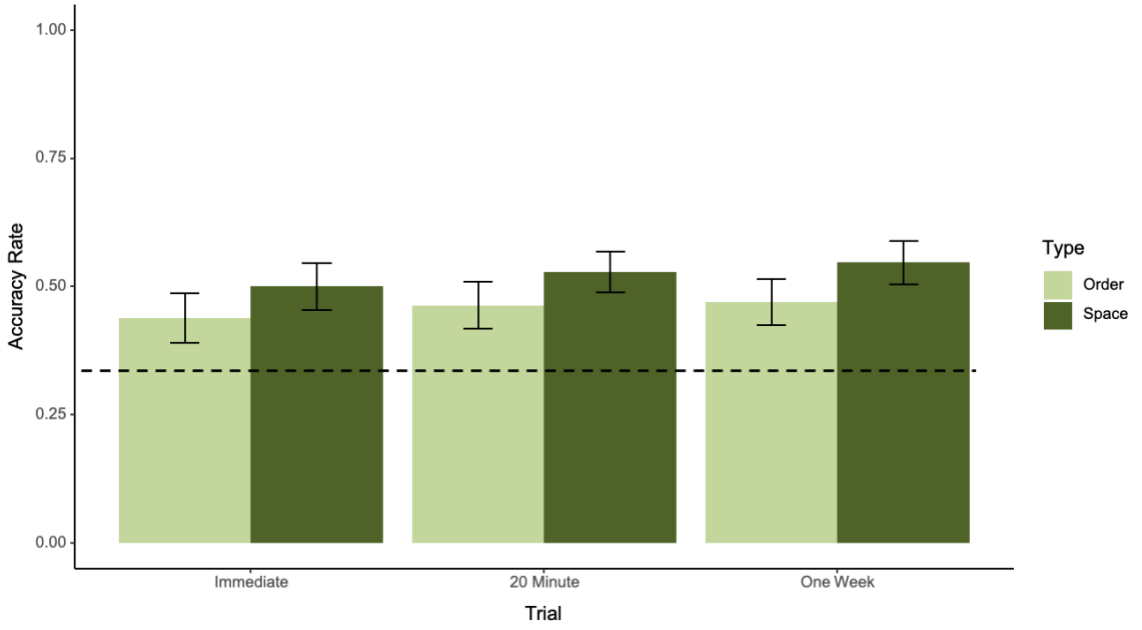
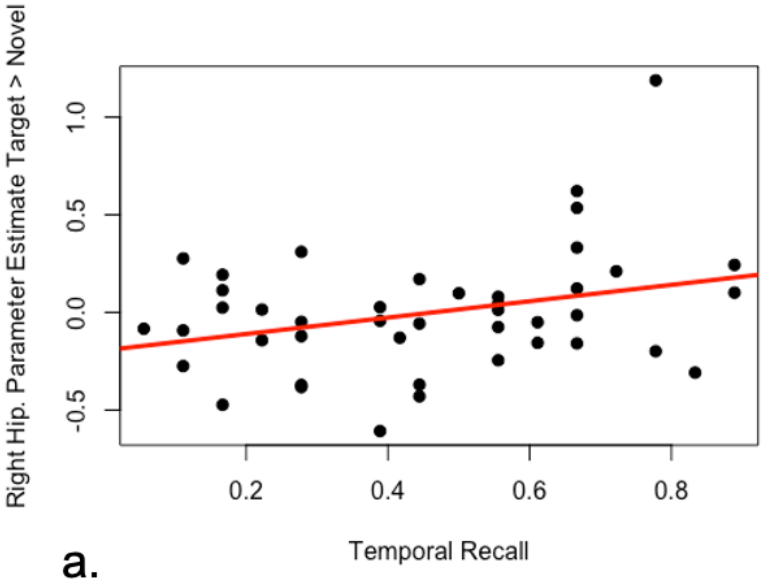


Figure 4: Behavioral Performance Results from ANOVA on behavioral data. Toddlers performed better on the spatial aspect of the task than the temporal aspect. Chance level is marked at 0.33.

4.2 fMRI Results. Given that the behavioral results indicated no performance difference as a function of testing occasion, and in order to accurately capture behavioral memory ability as a whole, we calculated the average memory performance across all testing occasions separately for spatial and temporal memory and correlated these averages with hippocampal activation. We found a significant correlation between activation for the Target compared to Novel (Target > Novel) contrast in the right hippocampus for temporal order memory ($r(41) = 0.31$, $p =. 04$; Figure 5a). However, we did not find a correlation between activation in this contrast and spatial location ($r(41) = -0.095$, $p = .55$; Figure 5b). The difference between these two correlations was significant (Steiger's $z = 2.88$, $p = .004$).



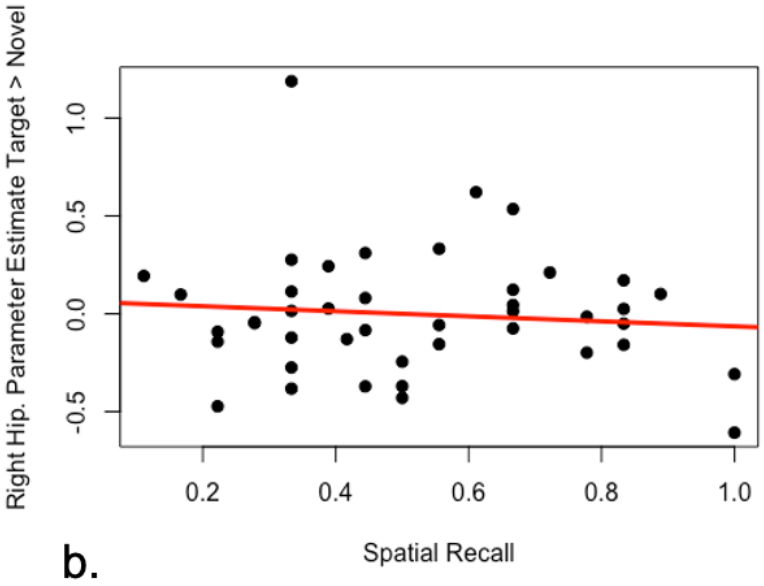


Figure 5: a) Association between activation in the right hippocampus and memory for temporal order ($r(41) = 0.31$, $p < .04$). **b)** Association between activation in the right hippocampus and memory for spatial location ($r(41) = -0.09$, $p = .54$).

Additionally, when we correlated activation in the Reversed > Novel contrast in the right hippocampus, we found the same pattern of results, such that there was a significant correlation with memory for temporal order ($r(41) = 0.43$, $p = .004$), but not for spatial location ($r(41) = 0.01$, $p = .94$). The difference between these two correlations was also significant (Steiger's $z = 2.43$, $p = .015$).

In the left hippocampus, the correlation between the Target > Novel contrast and temporal memory was not statistically significant ($r(41) = 0.22$, $p = .16$), and it was smaller than that in the right hippocampus (Steiger's $z = 1.66$, $p = .04$ one-tailed). In contrast, we found a significant correlation between temporal memory and Reversed compared to Novel (Reversed > Novel) activation ($r(41)= 0.36$, $p = .02$), which was not significantly greater than that found in the right hippocampus (Steiger's $z = 1.26$. $p = .10$). As in the right hippocampus, no significant association was found for spatial memory in the left hippocampus for either the Target > Novel contrast ($r(41)= -0.12$, $p =.44$) or the Reversed > Novel contrast ($r(41)= 0.09$, $p =.59$).

Finally, we conducted exploratory analyses of two additional cortical regions that are consistently found to be active during episodic retrieval, the parahippocampal gyrus and the angular gyrus. We found that the right parahippocampal gyrus ($r(41) = 0.35$, $p = .02$) and right angular gyrus ($r(41) = 0.33$, $p = .03$) for the Target > Novel contrast were significantly correlated with memory for temporal order, similar to the hippocampus. This was not the case for spatial memory (right parahippocampal: $r(41) = -0.17$, $p = .29$; right angular gyrus: $r(41) = 0.08$, $p = .60$). Correlations with memory for temporal order and Target > Novel activation was marginal but not significant in both the left parahippocampal gyrus ($r(41) = 0.30$, $p = .051$) and left angular gyrus ($r(41) = 0.29$, $p = .06$); neither spatial or temporal memory was significantly correlated with activation in the left parahippocampal gyrus ($r(41) = -0.15$, $p = .34$) or left

angular gyrus ($r(41) = 0.07$, $p = .67$) was significantly correlated with spatial memory. In the Reversed > Novel contrast, bilateral activation of the angular gyrus was significantly correlated with temporal memory (right: $r(41) = 0.35$, $p = .02$; left: $r(41) = 0.31$, $p = .04$), but not the parahippocampal gyrus (right: $r(41) = 0.23$, $p = .14$; left: $r(41) = 0.13$, $p = .41$). No aspect of spatial memory was correlated with Reversed > Novel contrast activation in the parahippocampal gyrus (right: $r(41) = -0.02$, $p = .91$; left: $r(41) = -0.05$, $p = .75$) or angular gyrus (right: $r(41) = -0.00$, $p = .96$; left: $r(41) = 0.002$, $p = .99$).

4.0 Discussion

The present study was designed to examine the association between memory for spatio-temporal information and hippocampal function in toddlers. In a previous study, hippocampal activation for a song was observed to be correlated with memory for aspects of an event that occurred while the song was playing (Prabhakar et al., 2018). The present study was designed to extend these previous findings in two ways. First, we were interested in establishing whether songs could be used to tag specific aspects of a past episode, as opposed to capturing the broader context as was the case in Prabhakar et al. (2018). For this reason, we tested toddlers' memory for specific spatio-temporal features of a discrete event associated with the playing of a song. Second, memory assessments occurred at multiple time-delays including immediate memory, 20-minute delay, and a 1-week delay. Previous methods for assessing memory in this age group have primarily focused on either temporal aspects of memory (e.g., imitation of actions in the order that they had been learned; Bauer, 2008) or linked spatial and temporal aspects of memory (Kirkham et al., 2007; Ribordy Lambert et al., 2016). The Tablet Song Game used in this study has the advantage of assessing, within the same task, the retention of both spatial and temporal

information, and critically, is integrally associated with the song as it is played and is therefore more salient.

We first determined that toddlers' memory for spatial features was significantly better than their memory for temporal features, regardless of time delay. We cannot exclude the possibility that reinforcement of spatial locations, but not temporal order, with the song may have preferentially supported spatial recall. However, toddlers played the game by placing the characters in a spatial location in a certain order. Therefore, they could not have known that it was spatial location alone that triggered the song. Furthermore, the full spatio-temporal sequence was shown again after toddlers completed their attempt regardless of their success. Better retention of spatial details is consistent with previous research showing clear evidence that infants notice the location of objects and retain information about it. For example, Richmond et al., (2015) demonstrated that 18- and 27-month-olds exhibited a visual preference for objects that had switched on a screen indicating that they had encoded their location. Just after their second birthday, however, toddlers experience significant difficulty at retaining unique associations between objects and their location, particularly if the locations are similar and toddlers are not provided with object cues to orient them in their search (Newcombe et al., 2014). Development during early childhood brings about the ability to remember more specific spatial associations enabling the ability to minimize interference from having learned associations between objects and similar locations (e.g., Newcombe et al., 2014; Ribordy Lambert et al., 2016).

Previous research has also demonstrated that infants and young children retain information about temporal aspects of their experiences. Even young infants demonstrate tracking of temporal order rules in statistical learning paradigms (Tummeltshammer et al., 2017), and utilize temporal order information together to track object locations presented on a screen

(Kirkham et al., 2007). Moreover, in the domain of declarative memory, infants have demonstrated retention of temporal information with their imitation behavior and, although abilities to retain ordered actions are detected at the end of the first year (e.g., Carver & Bauer, 2001), the utilization of enabling actions in these young infants suggest that memory for temporal order requires substantial cueing and scaffolding. Development into the third year affords more independent recall of ordered actions of arbitrary, not enabling actions (Bauer et al., 1998).

Despite these remarkable abilities and early development, these studies have not compared memory for spatial and temporal features within the same paradigm, raising the questions of whether we might find the same advantage for memory for spatial location compared to memory for temporal order in toddlers that is found in older children (Lee et al., 2016). Our results are consistent with findings confirming that retaining temporal order is more challenging. Nevertheless, we cannot exclude that some aspects of our paradigm may have facilitated retention of spatial locations. Locations on the screen in our tablet game were marked by meaningful images (e.g., school, doctor, etc.). Although the use of these locations was advantageous for ecological validity, it is possible that memory for the association between characters and location was facilitated by the overlap between the physical location on the screen and the meaningful place appearing in that location. The fact that similar age toddlers have been found to have a difficult time retaining arbitrary associations between co-occurring objects (as pictures of characters and pictures of locations are co-occurring; Johnson et al., 2020) suggests that physical location may be the primary reason for stronger performance.

The difference between spatial and temporal memory was retained across delays, and no decline in performance was observed. Although declines during the one week delay were

expected, previous literature has consistently showed that repeated exposure and opportunity to imitate supports retention even in infancy (Bauer & Leventon, 2013). Future studies may include longer delays in order to probe the neural substrates of retention and forgetting. Our paradigm was designed to provide repeated opportunity for the toddlers to learn the association between the game and the song used to tag the experience to be delivered during sleep to probe hippocampal function. However, it could be modified to include behavioral assessments after the neuroimaging session to examine how hippocampal activation during sleep may predict long-term retention.

Our fMRI results revealed that toddlers' ability to recall the temporal, but not spatial, features of the game was significantly correlated with hippocampal activation in the right hippocampus. This supports the claim that songs can be successfully used, not only to tag the context of children's experiences (Prabhakar et al., 2018), but also more specific events or features of events, underscoring that this experimental approach can be used to probe various aspects of children's memories. Moreover, not only was memory for temporal features associated with activation in the right hippocampus for the target song presented in the identical form as during study, but also when it was played backward. When played backwards, the correlation with performance was significant bilaterally. In Prabhakar et al. (2018), only the correlation between behavioral performance and activation for Target > Novel was statistically significant; the correlation with Reversed > Novel was in the same direction but not reliable, leaving open the question of whether the song ought to be presented in its exact form in order to reactivate aspects of the original memory. The current findings provide evidence that hippocampal activation can also be triggered by the highly similar reversed song, suggesting some degree of flexibility in memory reactivation and, possibly, retrieval. Nevertheless, we

recognize that the level of similarity is high between target and reserved songs given that the elements of the original song (e.g., pitch, tone, timber, tempo, etc.) are maintained in the reversed versions of the songs and only the song's melody differs. Future research should confirm whether bilateral hippocampal recruitment is more likely under increased flexibility demands. Finally, given the presence of a song heard exactly as it was previously heard in our fMRI task, additional research should investigate whether reinstatement of a memory must first occur exactly as it was previously experienced in younger infants before it can be reinstated flexibly.

It is not clear why only memory for temporal order was associated with hippocampal activation in this study. Associations with retrieval of spatial features of episodic memory have been reported previously in fMRI studies with adults (Burgess et al., 2002; Moscovitch et al., 2005) and children (DeMaster et al., 2013), and hypothesized in toddlers (Sluzenski et al., 2004). It is possible that the high level of performance obtained here, matched with restricted range and given that only two games were played, reduced the chances to identify associations. The association with temporal order is interesting in its own right for at least two reasons. First, temporal order in imitation paradigms with infants and young children has been long considered a signature of an emerging episodic memory (Bauer, 2008). Second, the current results provide the first evidence of a link between the hippocampus and temporal memory in very young children, as it has been hypothesized for years (Bauer, 2005, 2008; Pathman & Bauer, 2012).

We had predicted that activations would be stronger in the right compared to the left hippocampus, based on previous findings by Prabhakar et al., (2018) and knowledge that changes in hippocampal structure may occur in the right hippocampus earlier than those in the left hippocampus (Uematsu et al., 2012). The stronger associations between activation of the

right hippocampus and temporal memory are consistent with this prediction. On the other hand, associations between activation in both the left and right hippocampus for the song played backward and temporal memory underscores bilateral functionality. Previous research has found that the hippocampus undergoes substantial volumetric increases in the first few years of life, particularly in the second and third years (Gilmore et al., 2012; Uematsu et al., 2012). This is about the same time that episodic memory emerges, particularly spatio-temporal contextual memory (Gomez & Edgin, 2016; Mullally & Maguire, 2014). It is believed that all of the subregions of the hippocampus are active when encoding or recalling both spatial and temporal features, but that the CA2 may have a greater pattern of activity in response to temporal features than to spatial features (Mankin et al., 2015). These findings, coupled with knowledge from animal studies that indicate hippocampal-dependent learning and memory emerge at timepoints consistent with the second and third years of human life (Dumas & Rudy, 2009; Raineki et al., 2010), indicate that these early memory abilities are hippocampally linked, but questions remain about specificity of that link regarding temporal memory and functional lateralization of the hippocampus.

Finally, we investigated two additional cortical regions, the parahippocampal and angular gyri, which are consistently found to be associated with episodic memory retrieval (Smith et al., 2004). In both regions, we found a similar pattern of results to the hippocampus in both the Target > Novel and Reversed > Novel contrasts that while hippocampal activation was correlated with temporal memory, it was not correlated with spatial memory. These findings underscore that hippocampal development does not operate in isolation to support the emergence of episodic memory abilities in early childhood. Future studies ought to investigate the contribution of

structural and functional connectivity of the hippocampus to cortical regions to the emergence of episodic memory.

There are several limitations in the present study. First, it is possible that children who slept easily represent a unique subgroup of participants and, therefore, it is possible that these results do not generalize to all children. The results of our preliminary results reveal, however, that there were no obvious differences between toddlers who did or did not successfully complete the neuroimaging session. Second, our lack of electroencephalography data prevents us from linking our results to specific sleep stages. Although we did not advance any prediction that requires the examination of sleep stages, future research would benefit from this characterization. Third, the task required toddlers to attend to both spatial and temporal information; it is possible that this may have interfered with the more demanding task, if this is the case, temporal order may be underestimated in this task, even though toddlers performed above chance across tasks.

Taken together, our findings reveal new links between hippocampal function and memory for temporal order, as assessed with a unique game event. These results contribute to a nascent literature on hippocampal and cortical contributions to early memory functioning and confirm that songs can be used to tag discrete episodes.

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Chapter 2

Memory for Space and Time in 2-year-olds

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Abstract

Although the capacity to remember spatial and temporal information may develop at different rates throughout childhood, its early development has rarely been examined within the same participants, using the same task, and across different time delays elucidating retention of different aspects of early episodic memories. We used a novel tablet game to investigate memory for objects' spatial locations and temporal order in a sample of toddlers ranging in age from 2 years to 2;8 years (*M* = 2;4 years, *SD* = 2 months; N = 73). We examined performance both immediately after an initial and an additional demonstration, following a 20-minute delay, and 1 week after learning; performance was also assessed following a new demonstration after the 1-week delay test. Using a linear mixed model, we found that toddlers remembered spatial locations better than temporal order, and temporal memory decayed more quickly and did not benefit from reminders compared to spatial memory, underscoring that early memory fragility may depend on the type of information being retained.

Keywords: episodic memory, spatial memory, temporal memory, memory development, relational binding

Introduction

Early childhood is a period of rapid learning and knowledge expansion (Atherton & Nutbrown, 2013; Bauer et al., 1999; Rowe et al., 2012). During this period, the emergent capacity to recall prior experiences begins to support children's ability to explore and learn about their environment (Gopnik, 2020) as well as share their experiences (Nelson & Fivush, 2004). Episodic memory, or the ability to recall specific events, involves retaining memory for the spatio-temporal context in which they occurred (Eichenbaum, 2017a, 2017b) and it has been argued that its early development may support the capacity to accumulate and share knowledge (e.g., Bauer, 2021). To date, there is a paucity of studies with children between 2- and 3-years of age examining retention of both spatial and temporal details within the same individuals and within a single task to enable a direct comparison of memory for these details. Moreover, no studies have examined 2- and 3-year-olds' retention across multiple delays. These are significant limitations in the current literature because important improvements in memory are expected at the transition from infancy into childhood, and these differences may depend on the nature of the information being recalled.

A direct comparison of toddlers' capacity to form and retain spatial and temporal associations within the same task provides an avenue to elucidate the early development of associative components of episodic memory. Research in children older than 3-years shows that memory for spatial information may emerge earlier and develop faster, reaching adult-levels earlier than memory for temporal order (Lee et al., 2016; Pathman et al., 2018a), suggesting the prediction that the emergence of memory for temporal order in early childhood (< 7 years) may be delayed compared to memory for spatial context. Although evidence contrasting this prediction has also been reported, such that spatial memory exhibited a more protracted

development from childhood into young adulthood (Guillery-Girard et al., 2013), there were differences in cognitive demands between the tasks used to assess each memory type, making it difficult to make direct comparisons between these two aspects of memory content. Nevertheless, there is evidence of memory for spatial context (Newcombe, 2019), as well as memory for temporal order (Bauer & Leventon, 2013; Bauer & Lukowski, 2010) in infancy, which suggests the capacity to remember spatial and temporal aspects of an event may emerge at the same time. Thus, it is unclear whether an advantage of spatial over temporal memory would be evident in early development. Hence, the goal of the present study is twofold. First, we sought to examine memory for events and their association with spatial and temporal context within a single task, as well as to assess these associations over varying delays. Second, we sought to examine whether spatial and temporal memory performance on our task (adapted from Prabhakar & Ghetti, 2020) showed similar results to a previously validated assessment after multiple delays to establish whether the results converge with tasks with different motor demands.

Memory for Spatio-Temporal Context

A nascent ability to retain spatial and temporal information regarding an experience can be detected in infancy (e.g., Bauer et al., 2000). With regard to memory for spatial information, Richmond and colleagues (2015) reported that during memory test trials, even 9-month-old infants looked longer at two objects that had switched their spatial position from the encoding phase (relative to a third object that remained in the original position), indicating recognition of spatial novelty and memory for the initial positions. However, 9-month-olds showed this result only if sufficient exposure was allowed during study, otherwise only toddlers (e.g., 18-month-olds) responded to the location switch with their looking behaviors. These results underscore encoding constraints to learning item-space associations in the first year of life. However, even

after the first 12 months of life, toddlers show difficulty recalling memories encompassing arbitrary item-space context associations if they are tasked with remembering more than one single object-location association. For example, in a study requiring toddlers to remember in which of 4 containers a toy in one room was hidden and in which of the same 4 containers a toy was hidden in a second room (Newcombe et al., 2014), 15- to 20-month-olds did not remember the unique association between toy and container (i.e., one container hid the toy in one room and another container hid the toy in a different room, and not the other way around). Toddlers aged 21- to 26-months could recall which specific toy went in which specific container in each room only when parts of the toy were provided to cue the memory, while the older toddlers (between the ages of 34- and 40-months) performed significantly above chance on the same task without needing any cues. In another line of research, toddlers as young as 18-months accurately retrieved toys hidden across several locations in two different rooms, but not if those locations lacked visual cues differentiating them (Ribordy et al., 2013). At approximately 25-months or later, toddlers could identify the correct location of a previously hidden toy without a local cue, but only if one object was hidden in one of the locations as opposed to a different toy hidden in each location, and at 43-months they were able to recall multiple objects' locations without any cues (Ribordy et al., 2013). Finally, using functional neuroimaging methods to determine possible neural explanations for spatial memory abilities in toddlerhood, Prabhakar and colleagues (2018) demonstrated correlations between toddlers' accuracy in their recall of which room (out of two) they had encountered a novel song and hippocampal activation for the same songs in 25- to 32-month-old toddlers. Overall, this literature suggests that at about 25-months of age, toddlers may be able to form and retain memories for unique object-spatial location associations, when more than one object and more than one location are encountered. However,

difficulties persist if more than one such association is being learned. Overall, this research suggests that toddlers rapidly improve their spatial memory abilities as they age and develop. Between 24 and 36 months, toddlers are successful at recalling unique associations between objects and spatial locations, even after delays (Newcombe et al., 2014).

Despite clear evidence of spatial memory in 2- and 3-year-old, its development continues to improve in childhood. Between 3.5 and 7 years, children show improved ability to retain multiple associations and locate 3 hidden treats among 18 locations (Ribordy Lambert et al., 2016). Although younger children (< 5.3-yeara) make more errors overall, the nature of mistakes was found to differ as a function of age with older children (> 5.3-years) choosing locations that were near the target locations when they made mistakes instead of choosing previously visited locations, whereas younger children did not show this bias toward nearby locations and chose both nearby and previously visited locations equally. Thus, older children not only remember locations better than younger children, but even when they cannot recollect precisely, they may retain an approximate memory for the location which might constrain the types of errors.

The ability to retain item-time associations, including temporal order, may also exhibit some fragility at the transition from infancy to childhood. Infants and toddlers under 32-months can demonstrate action sequences in a given temporal order when those actions are functionally dependent (Bauer, 1992; Bauer et al., 2000). In contrast, fully arbitrary sequences of actions with no functional relation among them pose significant challenge. For example, when faced with one exposure to a non-arbitrary temporal sequence, in which the completion of an action facilitated the completion of the next action, 16- to 20-month-old infants could replicate a given sequence even after a month delay. However, 13-month-old infants required multiple exposures in order to replicate the same sequences at all (Bauer & Leventon, 2013). Early ability to retain arbitrary,

non-functionally dependent, temporal associations in which there is no pre-existing or enabling relation among subsequent actions, over a delay, has not been observed until 28-months of age (Bauer et al., 1998). Importantly, Mooney and colleagues (2021) discovered an association between hippocampal activation in response to a previously learned song compared to a novel song and the temporal order of the actions that triggered that song in a touchscreen table game in 24- to 32-month-old toddlers, underscoring that hippocampal function can support temporal memory at this age. The role of the hippocampus in retaining temporal associations between sequences of actions during deferred imitation has been established with studies of amnesic patients (McDonough et al., 1995). As is the case for memory for spatial details, temporal memory continues to improve beyond the age 3, including during preschool years where marked improvements between 3- and 4- year-olds (Prabhakar & Ghetti, 2020) and beyond (Loucks & Price, 2019; Pathman et al., 2018b; Pathman & Ghetti, 2014).

Overall, these results suggest that although memory for spatial and temporal information shows vast improvement during development, 2- and 3-year-olds demonstrate the ability to retain arbitrary information about spatial and temporal context. These early capacities may reflect sufficient integration of the dentate gyrus and CA3 into the hippocampal circuitry (Insausti et al., 2010; Lavenex & Banta Lavenex, 2013), which are responsible for precise and flexible episodic memories (DeMaster et al., 2016; Ghetti & Fandakova, 2020; Lee et al., 2014).

To date, almost no studies with children younger than 36-months have examined arbitrary spatial and temporal associations using the same paradigm to test the two components within a shared learning scenario. One exception is the study conducted by Burns and colleagues (2015) involving the comparison of memory for 2D vs 3D stimuli. In this study, toddlers between 24- and 41-months of age learned a spatio-temporal sequence in which individual

characters were matched with individual hats (what-what associations), with boxes (what-where associations) and with the order in the sequence they were acted upon (what-when associations). They found that children performed above chance across ages and type of layout and that only older children in the 3D task tended to remember the events configurally (remember what-where-when or nothing) underscoring a later emergence of integrated memory representations. The trajectories of memory retention for spatial and temporal features across multiple delays were not examined in this study, preventing conclusions as to whether even a subtle fragility of one component of memory representations may delay the emergence of configural memories.

These abilities may develop and emerge together but may likely have dissociable developmental trajectories observed in spatio-temporal associative abilities in older children (7- to 11-years; Lee et al., 2016, 2020). Measuring memory for spatial and temporal associations within the same task and assessing the components of success in an incremental rather than all-or-nothing fashion, will allow for a direct comparison of these abilities during toddlerhood. The retention of arbitrary associations is present during this period, but the developmental trajectory is unclear.

Memory across Delays

The retention of spatial and temporal associations over a delay has been assessed substantially with very young children. There is a wealth of evidence that robust forgetting is experienced from infancy through early childhood (e.g., Bauer, 2005). The rate of forgetting in toddlerhood decreases with age and memory can be retained for longer durations. In a study with 16- and 20-month-olds, toddlers required only one exposure to replicate an imitation sequence after a delay of one month, while 13-month-olds required multiple exposures. Additionally, Bauer and colleagues (1998) found that it was not until 28-months of age that toddlers could

retain and reproduce arbitrarily ordered actions immediately as well as after a two-week delay. In a similar line of work, Saragosa-Harris and colleagues (2021) found evidence that associative memory accuracy increases from ages 3 to 5 years across delays, but the age differences were even greater when examining them at the one-week delay, consistent with the idea that younger children experience more forgetting (see also Benear et al., 2021; Scarf et al., 2013 for additional evidence of age-related differences in forgetting). While there are substantial age-related differences in memory retention over delays, it is still unclear whether retention over delays differs as a function of the type of information, including spatial and temporal. A better understanding of differences in memory decline as a function of detail would provide new insight into the nature of memory content and experiences in young children.

Although there is clear evidence of strong forgetting in toddlers under 24-months, it remains uncertain the extent to which apparently forgotten memories may still benefit from re-learning as suggested by saving effects (Cornell, 1979; Morgan & Hayne, 2006). Savings effects are observed when individuals require fewer repetitions to achieve a certain level of learning if some retention persists than when they initially learned something (Ebbinghaus, 1885). Savings in memory are speculated to occur through an integration of the memory formed through relearning with a previously formed, but partially inaccessible, residual memory trace (Isurin & Seidel, 2015). It has been argued that there are greater benefits of re-learning in toddlers over 18-months, which suggests that while memories may be more likely to be lost in infancy, they may become less accessible in toddlers whose memory traces may persist in some form (Bauer, 2005). However, it is currently unclear whether the opportunity to relearn equally benefits retention of spatial versus temporal information. If an advantage is observed in the retention of spatial versus temporal information, it is also possible that memory for spatial detail would

benefit more from relearning. Alternatively, if hypothesized difficulties with long-term retention of temporal information are due primarily to a retrieval failure (as opposed to a storage failure), then re-learning may be particularly beneficial for temporal information.

The Present Study

The primary goal of this study was to examine memory for spatial and temporal information within the same task and posing similar demands. We also sought to investigate the impact of delay and re-learning on memory for spatio-temporal information. We adapted a task from Prabhakar & Ghetti (2020), which was also used in Mooney et al. (2021). This task was developed to measure both spatial and temporal memory and will be compared to recognized associative memory paradigms to establish support for this measure. The task, a Tablet Matching Game, involved toddlers pairing 3 characters on the screen to 3 specific locations in the correct temporal order, following a demonstration. This task yielded a measure of spatial memory (determined by the number of correct spatial locations) and temporal memory (measured by the number of characters moved in the correct order). Two versions of the task were administered to each toddler in order to maximize trial numbers. Additionally, we administered an Imitation Puzzle Game, which also required remembering how to assemble a puzzle by placing its 3 pieces in certain spatial positions and a given order. This is a previously validated task to assess memory for temporal order in toddlers as young as 18 months (Barr et al., 2016; Dickerson et al., 2013), but we sought to extract a measure of spatial memory as well in order to compare the pattern of results in this task to our own.

We expected toddlers to remember spatial locations better than temporal relations and that longer time delays would result in disproportionately greater loss of memory for temporal order compared to spatial position, given the extended developmental trajectory of temporal

memory. We chose our delay lengths based on those commonly used in the literature. Typically, immediate recall is measured immediately following learning (Bauer et al., 1998), use of a 20-minute delay in the neuropsychological literature has been used as a signature of long-term memory (e.g. Vargha-Khadem et al., 1997), and a week delay requires retention across naturalistic time scales (Bauer, 1996; Bauer & Hertsgaard, 1993). Finally, we proposed two alternative expectations regarding savings. If temporal memory is disadvantaged due to difficulties with integration and retrieval, it may benefit more from re-learning compared to spatial information that is more easily retrieved. However, if the development of spatial memory is more advanced, it may benefit more so from relearning compared to temporal memory.

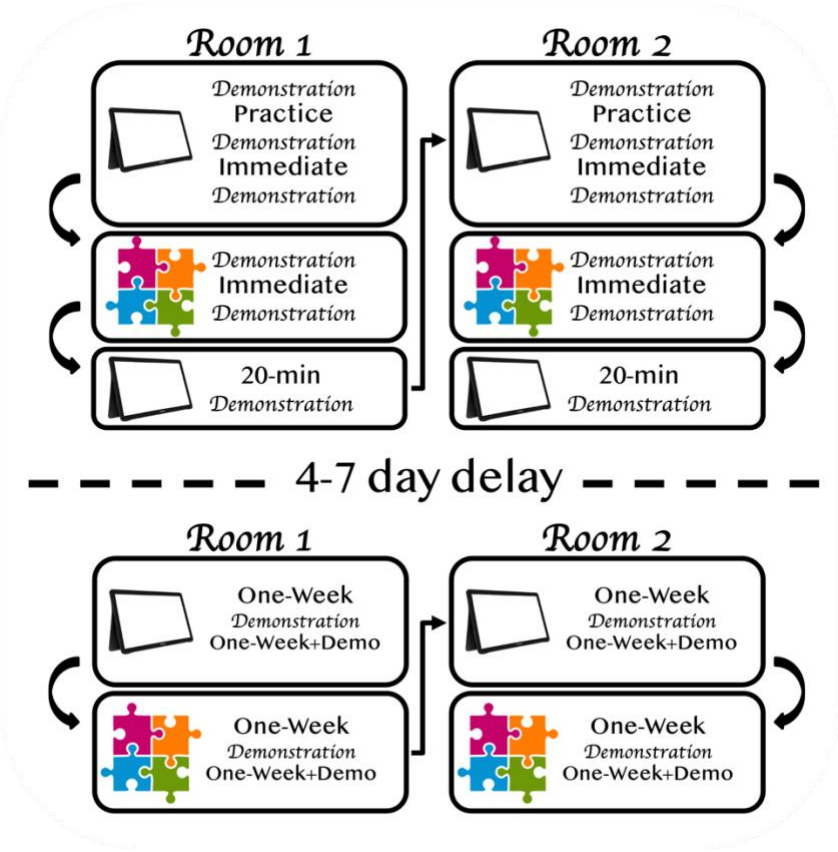
Methods

Participants. We assessed 73 typically developing toddlers (*M* = 2;4 years, *SD* = 2 months; Range = 2 years to 2;8 years; 58% Females). Participants included toddlers who were White (*n* = 46, 63.1%), African American/Black (*n* = 3, 4.1%), Asian/Asian American (*n* = 3, 4.1%), Multiracial (*n* = 12, 16.4%), and of unreported (*n* = 9, 12.3%) racial backgrounds; as for ethnic background, the sample included 23 (31.5%) Hispanic/Latinx toddlers, 40 non-Hispanic/Latinx (54.8%) toddlers, and 10 (13.7%) unreported. Parental income was also reported as ranges of $15,000 – $25,000 (*n* = 2; 4.9%), $25,000 – $40,000 (*n* = 4; 6.6%), $40,000 – $60,000 (*n* = 9; 14.7%), $60,000 – $90,000 (*n* = 20; 24.6%), over $90,000 (*n* = 31; 44.3%), and unreported (*n* = 7; 4.9%). Participants were recruited from community events or through a database of families contacted after childbirth and consented to be contacted about potential research participation. Toddlers were given a few books for their participation. Data collection was completed at the same time as data collection for Mooney et al. (2021), which employed the same task. None of the toddlers participating in this study were included in this previous study.

Materials and Procedure

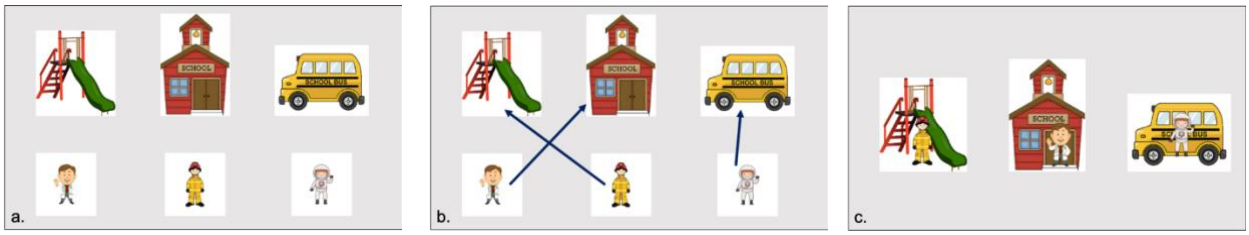
The experimental procedure included two laboratory visits. These visits were scheduled to be one week apart, $M = 6.12$ days, $SD = 1.60$ (See Figure 1).

Figure 1: Procedure Overview. Participants completed four trials (immediate, 20-minute delay, one-week delay, one-week delay+demonstration) of the Tablet Matching Game and three trials (immediate, one-week delay, one-week delay+demonstration) of the 3-piece Imitation Puzzle Task.



Session 1. During Session 1, toddlers first visited one room where they completed one version of the Tablet Matching Game, which involved learning to input a sequence of actions on a tablet to achieve a goal (turn on a song). The sequence required remembering the location of certain characters and the order with which they were placed at that location. The Tablet Matching Game began with the toddler being shown how to select the correct character image from an array of three characters (e.g., Astronaut, Doctor) and moving them sequentially, one at a time, to a location (e.g., Slide, School; see Figures 2a-c). We ensured there was no semantic match between the characters and their locations to prevent semantic knowledge from influencing toddlers' memory (Sipe & Pathman, 2021). The experimenter demonstrated the spatio-temporal sequence without naming the specific objects or locations, but using vague references (e.g., "Let's put this here") to prevent facilitating the performance of toddlers with better vocabulary skills. After toddlers were shown the sequence, they were asked to reproduce it (i.e., immediate – after first demonstration). We informed toddlers that the song would be played if they performed the task correctly, but it was actually based only on accurate spatial recall. Based on extensive pilot data, many toddlers switched the order of two actions and thus failed to reproduce the entire spatio-temporal sequence correctly when they were first taught it. We reasoned that letting the correct spatial position of the character suffice to hear the song (i.e., perfectly spatial matching irrespective of temporal matching performance) would prove helpful in supporting toddlers' motivation to stay on task.

Figure 2: Character-location matching tablet game. a. Toddlers are shown an array of three professional characters and three arbitrary locations. **b.** A specific matching procedure is performed in a specific order. **c.** Characters are matched to their prospective locations.

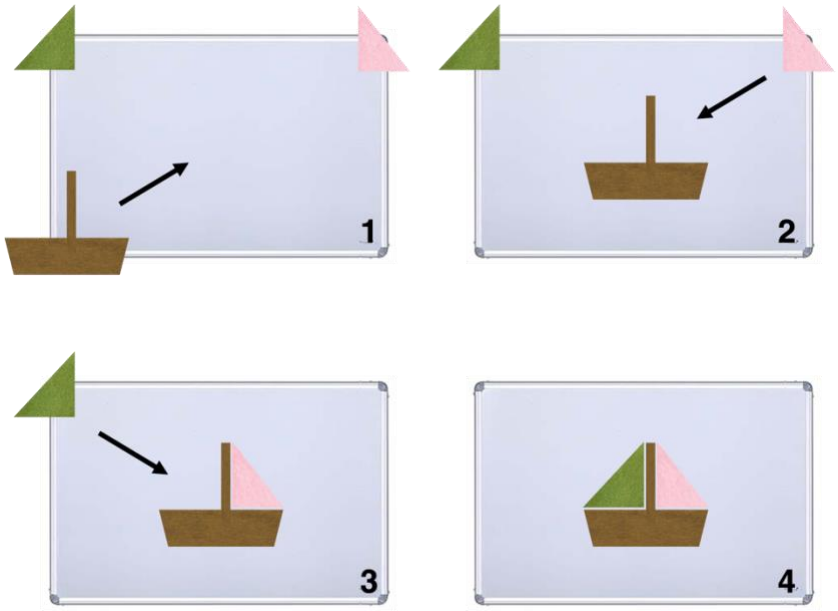


Location recall accuracy was calculated by the number of correctly placed characters out of 3. Since more than one character could be placed in the same location, chance performance was 0.33. Order recall accuracy was calculated as the number of characters chosen in the correct order. Chance performance level once again amounted to 0.33 after accounting for the dependency in temporal order trials. This chance comparison was calculated differently than chance for spatial memory, however, because the toddler's first choice in the sequence determined their possible chance performance and because the third choice entirely depended on the first two choices (i.e., it was impossible to assign the same order to multiple objects). If the first choice was correct, then chance across the task was 0.415 (i.e., the mean of 1/3 in the first trial and 1/2 in the second). If the first choice was the second-choice character, then the second choice was automatically incorrect and chance is 0.167 (i.e., the mean of 1/3 in the first trial and 0 in the second trial). Finally, if the first choice was the third-choice character, then the second choice could be correct or incorrect and chance corresponds to 0.415 (i.e., the mean of 1/3 in the first trial and 1/2 in the second trial). We averaged those three possible chance levels (0.415, 0.167, and 0.415) and determined 0.33 was the average potential chance level. Once the first practice attempt (immediately after first demonstration) was complete, the sequence was shown to the toddler again to provide an additional learning opportunity. After the experimenter completed their second demonstration, there was an immediate testing timepoint for the toddler (i.e., immediately after second demonstration). Together, the experimenter and participant then completed their third demonstration to ensure the toddler was exposed to the correct sequence again regardless of their immediate testing performance. After a delay of approximately 20 minutes, toddlers were tested on their ability to complete the Tablet Matching Game without a demonstration immediately preceding (20-minute delay). Following this 20-minute delay

timepoint, the experimenter once again completed the correct spatio-temporal sequence to ensure the toddler was exposed to the correct sequence regardless of their performance on the delay timepoint, this provided a final learning opportunity at Session 1.

During Session 1, toddlers also completed a 3-piece Imitation Puzzle Task (Barr et al., 2016), which was administered following the third demonstration and before the 20-minute delay test of the Tablet Matching Game. Two different imitation task puzzles were presented (e.g., boat, flower) in each room. Stimuli consisted of 3 abstractly shaped pieces attached via magnets to a magnetic 11"x 14" dry erase board. The pieces were initially placed in three of the four corners of the board, closest to their correct location to facilitate the toddlers' movement of the magnetic pieces. During Session 1, children were first shown the correct assembly (spatio-temporal order) of each imitation puzzle (see Figure 3), with the experimenter verbally emphasizing the order that the pieces are selected and moved (e.g., "first, this piece goes here"). Subsequently, the toddler was asked to complete the Imitation Puzzle Task (e.g., "can you show me how to make the puzzle?"; immediate recall), and then a final demonstration of the procedure was performed by the experimenter to ensure equal exposure to the correct sequence of assembly for all participants. Location accuracy recall was calculated as the number of puzzle pieces placed on the correct section of the board. We elected to use this method to assess accuracy, as opposed to the point in which the individual puzzle pieces touched other puzzle pieces (Subiaul et al., 2016) to reduce the motor demands of the task and make it more comparable to the Tablet Matching Game. Results using the original method are reported in the Supplemental materials (Supplemental Figure 1). Order accuracy recall was calculated as the correct number of pieces selected in the correct order.

Figure 3: 3-piece Imitation Puzzle Task. Toddlers are shown a 3-piece puzzle sequence on a magnetic white board with felted magnetic pieces. Complete puzzles represented known objects (e.g., boat, plane, flower, etc.).



After completing these tasks in the first room, toddlers were given a break before visiting a second room. There, toddlers followed the same procedures of the first room with a new version of the Tablet Matching Game and with two additional puzzles not used in the first room (e.g., train, boat). We counterbalanced across participants which version of the Tablet Matching Game and which puzzles were completed in the first and second room.

Session 2. After reacclimating toddlers with the lab, they once again visited the first room, and completed the Tablet Matching Game after a delay (one-week delay). After they demonstrated their recall, the experimenter demonstrated the correct sequence and toddlers were provided with one more opportunity to complete the sequence (one-week+demonstration).

The Imitation Puzzle Task was completed after the Tablet Matching Game once again and toddlers were initially asked to assemble the puzzle (one-week delay) without first observing a demonstration. After the toddlers' attempt, the experimenter demonstrated the correct puzzle assembly, and then toddlers were instructed to assemble the puzzle one final time (one-week+demonstration). After completing these procedures in the first room, they moved to the second room where they completed the other versions of the task in the same manner. First and second rooms, as well as tasks completed in each room, were the same across Session 1 and Session 2.

Results

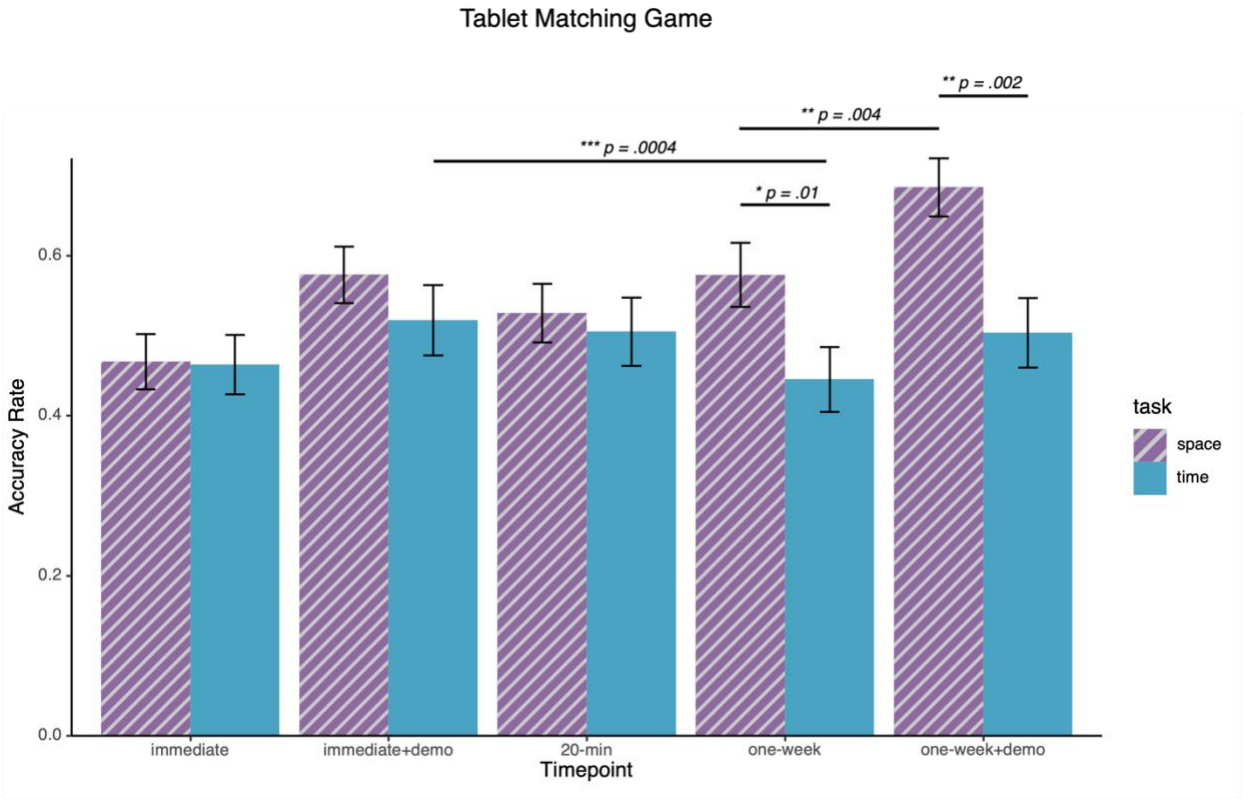
For the Tablet Matching Game, accuracy rates were calculated for memory for correct spatial locations (i.e., rate of correct placement of characters at the correct location) and memory for temporal order (i.e., rate of correct order with which characters are moved to be placed in locations, regardless of correct spatial matching). We conducted a linear mixed model (see Figure 4) evaluating the effects of age as a continuum, delay (immediate/after learning,

immediately after an additional demonstration, 20-minute delay, one-week delay, and one-week+demonstration), and detail type (spatial location or temporal order). Our model intercept was set at the immediate test after 2nd demonstration and the spatial task was used in the intercept. This was done in order to assess whether differences in memory over time and between task types were reflective of a deviation from the traditionally superior memory type (i.e., location) and ensured sufficient opportunity to encode (i.e., after two exposures). Our mixed model revealed a significant effect of delay, $F(4, 912.58) = 2.46$, $p = .04$, and of detail, $F(1, 899.71) = 11.14$, $p = .0009$. This indicates that children perform better on memory for locations, $M = 0.54$; $SD = 0.37$, than for the order with which individual characters visited the locations, $M = 0.47$; $SD = 0.41$. However, there was also a significant interaction between delay and detail ($F(4, 899.25) = 2.56$, $p = .037$) that was driven by several findings. First, spatial memory was better than temporal memory only after a delay (one-week delay $t(1,901) = -2.59$, $p = .01$), and after relearning (one-week delay+demonstration; $t(1,899) = -3.15$, $p = .002$), whereas no differences were found in the immediate test, $t(1,898) = 0.25$, $p = .80$, the test following a second demonstration, $t(1,896) = -1.25$, $p = .21$, and in the 20-minute test ($t(1,897) = -0.19$, $p = .85$), suggesting that the advantage of spatial memory is evident only after delay (i.e., one-week delay). Moreover, temporal memory declines significantly from immediate+demonstration to the one-week delay, $t(1,908) = -3.53$, $p = .0004$, but that was not the case for spatial memory, $t(1,910) = -0.84$, $p = .40$.

Finally, there were no differences between the immediate timepoint and at one-week delay+demonstration performance in the temporal portion of the task, $t(1,912) = -0.73$, $p = .47$, yet memory for spatial locations was better after re-learning compared to initial learning, $t(1,325) = 2.918$, $p = .004$, indicating that a reminder after a delay was effective only for spatial

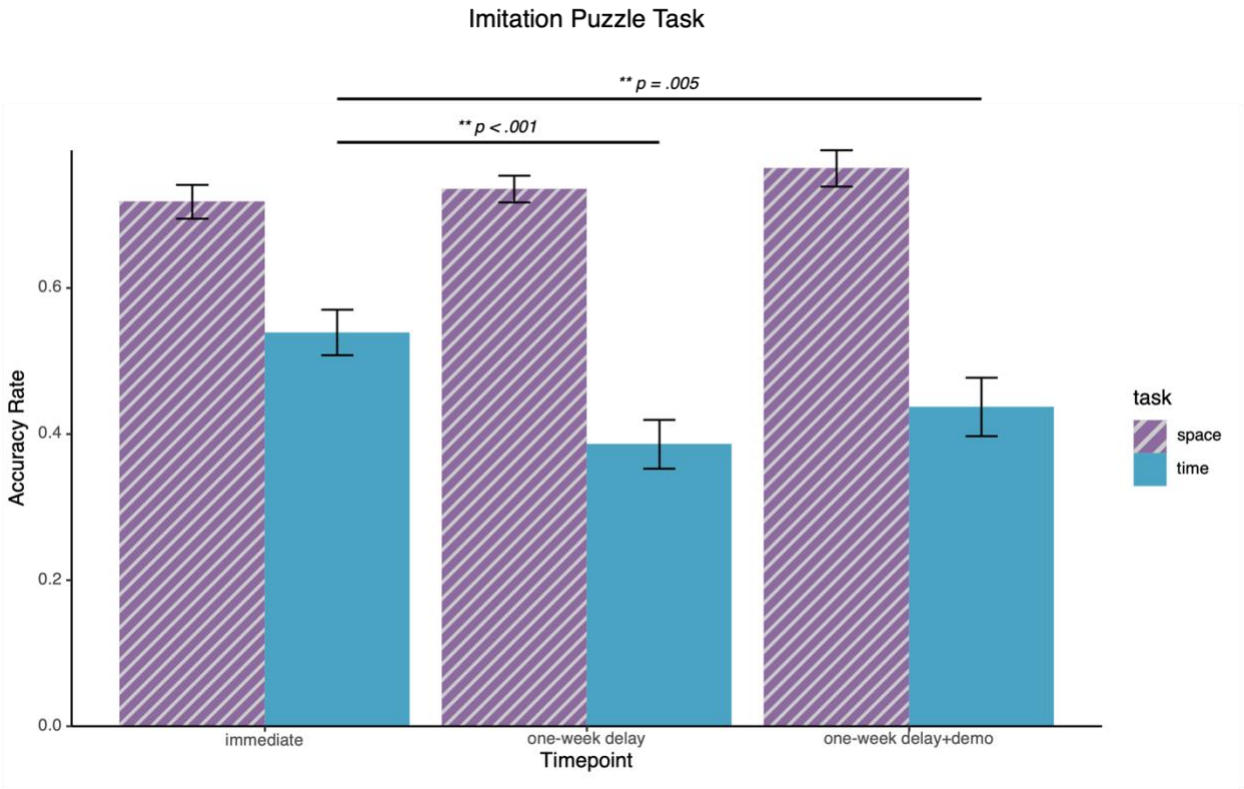
details. There was only a non-significant trend of older toddlers outperforming younger toddlers, $F(1, 186.49) = 3.12$, $p = .08$. Participants performed above chance, on average, across all trials, $t(1,972) = 16.39$, $p < .001$.

Figure 4. Tablet Matching Game Accuracy. Results from mixed model. Toddlers performed better on spatial memory details compared to temporal memory details, specifically after a one-week delay. Timepoints consist of: immediate (recall following learning), immediate+demonstration (recall following a demonstration of the correct sequence), 20-min (recall 20 minutes after learning), one-week (recall one-week after learning), and one-week+demonstration (recall following a final demonstration of the correct sequence).



Additionally, we conducted a repeated measure linear mixed model evaluating the Imitation Puzzle Task (see Figure 5). For this task, we investigated spatial proximity only (See supplemental materials for spatial orientation and proximity analyses). Consistent with the previous literature on this task (Dickerson et al., 2013), we investigated approximate location accuracy of pieces as a measure similar to the spatial demands of the Tablet Matching Game and seemingly less difficult in terms of motor demands. The linear mixed model again evaluated the effects of age, delay (immediate, one-week delay, after one-week+demonstration), and detail type (location or order) in the context of spatial proximity. Our mixed model revealed a significant effect of delay, $F(2, 665.90) = 13.86$, $p < .001$, and of detail, $F(1, 672.10) = 194.88$, $p < .001$. There was also a significant interaction of delay and detail ($F(2, 663.35) = 4.84$, $p = .008$). As in the Tablet Matching Game, there was no significant effect of delay for spatial trials ($t(1, 671) = 1.55$, $p = 0.63$, whereas for temporal order, toddlers performed significantly better at the immediate timepoint compared to the one-week delay, $t(1, 667) = 6.07$, $p < .001$, and the one-week delay+demonstration, $t(1, 669) = 3.60$, $p = 0.005$. Unlike the Tablet Matching Game , toddlers remember more about spatial location than temporal order starting from immediate assessment in the Imitation Puzzle Task, $F(1, 194) = 5.95$, $p < .001$.

Figure 5. Graph of Imitation Puzzle Task. Results from mixed model. Toddlers performed better on the immediate recall, than on either the one-week delay or one-week delay+demonstration. Toddlers also performed better on location accuracy than on temporal order. Timepoints consist of immediate (recall following learning), one-week (recall one-week after learning), and one-week+demonstration (recall following a demonstration of the correct sequence).



Finally, the one-week delay+demonstration memory was not significantly greater than memory at the one-week delay, $t(1, 666) = -2.36$, $p = 0.17$. The difference between the immediate recall and the one-week delay+demonstration recall indicates significant temporal memory decline across delays that does not benefit from reminders or savings.

In addition, there was a significant effect of age, $F(1, 66.89) = 9.50$, $p = .003$. This is indicative of older toddlers performing better than younger toddlers, which did not interact with any of the other variables. Participants performed above chance, on average, across all trials, $t(1,742) = 21.34$, $p < .001$. Results obtained using an alternative coding scheme for spatial memory are reported in the Supplemental Materials (Supplemental Results and Figure 1).

All findings are reported in Table 1. Performance on the two tasks was correlated. This was the case both within task (correlation between spatial and temporal memory for each task), $rs > .30$, $ps < .05$, and between tasks (imitation vs. tablet) across ages and delays, $rs = .26$, $ps < .05$.

Table 1

Means and standard deviations for the Tablet Matching Game and Imitation Puzzle Task across different trials.

	Tablet Matching Game				Imitation Puzzle Task			
	space		time		space		time	
Delay	*M*	*SD*	*M*	*SD*	*M*	*SD*	*M*	*SD*
Practice	0.47	0.30	0.46	0.32				
Immediate	0.58	0.30	0.52	0.38	0.72	0.20	0.54	0.27
20-min	0.53	0.31	0.51	0.36				
One-week	0.58	0.34	0.45	0.35	0.74	0.16	0.39	0.29
One-week+Demo	0.69	0.31	0.50	0.37	0.76	0.21	0.44	0.34

Note. M and *SD* represent mean and standard deviation, respectively.

Discussion

The primary goal of this study was to compare retention of memory for spatial versus temporal details within the same task and across several time intervals and opportunities to learn. The examination of the ability to retain these details is critical to our understanding of the early foundations of episodic memory (Bauer & Lukowski, 2010). In order to achieve this goal, we adapted a touchscreen tablet-based matching task (Prabhakar & Ghetti, 2020) that proved successful at engaging 2-year-olds, assessed arbitrary spatio-temporal associations, and is a promising complement to other associative memory tasks. We additionally assessed memory on an Imitation Puzzle Task requiring toddlers to place puzzle pieces in a certain spatial location and temporal order to gain evidence of the robustness of our findings on the table task.

Although there is ample evidence that the ability to remember specific events emerges in the first three years of life (Bauer, 2005; Bauer et al., 2000), very few studies have investigated the retention of spatial and temporal components within a single task and to our knowledge no study has examined 2-year-olds' retention of spatial and temporal details concomitantly across several delays. Although there is a wealth of literature supporting improvement of spatial (Newcombe et al., 2014, Ribordy et al., 2013) and temporal (Bauer et al., 1998, Bauer & Leventon, 2013) memory abilities during the infant and toddler years, more work is needed to understand early development of spatio-temporal memory and its persistence over delays. The present study aimed to begin to fill these gaps in the literature.

We expected, consistent with previous literature in older children (Lee et al., 2016; Pathman et al., 2018), that 2-year-olds would have better spatial compared to temporal order recall. With regard to delay, we expected that memory loss over delays (Bauer, 2005; Bauer et al., 1998; Bauer & Leventon, 2013) would be more pronounced for temporal details. Children

performed better on the spatial memory aspect of both tasks, which is expected based on investigations of memory abilities discussed earlier (e.g., Scarf et al., 2013). A key aspect of episodic memory is the ability to bind or associate together the various elements of an experience to retain information about the co-occurrence of these elements (Eichenbaum & Cohen, 2004). Previous work indicates that limited binding of either spatial or temporal information may also contribute to difficulties with recall of early episodic memories as a whole (Burns et al., 2015; Ribordy Lambert et al., 2016). With the comparison of our Tablet Matching Game to the Imitation Puzzle Task, we expand upon previous findings (Bauer & Leventon, 2013) that memory for item-space associations may be stronger earlier in development than item-time associations. While the current study did not directly examine the hippocampus, a brain structure known to support relational binding abilities, it undergoes volumetric changes for subregions at different rates and on different timescales during development (Lee et al., 2014, 2020), with the hippocampus being particularly adept at bridging gaps or identifying differences in associations (Staresina & Davachi, 2009). Spatial details, while visually salient, may be more readily differentiated than temporal details which have fewer tangible indicators. Moreover, a previous study using the same behavioral paradigm (Mooney et al., 2021) reported a correlation between memory for temporal order across delays and hippocampal activation associated with the song played at the completion of the task; the correlation with spatial memory was not significant. It is possible that higher performance levels reduced the score range and thus the probability of finding a significant correlation with spatial memory. However, it is also possible that the availability and utilization of additional cues (e.g., landmarks at spatial locations provided by a meaningful object) may have reduced hippocampal contributions, and, more generally, retrieval demands during task completion. This is consistent with research showing that children 18-

months to 5-years remember the location of hidden objects better if they are marked by a proximal landmark compared to if they are not and allocentric spatial representation is required (e.g.,Ribordy et al., 2013). However, even when memory for location and temporal order were compared for tasks requiring allocentric representations, children under 5-years seemed to struggle more with recalling temporal information (Ribordy Lambert et al., 2016), suggesting that the availability of local cues may not fully explain the difference. Moreover, we note that the patterns of results for spatial memory are similar to those of the puzzle task in which no local cues were used. Nevertheless, research comparing memory for spatial, temporal and spatio-temporal associations in young children is rare, and further research with the Tablet Matching Game should be conducted to directly compare memory performance with and without meaningful or arbitrary local cues, with and without stochasticity of spatial-temporal relations. As such, we assert that the task demands are as consistent as possible across spatial and temporal memory.

We also examined whether toddlers' spatial and temporal memory performance decayed differently over time after multiple delays. The fact that levels of performance for spatial and temporal memory were comparable after the first demonstration on the Tablet Matching Game suggests that the differences observed cannot be readily accounted for by difficulties with encoding temporal information when task demands between spatial and temporal conditions are matched. Instead, these differences likely have to do with how these different aspects of memory become solidified and are then retained over time. Consistent with previous research demonstrating consistent memory loss over time (Bauer, 2008; Bauer and Leventon, 2013), the accuracy results from the Tablet Matching Game and the Imitation Puzzle Task indicate some degree of forgetting over time. Based on the current results showing no differences between

spatial and temporal information at the immediate delay in the Tablet Matching Game, one could extrapolate that hippocampal contribution to encoding at this early age may operate similarly for spatial and temporal information, and that differences may emerge during storage or retrieval. Continuous improvement of relational binding occurs throughout development, and dependence on the hippocampus is likely one of driving factors (Lee et al., 2016, 2020; Mooney et al., 2021). Recent work, investigating the interaction of hippocampal recruitment during encoding and memory performance, suggests that the degree of hippocampal utilization varies by both age, with older children recruiting the hippocampus more, and performance, with greater hippocampal activation during encoding predicting better subsequent performance (Geng et al., 2019; Ghetti et al., 2010). Differences in hippocampal activation as a function of age and performance are found during retrieval (Sastre et al., 2016) and extend into adolescence (Selmeczy et al., 2019), suggesting that hippocampal function along with its connectivity with relevant cortical regions (Tang et al., 2020) might help explain early memory retention as well. Future studies should examine how the contribution of these brain regions changes with the opportunity for repeated learning in predicting retention over varying delays at different early ages.

The development and persistence of memory ability is not the same across spatial and temporal details. Memory for space and time may employ unique cognitive processes (van Asselen et al., 2006) and brain networks (Ekstrom & Bookheimer, 2007; Staresina & Davachi, 2009). Moreover, there is evidence that spatial and temporal features may be differentially associated with different hippocampal subregions (Kyle et al., 2015; Lee et al., 2020). The significant interaction of delay and type of information revealed that spatial memory persisted more than temporal memory after a delay. After a one-week delay, temporal memory declined

significantly in both tasks, while spatial memory did not. We expected that spatial and temporal memory would exhibit different developmental trajectories in toddlerhood, with temporal memory ability developing later than spatial memory (aligning with previous research with older children and adolescents; Lee et al., 2016, 2020; Picard et al., 2012). We found that toddlers retained considerable information, but that improvement in memory after a new demonstration a week after initial learning only benefitted spatial memory. This is consistent with the hypothesis that more persistent spatial memory representations may show savings during subsequent learning opportunities. In sum, in our sample of 24- to 32-month-old toddlers, spatial memory is on average superior, resists decay, improves with age, and benefits from relearning to a greater extent than temporal memory.

The fact that a difference between memory for spatial and temporal aspects of the task was found in the immediate test in puzzle task, but not the Tablet Matching Game, underscores the potential that other factors, including motor demands necessary to demonstrate memory, may additionally contribute to the pattern of results. It is possible that toddlers' focus on placing and orienting puzzle pieces may have interfered with processing temporal information. Differences in the saliency or importance of spatial and temporal features of events may play a large role here. For example, an additional spatial demand and critical requirement of the Imitation Puzzle Task, unlike the Tablet Matching Game, is that each piece must be correctly positioned relative to each other to complete the final figure. Additionally, toddlers may face some challenge due to the unique motor demands in each of the tasks, motor skills such as those needed to use a touch-screen tablet as well as the fine motor skills associated with moving and orienting puzzle pieces. Evidence of reduced memory for temporal information starting at the immediate test may suggest that the placement of puzzle pieces takes precedence, and the pattern of results is

different in the puzzle task if performance on the puzzle task is assessed based on stricter criteria for puzzle piece placements (Supplemental Figure 1). The failure to find reliable saving effects on the puzzle tasks similarly suggest that other demands may have interfered with performance. These considerations underscore the importance of matching motor or other memory-unrelated demands. Our Tablet Matching Game also limits the spatial locations available for choice, making it more directly comparable to the measure of temporal memory (for both measures there are only three choices in location/character). Despite these potential limitations, the Tablet Matching Game and the Imitation Puzzle Task both allowed for distinction of the retention of spatial and temporal details.

Other considerations regarding the memory development of the toddler years are the emergence of several other aspects of cognition, including the emergence of the sense of self, abstraction, and language abilities (Alberini & Travaglia, 2017). As the ability to recognize oneself and one's body as an individual entity emerges around 24 months with sense of their action on the world emerging around 14 months (Rochat, 2010), so too may emerge the ability to spatially place and recall items and events in relation to oneself. Similarly developing language abilities may impact toddlers' ability to create and maintain memories for that type of information, given the explosion of language abilities during this age. Spatial descriptors such as 'under' and 'next to' begin to emerge around 14-months of age, continuing until approximately 30-months (Shimpi & Waterfall, 2019) while temporal descriptors such as "before" and "after" emerge between 36- and 52-months (Zhang & Hudson, 2018). However, to date there is no evidence indicating whether these language abilities predate memory abilities or are dependent upon them. Future directions should include a systematic investigation of the role of arbitrary vs functionally dependent actions within a methodologically similar task as well as a systematic

investigation of the role of these language abilities in conjunction with the development of spatio-temporal memory associations. We can begin to unravel the true nature of episodic memory development only by conducting a thorough review of how other cognitive skills contribute to spatio-temporal memory.

Our research aligns with existing studies on memory for spatial and temporal details in older children. For example, 3- and 4-year-olds tested with this same task exhibited recall of spatial and temporal information (Prabhakar & Ghetti, 2020), with better memory for temporal order. The continued improvements in precision, flexibility during childhood in both spatial and temporal memory tasks (Arterberry & Albright, 2020; Benear et al., 2021; Canada et al., 2020; Newcombe & Huttenlocher, 1992; Ribordy Lambert et al., 2016) suggests continued refinement of the same abilities detected in toddlers. Continuity can also be gleaned from studies examining retention over delays in older children. The ability to remember associative pairs over delays improves with age; 4- and 5-year-olds retain this memory over intervals of 5 minutes, 24 hours, and one week. In contrast, 3-year-olds struggle to maintain such memory for a week-long delay despite initial successful recall at shorter intervals (Saragosa-Harris et al., 2021). The toddler years are pivotal, setting the foundation for these and further memory enhancements.

Ultimately, episodic memory has vast implications on how we can successfully navigate our lives. Episodic memory is necessary to navigate many daily challenges, such as memory guided planning—the ability to utilize past experiences and knowledge to develop plans in new contexts (Blankenship & Kibbe, 2019; Prabhakar & Ghetti, 2020). The relative fragility of memory for temporal compared to spatial memories provides insight on the kind of situations that may prove particularly challenging for young children. For example, it is possible that reduced memory for temporal information may help explain why young children encounter

disproportionate difficulty with bridging current memory states to future-oriented thought even when the future is immediate (Blankenship & Kibbe, 2022; Kliegel & Jäger, 2007; Prabhakar & Ghetti, 2020; Ślusarczyk et al., 2018).

More generally, characterizing the developmental trajectory of spatial and temporal memory can provide insight on how different aspects of memory can guide young children as they face novel situations or learning challenges. Taken together, our findings contribute to a growing of literature on early memory functioning and confirm unique developmental trajectories of spatial and temporal memory.

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Chapter 3

Hippocampal Contribution to Context Discrimination in the Second Year of Life

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Abstract

Research has suggested that the ability to retain distinguishable memory representations of similar events emerges in the third year of life in correspondence to refinement of hippocampal processes. However, forms of event memory discriminations may be detectable earlier than previously thought. In the present study, we familiarized fifty-eight 18 to 23-month-old infants to one face-song and two word-object associations in each of two similar contexts. In a canonical word learning task, infants showed memory for the object labels. On an eye-tracking task, infants were presented with songs and words and they showed evidence of a visual preference for faces and objects associated with corresponding auditory stimuli. This preferential looking for words was only evident when the distracter object came from a different context compared to the same context. In response to the same words and context-associated songs being heard, significant clusters of hippocampal activation were observed.

1. Introduction

Young children show remarkable learning abilities (Bjorklund, 2022), which enable them to explore their world and eventually share their experiences with others (Fivush et al., 2011). Early childhood is characterized by the burgeoning development of episodic memory, the capacity to recall specific past events within their spatial and temporal contexts, laying the foundation for the accumulation of knowledge among young learners (Atherton & Nutbrown, 2013; Bauer, 2021; Bauer et al., 1999; Eichenbaum, 2017a, 2017b; Gopnik, 2020; Nelson & Fivush, 2004; Rowe et al., 2012).

Infants, even as young as six months, exhibit the ability to recall specific actions after short delays, demonstrating early competencies in recall memory (Bauer, 2005). Early findings indicate that infants can demonstrate memory for spatial information, such as recognizing a change in the location of objects, albeit with age-dependent constraints on encoding item-space associations (Newcombe et al., 2014; Ribordy et al., 2013; Richmond et al., 2015). This body of work suggests a significant improvement in spatial memory abilities as children approach the age of 2- to 3-years, with the ability to recall specific object-location associations becoming more refined and less reliant on external cues (Prabhakar et al., 2018). In contrast, the development of memory for temporal information, such as the order of actions, appears to present challenges for younger toddlers, with more arbitrary sequences of actions requiring multiple exposures for successful recall (Bauer, 1992; Bauer et al., 2000). These burgeoning but immature abilities beg the question as to whether they suffice for forming and retaining discriminable memory representations of events that share some similarities in spatio-temporal structure.

1.1 Different Representations for Difference Events: Emerging Abilities

An essential facet of episodic memory is the ability to discriminate between similar events, enabling the individual to distinguish where and when a specific instance of an event occurred. Without the ability to discriminate between specific events, individuals would only retain general information about their past. This discrimination requires that memories are not only formed and recalled but are also

encoded within a spatial and temporal context. Greater memory performance in the same environment as learning is a long standing and well documented observation (Karpicke et al., 2014; Smith, 1979; Smith & Vela, 2001), which suggests that information about the context is integrated in memories and it is a powerful cue to reinstate a unique memory.

In her pivotal 1999 paper, Rovee-Collier fundamentally advanced our understanding of infant memory, underscoring the impact of context on memory retrieval. The mobile conjugate reinforcement task was used to assess infants' memory through a procedure where an infant's leg was attached via a ribbon to a mobile above their crib, enabling the infant's movements to cause the mobile to move. This setup allowed 2- to 6-month-old infants to learn that kicking their leg resulted in the mobile's movement. An increase in the infant's kicking rate when re-exposed to the same context without direct reinforcement indicated recall of the mobile conjugate training within a specific environmental context. These findings laid the groundwork for a new way to assess memory in infancy. Infants were able to recall specific actions (such as kicking their feet to move a mobile) when they are in the same context (in the same crib where they originally learned that kicking results in the mobile moving) where the memory was initially formed. This suggests that the context surrounding an event plays a crucial role in how memories are encoded and accessed, even from a very early age. The importance of context reinstatement in promoting early memory retrieval has been confirmed in several other studies across multiple methods (e.g., (i.e., visual preferences; Robinson & Pascalis, 2004). Although these results have been primarily interpreted as demonstrations of infants' retrieval rigidity requiring the highest degree of overlap between encoding and retrieval conditions (i.e, encoding specific principle; Tulving & Thomson, 1973), they also show that information about spatio-temporal context is retained in some form even in young ages.

With development, there is a notable shift from context-bound memory to a more flexible system. Robinson and Pascalis (2004) found that while infants showed difficulty recognizing objects in a changed background, toddlers around 18 months displayed a developmental leap, recognizing objects irrespective of the original context. This suggests an evolving capability for abstraction, enabling memory retrieval

beyond the confines of the initial learning environment. Such flexibility points to a maturation of the hippocampus, integral to developing a more adaptive memory system (Bernardi et al., 2020).

However, other results stand in contrast with these findings. For example, in a study requiring toddlers to remember in which of 4 containers a toy in one room was hidden and in which of the same 4 containers a toy was hidden in a second room (Newcombe et al., 2014), 15- to 20-month-olds did not remember the unique association between toy and container (i.e., one container hid the toy in one room and another container hid the toy in a different room, and not the other way around). Toddlers aged 21- to 26-months could recall which specific toy went in which specific container in each room only when parts of the toy were provided to cue the memory, while the older toddlers (between the ages of 34- and 40-months) performed significantly above chance on the same task without needing any cues. The need for cueing in this study may indicate an inability to effectively discriminate between contexts until 34-months of age, despite the potential retention of contextual elements discussed previously.

Similarly, Hala et al. (2013) suggested that context discrimination abilities did not emerge until 2.5 years old. When placing farm animals in a model farm, children in this study could accurately attribute who had placed which animal had been placed by which person when the spatial array of farm items remained intact. By age 4, children are able to accurately recall activities and the setting (context) in which the activities occurred. In a subsequent study the setting even served as a cue for recall of the activity (Bauer et al., 2016). When searching for three hidden treats, 3.5 to 7 year old children displayed a growing ability to correctly identify the specific locations where events (hidden treats) occurred, both when there was a single trial or multiple trials. This ability improved with age and suggests improvements in both spatial and temporal context discrimination (Ribordy Lambert et al., 2016).

In conclusion, based on the literature reviewed, there seems to be an apparent inconsistency regarding event representation in the second year of life. On the one hand, even relatively young infants respond to changes in context (e.g., Rovee-Collier, 1999) suggesting that specific information about event context is retained. On the other hand, studies that have specifically examined toddlers' discrimination

between similar events has documented clear difficulties (Bauer et al., 2016; Hala et al., 2013; Newcombe et al., 2014; Ribordy Lambert et al., 2016) suggesting that toddlers may retain sufficient information to trigger memory retrieval when the encoding context is presented, but the memory may not be precise enough to support its differentiation of similar events. However, the studies that have shown these limitations were uniformly conducted with paradigms in which toddlers are asked to respond to verbal cues or engage in object searches, requiring goal-directed memory behaviors. It is possible that tasks that decrease direct retrieval demands, such as those that revealed the context-reinstatement effects (Howe et al., 1993; Robinson & Pascalis, 2004; Rovee-Collier, 1999) would prove effective at revealing emerging abilities to discriminate similar events.

1.2. Preferential Looking and Associative Memory in Infancy

While very young children may not be fully capable of articulating what they remember, their eyes betray their memory. Preferential looking techniques exploit the inherent preference infants show for what they find interesting, including novelty. Assuming that a familiar visual has been sufficiently encoded into their memory, this preference for novelty provides an indirect measure of the infant's ability to recognize and remember visual stimuli (Fagan, 1970). Early work using visual paired comparison paradigms demonstrated that even infants as young as 2 months show a visual preference for new compared to old stimuli, they look longer at novel patterns and faces compared to familiar ones (Fantz, 1964).

Understanding this preference for novelty has given researchers a unique opportunity to explore recognition and memory in infants that cannot yet verbalize their memory for stimuli. One study suggested that 19- to 31-month-olds exhibit a preference for novel over familiar objects. However this preference was significantly weaker when the objects shared a common label, suggesting that label or conceptual similarity plays a special role in recognition and novelty preference in children under three (Daehler & O'Connor, 1980).

Visual preference has also been used to track memory for contexts or associations. By manipulating the distractors from completely novel to be a deviation from a previously learned association, infants' expectations are parametrically violated, eliciting more time spent looking at a distractor as it is more novel or more dissimilar to a previously learned association. This is theorized to be due to the need for additional learning to make sense of the new association (Roder et al., 2000). Consistently, two-year-olds, across two studies, displayed visual preference for objects in a pair that violated learned expectations, overcoming preference for centrally located stimuli (Johnson et al., 2020). Other research has illustrated that not only do infants respond to novelty but also show substantial capacity for relational memory and contextual discrimination. Studies by Richmond et al. (2004; 2015) reinforce these findings, demonstrating that infants' and toddlers' preferential looking toward stimuli that violate previously learned associations can be influenced by spatial relationships and degree of familiarization with learned associations. This provides support for a discerning preference for directing visual attention to opportunities for learning. These studies underline that preferential looking is not merely a response to novelty but a more complex interaction involving memory recall, degree of exposure, and even relational understanding.

When novelty or a violation of learning is not present, humans tend to look toward visual information that matches other information they are exposed to, such as sounds and smells. For example, Spelke (1979) presented 4-month-old infants with two events concurrently and an auditory stimulus that matched one of the events (e.g., a donkey jumping on a table and a person clapping hands – audio was clapping sounds). Infants looked significantly longer at the audio matching scene than the non-matching scene. Similarly aged infants looked towards scenes that matched the language they were hearing and matched learned words and phrases to images representing their meaning (Golinkoff et al., 2013; Hirsh-Pasek & Golinkoff, 1996). Finally, Yu and Smith (2011) reported that 14-month-old infants who formed strong associations between objects and the words associated with them looked longer at the correct

object referents during testing and showed fewer gaze shifts between matched and mis-matched, but still learned, object stimuli.

Most importantly, associative context can serve as a memory cue and promote looking toward learned or expected associations. In two studies, 6- to 12-month old infants were taught face and scene pairs. When tested, infants were cued with a learned scene three seconds before faces appeared; 9-month-old infants showed preferential looking behavior toward the matching face and were more accurate when delay between learning and testing was shorter (Richmond & Nelson, 2009). Similarly, 6-month-olds exhibited similar behavior and showed preferential looking when delay was minimal in a subsequent study, but interestingly 12-month-old infants did not show this pattern with either minimal or extended delays. Despite developmental improvements in associative memory, null findings in older children could spawn from multiple sources. Extended cueing time may be detrimental to older infants whose visual processing is faster or greater flexibility in memory representations could result in less rigid associations (Richmond & Power, 2014). Further investigating factors contributing to visual preference, Richmond et al., (2007) dissected preferential looking patterns, indicating that memory expression through preferential looking varies based on the timing and context of the memory test. They indicated novelty, null, and familiarity preferences shift depending on the conditions of the memory cue. Instigating retrieval with cuing of stimuli may also play a crucial role in directing attention to learned stimuli.

In summary, the spectrum of preferential looking techniques serve as an indirect indicator of memory in children who are too young to provide overt expressions of memory. By capitalizing on infants' visual preferences, researchers can infer the processes underlying recognition memory, yielding essential insights into developmental milestones reached during early life. These methodologies also facilitate the exploration of contextual discrimination by examining stimuli originating from identical or varied contexts. This allows for the assessment of whether associative preferences are more readily formed within consistent contexts compared to those that are contextually distinct, providing a deeper understanding of the complexity of early cognitive development.

1.3. Hippocampal contributions to memory development

The hippocampus is universally understood to be a brain structure of unparalleled importance for memory encoding, storage, and retrieval (Buzsáki et al., 2022; Eichenbaum & Fortin, 2003). Early life memories are rapidly forgotten, but latent traces of those memories can be reinstated later in life to create lasting memories for events – a process that appears to be heavily dependent on the hippocampus (Travaglia et al., 2016). Research in adults has extensively documented the hippocampus's role in discriminating between similar events (Capaldi & Neath, 1995; Smith, 1979), yet how this ability develops during the early stages of life remains understudied. The development of the hippocampus, in this case, may be the key through which long-term memory and context discrimination is achieved.

The emergence of memory capacities in early childhood is linked to the maturation of the hippocampus and associated neural circuits. Studies employing neuroimaging techniques have begun to unravel the timeline and manner in which the hippocampus becomes involved in memory processes (Ghetti & Bunge, 2012). Particularly, unique trajectories of development of different sub regions of the hippocampus may support differing maturation of abilities. The CA1, for instance, may mature early – as well as other regions like the subiculum, presubiculum, parasubiculum and CA2, while the CA3 and dentate gyrus (DG) may undergo a more protracted maturation. The CA1 lends itself well to early life acquisition of integrated sensory relations, relationships between items, gradual concept learning, and allocentric spatial memory; further supporting the early and rapid ability improvement of spatial memory in young children. Conversely, the CA3 and DG are integral to pattern separation and pattern completion as well as encoding of temporal associations as well as fast and flexible acquisition of spatial details (Lavenex & Banta Lavenex, 2013).

Hippocampal recruitment may very well be essential for memory, even in very young children. Ellis and colleagues (2021) observed heightened hippocampal activation in response to learnable temporal sequences in a statistical learning task in infants ranging in age between 3 months and 24 months. Although this study could not provide any insight on whether hippocampal function can support context

discrimination in infancy, it does underscore that task-related hippocampal activation can be reliably redetected at early ages.

In contrast, research from our research group has provided critical insights into toddlers' hippocampal activation responds to stimuli associated with specific episodic detail, including context discrimination, but this activation has been observed at the age when behavioral evidence is also observed (e.g., Newcombe et al., 2014). Specifically, one study showed greater hippocampal activation for a learned song (in the context of a play session) compared to a novel song; moreover, that activation was significantly correlated with the toddlers' memory for the context in which the song was heard (Prabhakar et al., 2018). Additional studies have demonstrated hippocampal activation for a learned song is associated with memory for the sequence of actions required to elicit that song in a memory game, emphasizing its role in processing temporal order of events (Mooney et al., 2021). Finally, in another study involving 25-32 month-olds, we observed a correlation between hippocampal activation for newly learned words (relative to novel words) and memory for those newly learned words and vocabulary more generally (Johnson et al., 2021). Overall, these results underscore that the hippocampus is engaged in variety of tasks that require encoding and retention of arbitrary associations between stimuli, but as noted earlier, behavioral manifestations of associated memory abilities are also evident. This raises the question of whether this would be the case in younger toddlers who struggle with behavioral tasks of context discrimination (Newcombe et al., 2014), but whose memory retains contextual features as indicated by context reinstatement effects (Johns et al., 2016).

1.4. Current Study

The current study is aimed at examining whether toddlers between 18- to 23-months of age are able to discriminate between events encountered in two contexts. Building on the previous behavioral and neuroimaging work, as well as incorporating methodologies from past eye-tracking work, the current study seeks to elucidate the early development of hippocampal function concerning memory for the ability to discriminate memory based on the context of learning.

To do so, we assessed memory for face-song and word-object pairings. Toddlers visited two rooms; in each room they learned a song paired with a 3D face block, followed by two words associated with novel objects. They visited the first room and then the second, before entering a third environment where they completed an eye-tracking task evaluating their ability to direct their gaze towards a learned stimulus when prompted by its corresponding auditory cue, either a song or a word. One week later, a follow-up session was conducted where toddlers completed similar procedures of learning and testing in all three rooms.

If infants can hold distinct memory representations for events occurring in each of the rooms, we expect greater visual preference for stimuli that match auditory cues compared to mismatched stimuli, particularly when the distractor stimulus is from the opposite context. If they are not able to discriminate between contexts effectively, we expect that there will be no difference in directed attention to the audio matched stimulus when the distractor is from the same or opposite context.

We also explored whether one individual learning opportunity suffices to exhibit the predicted behavior or additional exposure is necessary, given the vast evidence of the importance of repeated learning to demonstrate episodic-like memory (Fivush & Hamond, 1989; Meltzoff, 1988a, 1988b). To this end, we compared visual preferences assessed after the first learning sessions to those observed after the second learning session one week later.

Finally, we anticipate increased hippocampal activation in response to previously learned stimuli compared to new information and we expect this activation to positively correlate with visual contextual discrimination and memory performance, underscoring the hippocampus's role in memory retrieval and contextual processing in early childhood.

2. Methods

2.1. Participants

A total sample of 58 18-24-month-old toddlers participated (*Mean* = 20.16 months; SD = 1.50 months, range = 18.0-22.9 months; 34 males). A subset of 24 subjects successfully completed a nighttime neuroimaging session.

2.2 Materials

Song Memory Task. Stimuli for this task included 4 songs and two 3D blocks with cartoon faces. The 4 36-second songs (one with male vocals and one with female vocals) were broken up into two 18-second clips. Song vocals were in non-English languages (i.e., Portuguese, African dialects) which were unknown to children and their families. Song clips included relatively unique rhythms, tempos, and vocals. Two songs were used in the learning phase and behavioral testing phase of the task and the two additional ones were used as novel stimuli in the neuroimaging session. The use of songs as learned versus novel was counterbalanced across participants. Each of the two 3D blocks with a cartoon face (see Figure 1) were used during learning to be associated with each of the songs.

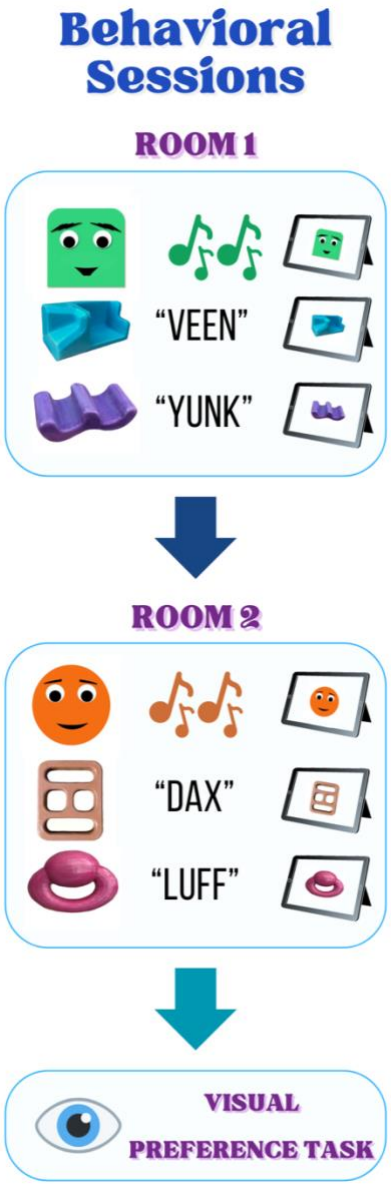
Word Memory Task. Stimuli for this task included 6 words and 12 unique toys.

The words were monosyllabic and consistent with the English phonotactic but did not carry any contextual or cultural meaning (e.g., "luff," "stip," "dax"). Four words were learned and tested behaviorally and the remaining two were used as novel stimuli in the neuroimaging session. Unique toys were created using a 3D CAD database specifically for this experiment and did not resemble everyday objects or toys that children may have previously encountered (see Figure 1). Four triplet sets were created from the 12 total toys. Within a given triplet, toys were counterbalanced to either be 1) "Named" (i.e., received a verbal label during learning when the toddler's attention was directed to the object to be manipulated ; 2) "Unnamed (i.e., did not receive a label but was manipulated in the same way as the named object) and 3) "Familiar" (i.e., object was presented as part of the set but was never the object of attention or directly manipulated. Names were counterbalanced across toy and triplet set; children learned

four words during the behavioral session and two additional unlearned words were utilized during the neuroimaging session.

Two separate rooms (i.e., Room A and Room B) in a hallway were prepared in the laboratory for behavioral sessions. Rooms were prepared with different colored plush rugs and different decorations on walls to provide two different contextual environments.

Figure 1. Behavioral session structure, consisting of similar procedures across two rooms each session, followed by eye-tracking; a song and two words per room was learned.



2.3. Procedure

The procedure included a total of two laboratory visits during the daytime held on average one week apart (M = 6.56 days, SD = 1.08) followed by a nighttime MRI visit, typically on the same day as the final behavioral session (n = 23), or the following day (n = 1). At the beginning of the first laboratory visit, parents or guardians completed consent forms and questionnaires regarding their child's demographics, temperament, verbal ability, motor skills, screen exposure, and sleep behavior. During this time, participants played with experimenters for comfort and familiarization.

2.3.1. Behavioral Sessions

Two behavioral sessions took place with an average of a week delay (M = 6.61 days, SD = 1.02 days), within each session, the same procedures/tasks with different content used in two rooms (see Figure 1). The procedure comprised of 3 phases: song-face association, two separate word-toy associations.

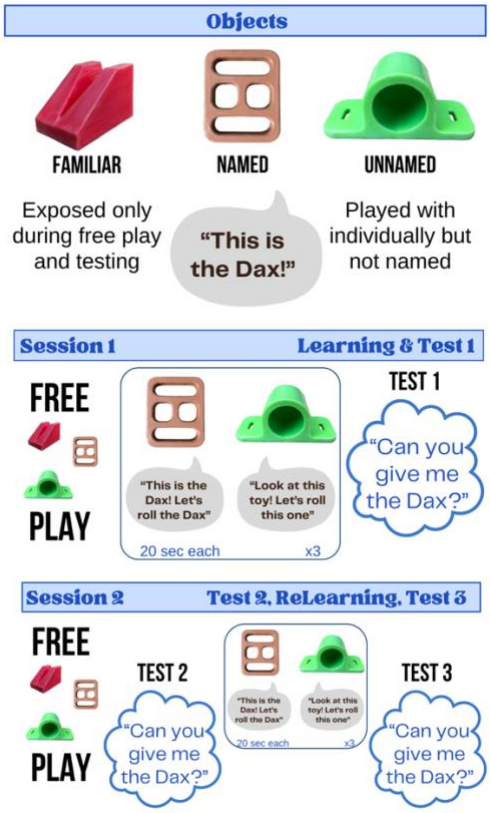
Song Learning. At the beginning of Session 1, after consent and familiarization, participants were transferred to either Room A or B (counterbalanced across participants). Once, in the room, participants began with song-face association task in which they were introduced to a colorful face that was printed on a 3D block and interacted with it for approximately 30 seconds. Children were then told that the character had a special song. The song played on a tablet while the face was being displayed on the screen. Participants listened to the song for 18 seconds, followed by a replay of another 18 seconds.

Word Learning Task. Subsequently, participants engaged in the first word-toy association task in which they first played with all three toys from one of the triplets for a free play/familiarization period of 1 minute while no name were given for the toys (see Figure 2). The experimenter then hid all toys except for one, the named toy, stating "Look at this (named toy name)," and encouraged the participant to interact with the toy for approximately 20 seconds. After placing the named toy out of sight, participants were presented with the unnamed toy, and encouraged to interact with it for approximately 20 seconds.

This process was repeated twice more, for a total of 3 exposures (20 seconds each) to both the named toy and unnamed toys. Then, all three toys (named, unnamed, and familiar) were placed in front of the participant, and the participant was asked to choose the named toy to put in a special box. If the child chose the wrong toy, or multiple toys, the experimenter corrected or redirected the participant. Once the correct toy was in the box, participants were shown an image of the named toy on the tablet screen while a looping audio of the named toy name played. The audio repeated the word a total of eight times. Finally, the same procedure was repeated with another triplet of toys and a new name toy association.

After completion of these activities in the first room, participants took a brief break then they were transferred to the second room and participated in the same procedures with a new set of stimuli.

Figure 2. Word task behavioral structure. Children played with three unique objects, afterwards one was named and interacted with, followed by interaction with another toy that was not named. Afterwards recollection for the named object was assessed.



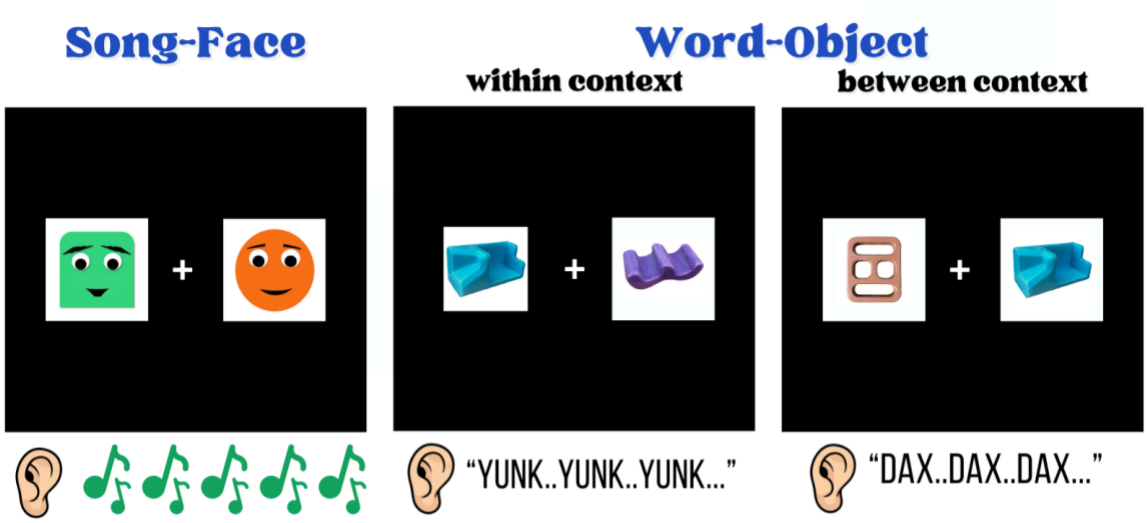
Eye-tracking Visual Preference Task. Throughout the behavioral tasks, each character block and named toy were also represented on a tablet screen as a 2D image. This was done to help the child understand that the 2D representation of the toys they would later see during the eye-tracking component were the same as the 3D objects in their hands during the game. A Tobii T-120 17 inch eye-tracker monitor was used to collect participant looking patterns. Participants sat on their parents' laps approximately 60-70 cm from the monitor and were given sunglasses to wear so that their eyes were not collected by the eyetracker. Tobii Studio's standard infant calibration was employed, consisting of five points for focus on the screen. Focus points were accompanied by a sound effect to encourage looking and the fixation was a cartoon cat in order to be more entertaining than typical fixations. The experiment proceeded when the gaze of the toddlers was captured at all five points. We used default Tobii fixation filter settings were used for eye-movement data reduction. The stimuli were 10 cm × 10 cm and consisted of the images previously displayed (see Figure 3). The eye-tracker task itself consisted of six trials. On each trial, one auditory stimulus was presented for 8 seconds with a fixation cross before two visual stimuli, the target and the distractor, appeared on the screen for 10 seconds.

On the 1st and 4th trial, the stimuli were face blocks and the auditory stimuli were one of the songs on one trial and the other song on the other trial. The position of the faces switched position between these two trials. The second/third and fifth/sixth trials, the stimuli were objects, and the auditory stimuli were words. The distractor used identified whether the trial was part of with between contexts' versus the "within context" condition, In the "between context" condition the distractor represented an object named in the other room, whereas in the "within context" condition, the distractor was the object whose name was learned in the same room, For the between context trials, one trial consisted of the first word task stimuli from each room and the other trial consisted of the second word task stimuli from each room; for the within context trials there was one trial per room.

Overall, within context trials consisted of images of toys from the word tasks from the same room, with the audio matching one of the images/toys; two of these trials exist, one representing the word

tasks from the first room and one representing the word task from the second room. This counterbalancing and trial setup was meticulously designed to assess the associative connections between learning and eye movements.

Figure 3. Eyetracking trials. Song trials consisted of faces from both rooms for both trials. Half of the word trials consisted of objects from the same learning contexts, while the other half were comprised of objects from different learning contexts (i.e., between contexts).



Session 2. During Session 2, experimenters reminded parents/guardians of MRI safety protocols and encouraged parents to ask any questions regarding the nighttime MRI session. Then, the experimenter led the child through a nearly identical procedure to Session 1 with one deviation. During the word-learning tasks, following free play with all three items in each triplet, participants were asked to identify the Named toy (i.e., "Can you put the X in the box?") before re-exposure to named and unnamed toys individually, and subsequent final identification.

2.3.2. Nocturnal Neuroimaging Sessions

Participants underwent their neuroimaging session during natural nocturnal sleep the same day or one day following the second laboratory visit (*M* = 7.22 hours, *SD* = 4.66 hours). During the nighttime visit, families arrived between 6PM and 11PM depending on their child's typical sleep schedule. Each successful session lasted approximately 2.5 hours (*M* = 112.3 minutes, *SD* = 55.35 minutes). The scanner bed was outfitted with pillows, various blankets, including a weighted blanket, and assorted stuffed animals for the child's comfort. Parents were encouraged to bring comfort items for their child, which were properly screened for MR safety prior to the scanning session. Once comfortable and sleeping soundly, approximately, 20 minutes following arrival, researchers placed earplugs and headphones on the participants for sound protection and auditory stimulus delivery. To confirm a child was asleep, researchers or parents would attempt moving the child's arm to see if the child would wake from the movement. If the child continued to sleep and did not show muscle tension, experimenters would begin the scan. The scan generally began on average 78.92 min (SD = 44.52 mins) after sleep onset and was completed within 43 mins (range: 29-61 minutes) after sleep onset (1 typical infant sleep cycle, Stern et al., 1969). This was done in order to increase the chances that children were in slow-wave sleep during the functional scans (e.g., Anders and Taylor, 1994; Mitra et al., 2017). A researcher was present inside the scanner room at all times within arm's reach of the child for the duration of the scan. Dim lighting allowed the researcher to see the child's face and body and monitor for signs of waking up, including

face, body, foot, and eye movements. If the child showed signs of waking at any point during the scan, the researcher would stop the scan prior to full wakefulness.

2.4. fMRI Acquisition and Design

Images were acquired via a 3T Siemens Magnetom Skyra MRI System at the University of California, Davis, using a 32-channel head coil. Functional images were acquired using a gradient echoplanar imaging pulse sequence [repetition time (TR), 1500 ms; echo time (TE), 24.20 ms; field of view (FOV), 216 mm; number of slices, 46; voxel size: 3 mm isotropic; 250 volumes acquired]. During the functional scan children heard ten, 18 second blocks of different stimuli: 4 learned words, 2 novel words, 2 learned songs, and 2 novel songs. 18-second blocks of silence separated the stimuli blocks. There were four functional runs per participant, with blocks counterbalanced within each run. This functional protocol lasted 25:32 minutes. A T1-weighted high-resolution magnetization-prepared rapid acquisition gradient echo (MPRAGE) scan in the sagittal plane was also obtained (TR, 2500 ms; TE, 3.24 ms; FOV, 224 mm; slice thickness, 0.70 mm) prior to the functional scan (7:08 min). Following the functional protocol, if the child was not showing signs of wakefulness, a T2-weighted scan was obtained (TR, 3200 ms; TE, 350 ms; FOV, 226 mm; slice thickness, 0.95 mm). Overall, with the localizers and phase map, the complete scanning protocol took 41:54 min to complete.

2.5 fMRI Data Processing and Analysis

2.5.1 Univariate Analysis. Data were preprocessed and analyzed using FEAT in FSL6.0. (https://fsl.fmrib.ox.ac.uk/fsl/fslwiki/). Preprocessing included slice timing and motion correction. FSL's motion outliers function (https://fsl.fmrib.ox.ac.uk/fsl/fslwiki/FSLMotionOutliers) identified motion outliers greater than 0.9 mm by measuring relative intensity differences and defining outliers using the upper threshold for creating boxplots. We excluded scans with more than 20 % of the volumes with motion outliers as defined by this function. This resulted in 0 runs being excluded for excessive motion because of an average of 4.5 % volumes affected in these participants. A total of 453 volumes were

rejected across 24 participants (average = 18.12 volumes per participant, range = 0-40 volumes) and they were corrected by including a confound matrix of outliers in the general linear model. The sample included in these analyses showed an average relative framewise displacement of 0.15 mm (*SD* = 0.13 mm, *range* = 0.04-0.84 mm) and an average absolute displacement of 0.37 mm (*SD* = 0.68 mm, *range* = 0.05-3.57) per run. Functional and structural data were all registered to a standard toddler template created by the University of North Carolina (26) from a sample of 95 toddlers (*M* = 18 months; Shi et al., 2011) and smoothed to 6mm. Each registration was visually inspected by investigators to ensure it was successful. We confirmed visually that all were successfully registered to the template. General linear models were conducted using FEAT in FSL to model each of the 10 types of blocks during the time series and were convolved with a double-gamma hemodynamic response function to yield various contrasts of interests.

2.5.2 Imaging Masks and Cluster Correction Analyses.

Our hypotheses centered on hippocampal function, and thus we focused our analyses to the right and left hippocampal masks, which were obtained from parcellation maps provided by the University of North Carolina 2-year-old template (right: 5538 voxels, 50 % probability; left: 5785 voxels, 50 % probability). Parameter estimates were extracted from these structurally defined hippocampal masks. We also investigated activation in the left and right parahippocampal gyrus (right: 8542 voxels, 50 % probability; left: 7585 voxels, 50 % probability; see Fig. 3b) and angular gyrus (right: 17,988 voxels, 50 % probability; left: 12,992 voxels, 50 % probability; see Fig. 3c) obtained via parcellation maps from the University of North Carolina 2-year-old template.

2.6 Eye-tracking Analysis and Technique

2.6.1 Data processing and filtering.

We employed Tobii Studio software to create areas of interest (AOIs) and assess looking behaviors within those AOIs. These AOIs encompassed individual square images (10 cm × 10 cm)

surrounding targets and distractors, so that each trial was composed of a target AOI and a distract AOI. These stimuli were approximately 4cm from the side in which they were placed (e.g., left edge of screen for the stimulus on the left), 2.5cm from the center fixation, and 8cm from the top and bottom of the screen. The analysis window was focused on a 3000ms period (across the entire 10000ms trial) beginning 200ms following the onset of stimuli. This was done for three reasons, 1) in order to allow infants the time to make an eye-movement following the onset of the stimuli, 2) in order to capture a true window of looking for infants, as many had to be directed to attend to the stimuli after the fixation and only 24% of participants produced any looking data in that time period and 3) to capture an accurate picture of participant looking based on trial number for total participants attending at a given epoch (Hyun et al., 2009; Oakes et al., 2017). For each trial we calculated a time-series based on 16.67 epochs. In each given epoch, it was determined whether each participant was attending to the target AOI, the distractor AOI, or neither (reported as NA for our analyses). Proportion looking toward the matching stimulus AOI was the focus of our analyses.

2.6.2 Statistical approach

The characteristics of eye-movement data allowed us to detect variations in gaze patterns throughout the analysis period (Oakes, 2012). Given the extensive number of time-based measurements (~180 across 3000ms) and the risk of increasing the overall likelihood of Type I errors through repeated t-tests across epochs, coupled with the fact that eye movements are sequentially dependent (meaning the position of the gaze at one time point is likely close to its position at the preceding time point), we opted to employ cluster-based permutation tests (Beckner et al., 2020; Cantrell et al., 2019; Leckey et al., 2020; Oakes et al., 2013, 2017).

We began by conducting uncorrected t-tests at each time point (epoch), which allowed us to identify clusters of significant consecutive time points. For each cluster, we summed the t-values to calculate the cluster's mass. To assess the significance of a cluster's mass, we compared it against a null distribution generated from random permutations of the observed data, ensuring the sequence of eye

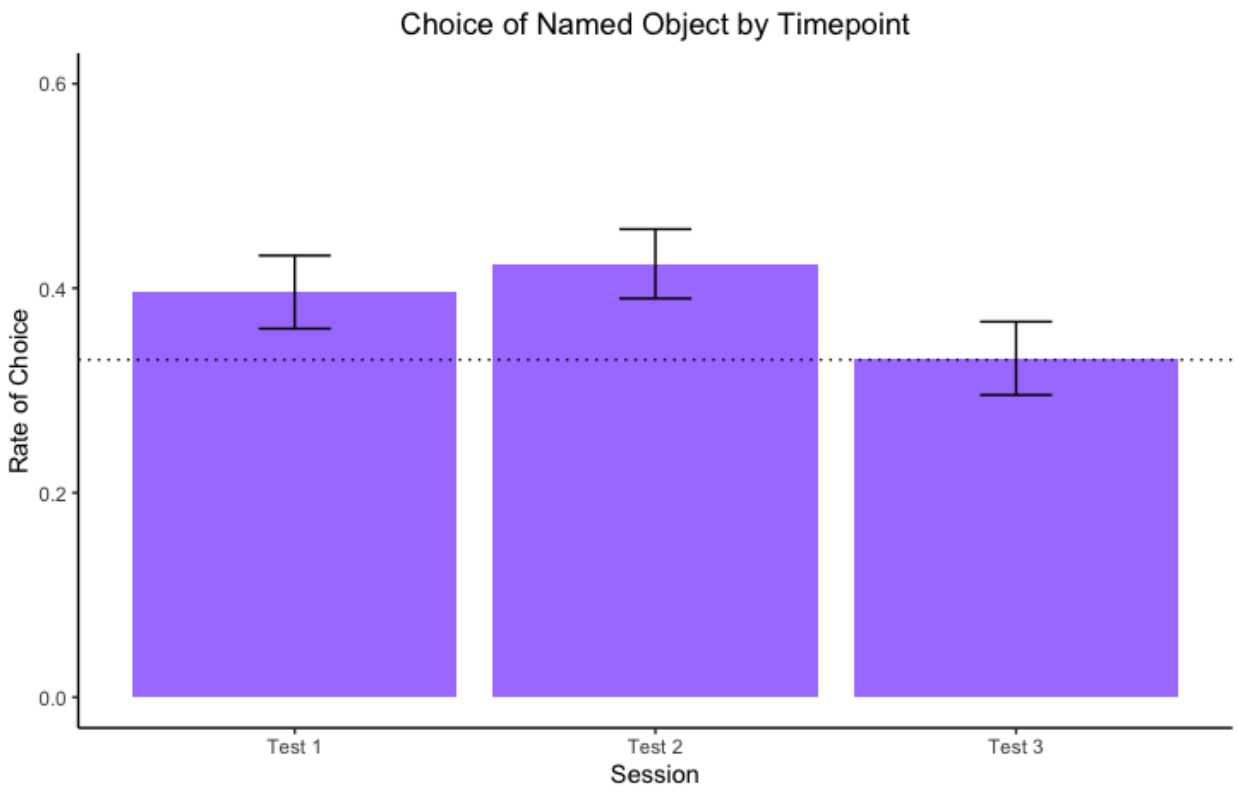
movements was preserved to acknowledge their non-independence at closely spaced intervals. The null distribution was created by shuffling the labels of variables of interest and determining the largest cluster mass in the permuted data, a process repeated 500 times. This generated an empirical, nonparametric distribution representing the expected cluster masses if trial types were drawn from identical populations. In this case, we shuffled (trial-by-trial) which of the two items was labeled as matching to compute the null distribution (thus, by chance, the matching stimuli was correctly labeled as such on 50% of the iterations in the null distribution). We then evaluated our observed cluster masses against this distribution, considering a cluster significantly different from chance if its mass fell in the top or bottom 2.5 percent of the null distribution, akin to a conventional two-tailed t-test with an alpha of .05.

3.0 Results

3.1 Behavioral Task Performance

Toddlers choice the named object greater than chance (0.33; three objects) at both Test 1, $t(1, 52) = 1.77$, $p = .04$, and Test 2, $t(1, 45) = 2.47$, $p = .009$. This was not the case at Test 3, $t(1, 43) = 0.03$, $p = .49$, but instead toddlers chose the novel object greater than chance, $t(1, 43) = 1.81$, $p = .04$.

Figure 4. Rate of choice for the named object across all three testing points.



3.2 Eye-Tracking Data Analysis

Face-Song Trials. Analysis of eye-tracking data for the face trials indicated that participants spent an average looking duration difference of 5.81 seconds (*SD* = 2.24 seconds) per trial. Looking behaviors for the matched stimuli vs the mis-matched stimuli differed significantly in terms of the percentage of time spent looking at said stimulus at the first session, $t(1, 50) = 3.43$, $p = .001$, but not the second session, $t(1, 43) = -0.98$, $p = .33$. In terms of the time-series permutation, toddlers looked significantly longer at the face paired with the song being played between 1784-1850ms during the first session compared to the second session (see Figure 5), potentially indicating that after multiple exposures infants habituate to the audio-visual matching preferential looking.

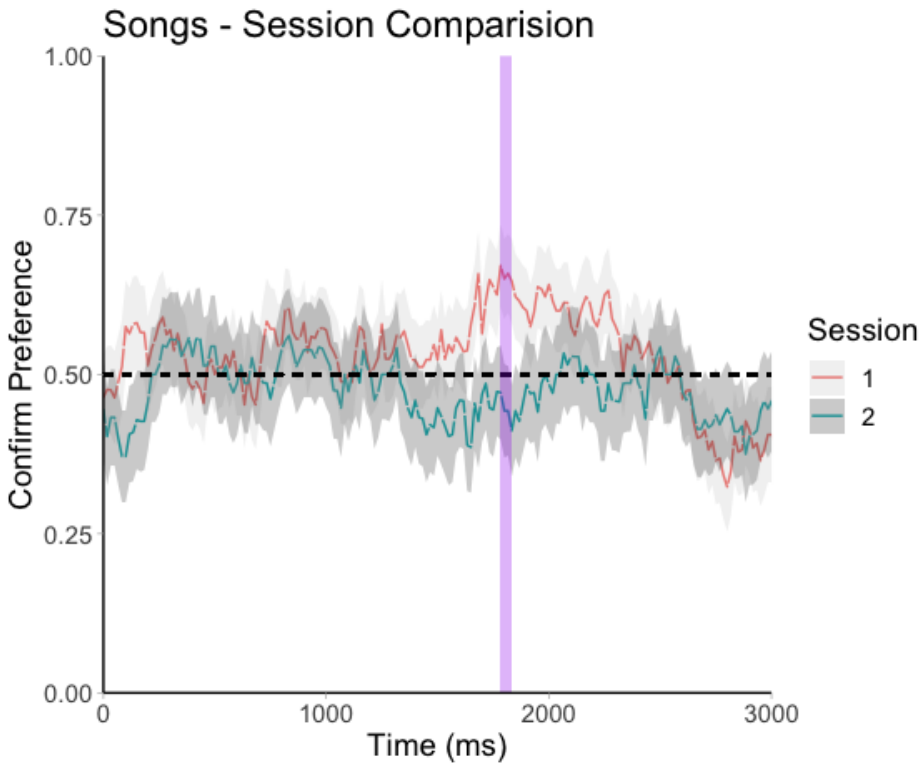
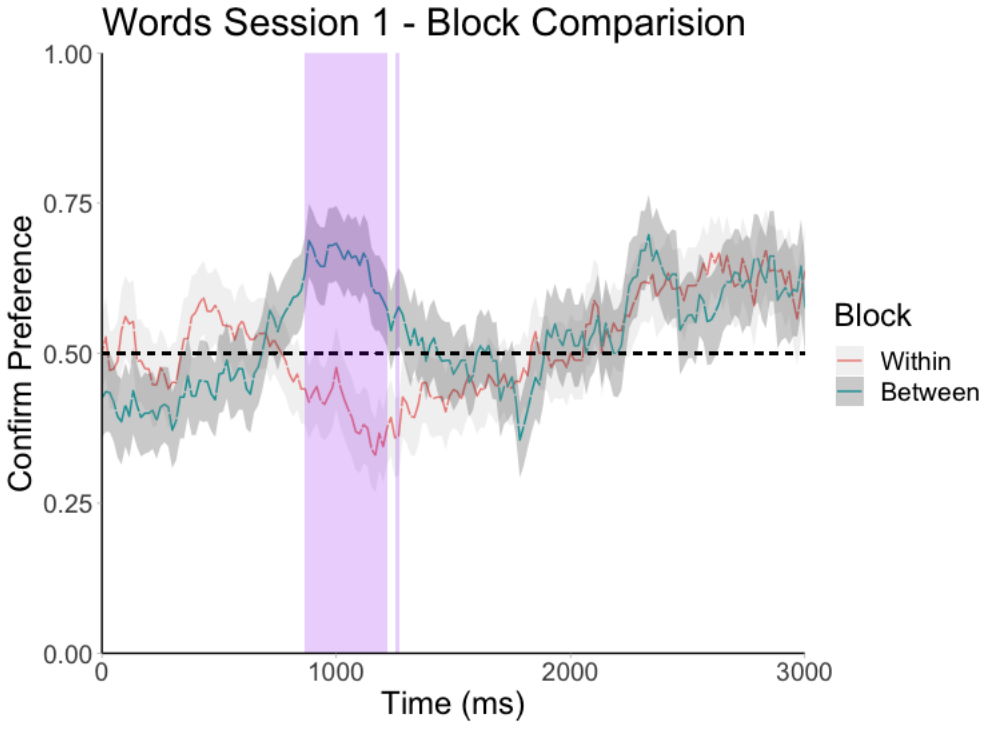


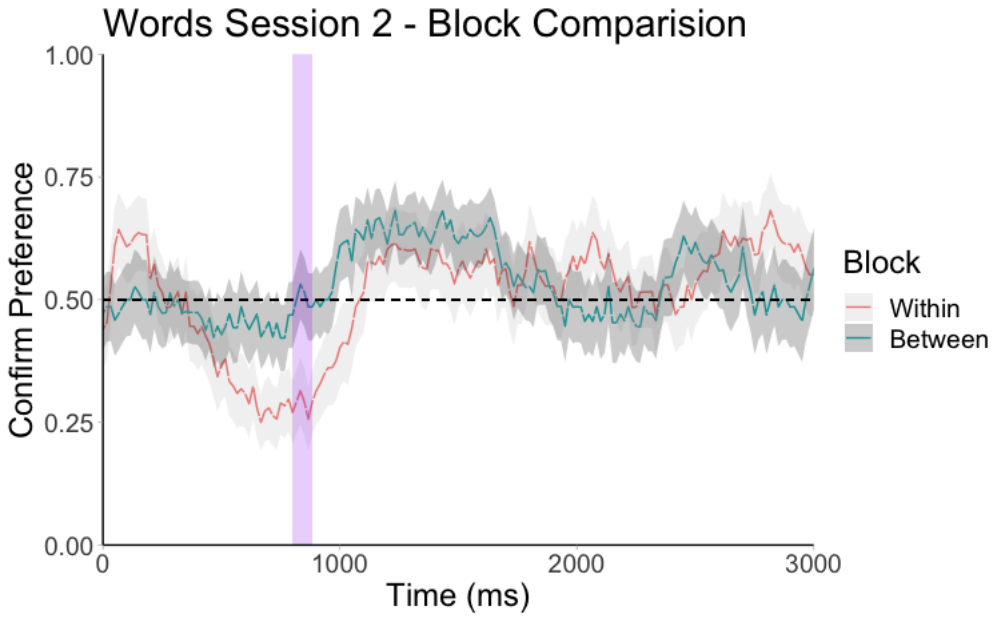
Figure 5. Song-face timeseries differences between sessions.

Object-Word Trials. Analysis of eye-tracking data for the within room toy trials indicated that participants spent an average looking duration of 4.49 seconds (*SD* = 2.19 seconds). Toddlers looked numerically longer at the matched stimuli vs the mis-matched stimuli, $t(1, 50) = 1.75$, $p = .08$. Looking patterns in the between room toy trials indicated that participants spent an average looking duration difference of 4.87 seconds (*SD* = 1.97 seconds). Toddlers did not look at either the matched or mis-matched stimuli more overall, $t(1, 52) = 1.64$, $p = .10$.

Furthermore, during the first session, between 867-1234ms, infants looked significantly, probability 1.4%, more towards the matching stimuli when objects presented came from different rooms than when objects presented came from the same room (see Figure 6a). This was also true between 1250-1284ms, with a probability of 65%. Similarly, during the second session, between 800-900ms (probability 32%), infants looked more towards the matching stimuli when objects presented came from different rooms than when objects presented came from the same room (see Figure 6b).



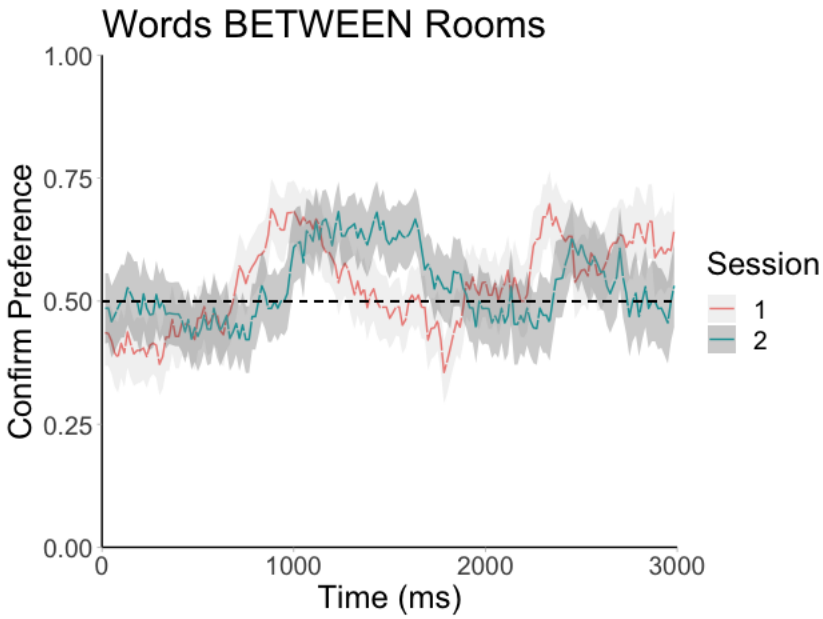
A.



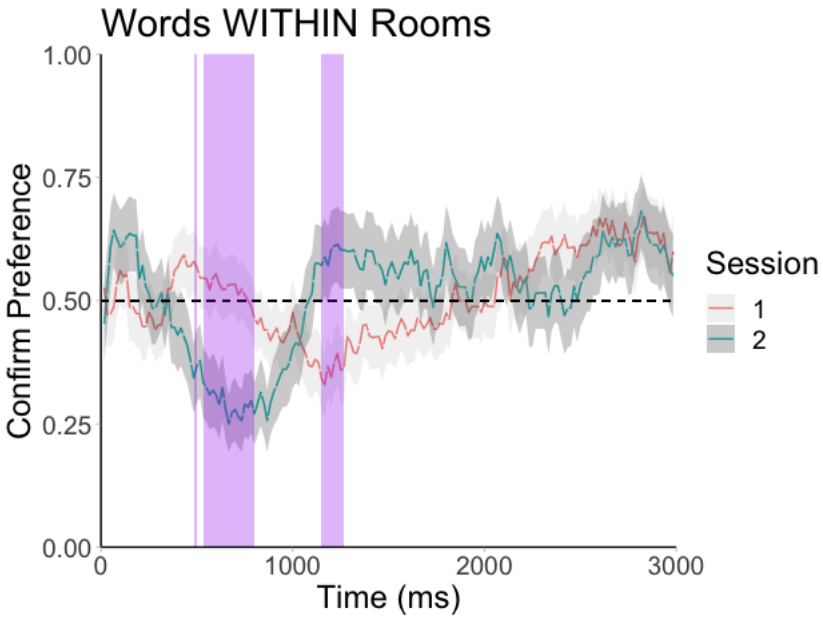
B.

Figure 6. Word-objects timeseries differences between types of trial at A) Session 1 and B) Session 2.

Comparing looking behaviors between the first and second sessions, we also observed no differences in the amount of attention directed toward the matching stimulus when the distractor object comes from the opposite context (see Figure 7a), likely indicating that contextual discrimination and therefore visual preference remains stable across multiple tests and learning experiences. When objects came from the same room, however, toddlers looked longer at the matched stimuli earlier in the trial (between 483-517ms, probability of 65%; 533-817ms, probability 4.4%) at the first session, but later in the trial (between 1150-1284ms, probability of 19%;) at the second session (see Figure 7b).



A.



B.

Figure 7. Word-objects timeseries differences between sessions is A) non-existent at the first session and B) reflects greater looking toward the matching stimuli earlier in the trial at the first session and later in the trial at the second session.

3.3 Eye Movement & Word Learning Behavior

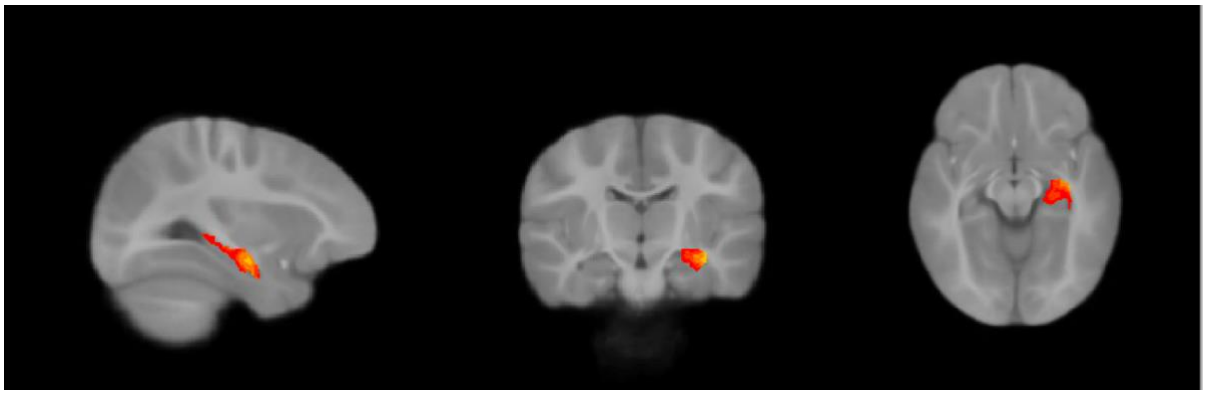
In the first session, we observed that the amount of time participants spent looking at objects corresponding to the words during the initial 3000 milliseconds of each trial correlated significantly with their ability to select the correct object later in test 2. This was true both when the objects presented visually were from different rooms, r(40)=0.31, p=.04, and when the objects were from the same room, r(41)=0.32, p=.04. These findings suggest that the participants' attention to the correct audio-visual association may support recollection of the association between the object and its verbal referent.

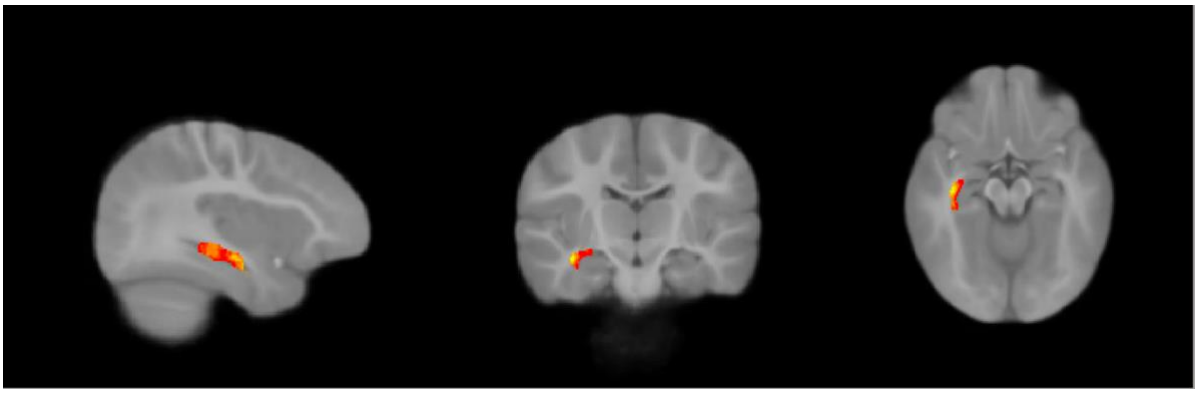
3.4 fMRI Findings

Univariate analysis of the fMRI data showed significant activation in the hippocampal regions during exposure to both familiar and novel stimuli. Specifically, when using a hippocampal mask there were significant positive clusters in the following contrasts: Learned Songs > Novel Songs (left: z = 2.3, p = .01, -31, -8, -12, z-min = 3.98, Figure 8a). There was also a significant negative cluster in Learned Words > Novel Words (right: z = 2.3, p = .04, 32, -13, -11, z-min = 3.06, Figure 8b).

Figure 8. Significant clusters of activation using a bilateral hippocampal mask. A. Positive cluster of activation for learned song blocks minus novel song blocks; X= -25, Y= -10, Z= -9. **B.** Negative cluster of activation for learned words blocks minus novel word blocks; X= 30, Y= -12, Z= -11.

A



B 

Discussion

Our findings build upon previous work that shows young children exhibit a burgeoning ability to discriminate between contexts in their associative memory (REF). Contextual information (cues) may support the representation of memories and in very young children may be essential (Newcombe et al., 2014). The primary aim of this study was to investigate the early development of contextual discrimination in learned association in toddlers aged 18 to 23 months. We explored whether these toddlers could distinguish between memories formed in different but similar contexts, focusing on their ability to associate visual stimuli with corresponding auditory cues. This was examined through two sets of paired associations: face-song and word-object pairings learned in distinct environments. To achieve these goals, we employed a dual-task approach where toddlers were exposed to learning sessions in two unique rooms, involving different face-song and word-object pairings. The assessment of their memory and contextual discrimination was conducted using a preferential attention task where the correct association was made by matching visual stimuli with auditory associates, amidst distractors from both the same and opposite learning contexts.

Our findings provide evidence that infants aged 18 to 23 months can discriminate between similar events, both for words and other content, when these events occur in different contexts. This capability to discern distinct memory representations earlier than the previously thought third year of life suggests a more nuanced understanding of early cognitive development. By showing that even younger toddlers can

use contextual information to enhance memory recall, our study challenges and refines the timeline of memory maturation in early development.

For both face-song and object-word trials, toddlers looked longer at auditorily matched stimuli compared to non-matched stimuli over the entire trial. Similarly aged infants also looked towards scenes that matched the language they were hearing and matched learned words and phrases to images representing their meaning (Hirsh-Pasek & Golinkoff, 1996; Golinkoff, Ma, Song, Hirsh-Pasek, 2013). These findings are also consistent with previous work that asserts that when cued with a portion of an association, toddlers will look toward the stimulus associated with the cue above other learned stimuli (Richmond & Power, 2014; Richmond & Nelson, 2009).

Furthermore, in our sample, there is evidence that in 18- to 22-month-olds context discrimination is beginning to emerge but may still be inadequate; for word-object trials, significant preferential looking toward matching stimuli occurred in the first session when objects were from different rooms, but this effect did not persist into the second session, hinting at the nuances and potentially unique trajectories in memory retention and retrieval over time and repeated exposure. Contextual discrimination aided associations as well, with toddlers looking more at the matched stimulus when the distractor came from the opposite context rather than the same. The ability to distinguish between the two events is likely a supportive factor in recognizing the correct association, within context associations as a result were more difficult and produced less robust looking.

Mather and Plunkett (2009) demonstrated that 22.5-month-olds can retain and utilize context to enhance their recall of novel objects. In their study, children were shown a known object (e.g., car) alongside a novel object (e.g., compass) and directed to look at one of them. When these objects were presented again later in the same context, toddlers looked significantly longer at the target before hearing its name, indicating pre-emptive focus based on contextual familiarity, highlighting how repeated contextual cues can prime young children to anticipate and focus on learning targets, enhancing their ability to remember and recognize both familiar and novel objects within consistent environments.

However, this study was done only with known objects, which may require less episodic memory compared to recently learned associations.

The beneficial effect of contextual reinstatement may also mean that deviating from the learning context has a detrimental effect, or at least that cross-contextual learning may support less specific and more generalized memory. Vlach and Sandhofer (2011) examined the effects of consistent versus changing contextual backgrounds on the generalization of word learning. Their study showed that toddlers were better able to learn and generalize new words when both the learning and testing occurred in the same contextual environment. When the contextual background changed between learning and testing, children struggled to generalize the words immediately. This underscores the importance of environmental consistency in early learning stages, highlighting how stable contexts can facilitate better memory and generalization among young children. Finally, Johns et al., (2016) discovered that learning words in redundant contexts, despite being less effective for recognition speed and accuracy, promoted the development of more stable and consistent semantic representations. This indicates a trade-off between the reinstatement of a specific memory and the generalized learning of word labels. In our study, learning word-object associations in only one context may have supported more specific memories and violations of associations are more distinguishable as a result.

Furthermore, our fMRI findings provide neurobiological support for the behavioral and eye-tracking results. Significant hippocampal activation during exposure to familiar compared to novel stimuli indicates that this brain region is actively engaged in processing memory for learned content. The differentiation in hippocampal response to learned versus novel stimuli suggests that the infants' brains are not only recognizing familiar information but also encoding and responding to novel information differentially. These hippocampal responses are correlated with eye tracking measurements of memory retention, providing additional evidence for the episodic memory dependence on hippocampal activity even in very young children. Lastly, the Context B > Novel contrast also elicited a significant hippocampal cluster, perhaps indicating temporal comprehension of the hippocampus, but future work

and analyses are essential to understand that relationship. One recent study indicated that hippocampal activation is correlated with recently learned words, but did not examine the role of context (Johnson et al., 2021), while another study implicated the hippocampus in temporal recall (Mooney et al., 2021). Without future work, we cannot directly infer that temporal context in event learning may elicit unique hippocampal patterns of activation. Therefore, future research ought to assess hippocampal involvement word learning specifically with distractors from different temporal contexts.

However, for slightly older children (25- to 33-month-old toddlers), there is more substantial evidence for the developing hippocampus's ability to support contextual discrimination (Prabhakar et al., 2018). When children learned nearly identical procedures in two different rooms associated with unique songs, memory for the room in which a specific song and an associated puppet friend was significantly correlated with hippocampal activation for the same learned song compared to a novel song. However, these findings are purely correlational and do not provide direct evidence that hippocampal activation is responsible for recalling the room where the song was heard, as the study did not assess this question directly in the scanner but instead employed targeted memory reactivation during sleep.

While our results showing hippocampal activation for memory are robust, our findings and the present literature regarding contextual discrimination are mixed. The developmental changes in subfield maturation and their roles in pattern separation and pattern completion may be the key to understanding the emergence of contextual discrimination after associative memory. In adults, the DG and CA3 are responsible for pattern separation and pattern completion, which form the basis for contextual discrimination. Pattern separation helps distinguish between similar experiences by creating unique, non-overlapping memories, mainly in the dentate gyrus and CA3 areas of the hippocampus. This is crucial for preventing memories from becoming incorrectly attributed to contexts. On the other hand, pattern completion helps recall a whole memory from just bits and pieces of information, due to the CA3's ability to connect related memories (Bakker et al., 2008; Rolls, 2013). Yet, in young brains, CA3 and DG development lag behind that the CA1, the region responsible for relationships between items and gradual

concept learning, in development (Lavenex & Banta Lavenex, 2013). Thus, one possible avenue for future work is to utilize representational similarity analysis to examine activity patterns across hippocampal subfields for stimuli from the same and different contextual settings. Using representational similarity analysis to understand brain patterns within and across contexts will help better understand the role of the hippocampus and its subregions in pattern separation and pattern completion. Future research should also consider longitudinal studies to track how memory discrimination abilities and the hippocampus develop in tandem over time.

All of these findings, taken together, indicate a fascinating relationship between unconscious neurocognitive mechanisms and active memory choices in young children. Within the context of cognitive theory, event segmentation theory may offer a nuanced view of how memories are influenced by the perceived beginnings and endings of events within a context (Kurby & Zacks, 2008). The cognitive process of breaking down continuous experiences into distinct events can significantly enhance memory retrieval by creating clear contextual boundaries, as such, adults and children process and recall segmented events with greater accuracy when these events align with perceived cognitive boundaries. These boundaries serve as mental markers that segment experiences into manageable units, making them more memorable and easier to recall. This segmentation is especially pronounced in structured environments where clear contextual cues are present, reinforcing the role of context in shaping memory encoding and retrieval (Zacks & Swallow, 2007). However, there may not be as much of a benefit for distinct events in early development, with generalization and knowledge building being a substantial goal and priority in early life (Keresztes et al., 2018).

In summary, the behavioral, eye-tracking, and fMRI results collectively suggest that associative memory capabilities and the ability to discriminate between named and unnamed referents are present in infants as young as 18 to 23 months. The hippocampus appears to be crucially involved in this process, as evidenced by its selective activation in response to learned versus novel stimuli and these findings provide a valuable contribution to the understanding of early memory development and the neural basis of

associative learning in infancy. Our complex findings, while informative and interesting, beg several more questions to answer about how these episodic memory abilities develop and at what ages can they be reliably observed. In our sample, the specific age range and small sample size may limit generalizability to development at large. And finally, the lack of direct within and between comparison for the song-face task make it difficult to compare findings between the song-face and word-object tasks directly.

Our study advances the understanding of memory discrimination and hippocampal function in infants, offering new insights into the cognitive and neural underpinnings of early memory development. These findings not only challenge existing models of memory maturation but also pose more questions about discrimination abilities and hippocampal contributions to the development of episodic memory.

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