ABSTRACT

Title of Thesis:	INVESTIGATION OF HIPPOCAMPAL NEURITE DENSITY AND DISPERSION AND THEIR RELATION TO MNEMONIC DISCRIMINATION IN PRESCHOOL-AGED CHILDREN
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Research has identified links between mnemonic discrimination, sleep, and the hippocampus. Mnemonic discrimination is a cognitive ability that allows for the discrimination between two similar stimuli. This ability relies on pattern separation, a neurocomputational process in which similar representations are stored orthogonally within the hippocampus, a region critical for memory. Sleep strengthens memory traces via a process called consolidation, which relies on the hippocampus. Assessments of hippocampal microstructure (i.e., internal make-up) have become preferred over assessments of macrostructure (i.e., volume) because the hippocampus has a complex organizational structure, and metrics of microstructure are more precise and able to detect subtle changes in tissue integrity. However, previous studies have not explored how mnemonic discrimination, sleep, and the hippocampus relate, particularly in a developmental population when all three are still undergoing maturational changes. In the following thesis, the relation between mnemonic discrimination, sleep, and the hippocampus was investigated in a sample of 63 habitually napping preschool-aged children. We hypothesized that mnemonic discrimination performance would be worse following a nap, as napping may

support gist memory but not precision memory, and that mnemonic discrimination ability would be significantly associated with hippocampal microstructure. A repeated measures ANOVA, linear regressions, and Bayesian probit regressions were conducted to test these hypotheses. Analyses revealed that relations between the variables did not reach significance. It may be that age contributes a substantial amount of variance to memory in early childhood, and that longitudinal methods may be more suitable for studying developmental populations as they investigate change with age as opposed to without it.

INVESTIGATION OF HIPPOCAMPAL NEURITE DENSITY AND DISPERSION AND THEIR RELATION TO MNEMONIC DISCRIMINATION IN PRESCHOOL-AGED CHILDREN

by

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Chapter 1: Introduction

The ability to store and recall information about past experiences is referred to as *episodic memory*. Episodic memory includes the ability to recognize previously encountered stimuli. The ability to discriminate between two similar stimuli is referred to as *mnemonic discrimination*, which relies heavily on *pattern separation*, a neural-computational process by which similar representations are stored orthogonally within the hippocampus (Stark et al., 2019). Like general episodic memory ability, mnemonic discrimination ability has been shown to improve between the ages of 4 to 6 years (Ngo et al., 2018, 2019; Rollins & Cloude, 2018). Better mnemonic discrimination performance has also been linked to both the volume and functional activation of the hippocampus in adults (Lacy et al., 2011; Stark & Stark, 2017) and the volume of the hippocampus in children (Canada et al., 2019), suggesting this region may be integral in the development of mnemonic discrimination abilities. Additionally, the hippocampus has been shown to be active during sleep, a period in which memory traces are strengthened (Marshall & Born, 2007), suggesting clear links between memory, sleep, and the hippocampus. The following thesis aims to explore the relation between mnemonic discrimination, sleep, and hippocampal microstructure in early childhood. To set the stage, literature on these topics in both adults and children will be reviewed. A novel study based on this past literature will then be outlined and the results will be discussed. Finally, the implications of the analysis for the greater field of developmental cognitive neuroscience will be considered.

The Mechanistic and Cognitive Role of Sleep on the Memory System and the Hippocampus

Sleep has been shown to be beneficial to the memory system because it provides an opportunity for the hippocampus to strengthen neural connections and reorganize memory traces

(Inostroza & Born, 2013; Rasch & Born, 2013). This period of reduced responsiveness to external stimuli allows for uninterrupted memory *consolidation*, a process by which the brain gradually transfers information from neocortical short-term memory stores to hippocampal long-term memory stores (Inostroza & Born, 2013; Rasch & Born, 2013; Stickgold, 2005). Memories are strengthened through distinct patterns of electrical activity that are observed in the hippocampus and occur primarily during sleep (Marshall & Born, 2007). In adults, retention of learned information is stronger following a period of overnight sleep compared to a period of wake (Benson & Feinberg, 1977; Heine, 1914; Jenkins & Dallenbach, 1924; Rasch & Born, 2013). This finding is also observed in children (Kopasz et al., 2010). Additionally, overnight sleep has demonstrated a benefit to hippocampally-dependent mnemonic discrimination in adults (Cellini, 2023; Doxey & Kirwan, 2015; Helm et al., 2011). One study in adolescents demonstrated a reduction in mnemonic discrimination ability following five nights of reduced overnight sleep (7.5 hours) compared to adolescents who slept for 10 hours a night (Saletin et al., 2025).

However, the role of daytime sleep (i.e. napping) in both early childhood and adulthood on memory is unclear due to mixed findings from studies investigating this relation (Cellini et al., 2020; Davidson et al., 2021; Dunstan et al., 2024; Kurdziel et al., 2013). In adulthood, napping demonstrates no benefit to mnemonic discrimination (Cellini et al., 2020; Davidson et al., 2021). One study on preschool-aged children found that naps provided a benefit to visuospatial spatial memory, such that memory between immediate and delayed retrieval was retained when the child had napped, but memory decayed when children were kept awake

(Kurdziel et al., 2013). To the author's knowledge, only one study has investigated the role of both daytime and overnight sleep on mnemonic discrimination in early childhood. In this study, Dunstan et al. (2024) found that mnemonic discrimination improved after overnight sleep for habitual nappers (children who nap at least 5 days a week) but worsened after a nap, which may suggest that naps promote generalization memory but not precision memory in nappers. In non-nappers (children who nap less than 3 days a week), there was no benefit of naps nor overnight sleep on mnemonic discrimination performance. These findings might suggest a differential role of sleep between nappers and non-nappers.

Spencer & Riggins (2022) proposed a theory that may explain the differences in findings in the role of sleep on memory for nappers and non-nappers. They posited that the gradual transition from biphasic sleep (i.e. napping) to monophasic sleep in early childhood is supported by the maturation of the hippocampus, which in turn increases the storage and efficiency of the hippocampal-dependent memory storage. This more effective memory system can store more information throughout the day and therefore does not require sleep-dependent consolidation mid-day (i.e. naps). Given this theory, as well as the previous findings in adults and non-napping children, it could be that napping does not provide an observable benefit to memory performance in these groups because the memory system is mature enough to be able to effectively consolidate throughout the period leading up to the retrieval task. However, it is important to note that this theory has not been empirically tested yet. The data being used for this thesis is part of a larger empirical study designed by Spencer & Riggins to investigate this overarching hypothesis. This thesis aims to investigate a portion of the data to determine how sleep and

mnemonic discrimination relate to hippocampal microstructure in habitually napping children, before the nap transition occurs. This question is an important first step, as it will establish baseline associations between mnemonic discrimination, sleep, and hippocampal microstructure in this sample.

Limitations of Hippocampal Macrostructural Studies

Much of prior research has focused on the association between hippocampal volume, or macrostructure, and memory performance in children. Many of these studies have reported mixed findings regarding hippocampal structure and memory, suggesting a complex relation between the two (Botdorf et al., 2022; Canada et al., 2019, 2021; Daugherty et al., 2017; Homayouni et al., 2023). However, a major limitation of using volume to assess hippocampal maturity is that volume is agnostic to neurophysiological processes that may affect tissue properties, such as synaptogenesis, myelination, and synaptic pruning (Callow et al., 2020; Canada et al., 2020). Prior research has established that these microstructural changes in tissue properties are a major driving force for cognitive development (Lebel et al., 2019; Lebel & Deoni, 2018; Tamnes et al., 2018). Thus, the field is turning to more precise neuroimaging techniques that allow for the detection of changes to tissue integrity, which may be more appropriate for regions that undergo rapid development during childhood, such as the hippocampus (Uematsu et al., 2012).

Assessing Hippocampal Microstructure Using Diffusion Magnetic Resonance Imaging

Assessments of hippocampal microstructure using diffusion-weighted magnetic resonance imaging (dMRI), a burgeoning neuroimaging technique, have been shown to predict memory performance over and above hippocampal macrostructure. This suggests that assessments of tissue integrity may be unique and possibly more reliable predictors of memory (Callow et al., 2020; Cherubini et al., 2010; den Heijer et al., 2012; Venkatesh et al., 2020). Diffusion tensor imaging (DTI) is one dMRI technique that looks at the diffusion of water molecules within a brain region, which better reflects tissue integrity than volume, which is a gross measure of tissue structure. Mean diffusivity (MD) is a common DTI metric, and to date, all studies conducted in children have shown a negative association between MD in the hippocampus and memory performance (Callow et al., 2020; Fjell et al., 2019; Solar et al., 2021; Vieites et al., 2024; Vinci-Booher et al., 2024). Excitingly, advances in dMRI techniques now allow for methods that can provide additional information about tissue architecture, such as neurite density and organization. These methods are especially useful in regions such as the hippocampus, which is predominantly composed of grey matter, a tissue that is more densely packed and less structurally organized than white matter (Chang et al., 2015; Nazeri et al., 2015, 2020; Zhang et al., 2012).

Neurite Orientation Dispersion and Density Imaging (NODDI)

One such dMRI method that accounts for the complex organization in gray matter structures like the hippocampus is neurite orientation dispersion and density imaging, or NODDI (Zhang et al., 2012). NODDI assumes that the region of interest (ROI) consists of intra-cellular

space, extra-cellular space, and cerebrospinal fluid and that all three contribute to diffusion differentially (this is dissimilar to DTI, which assumes equal contribution to diffusion across all cellular spaces). For this reason, NODDI has been shown to be more precise in its estimation of hippocampal microstructure than DTI metrics (Chang et al., 2015; Nazeri et al., 2015, 2020; Zhang et al., 2012). Furthermore, NODDI provides several metrics to characterize gray matter microstructure, two of which are the neurite density index (NDI) and the orientation-dispersion index (ODI). NDI estimates the density of neurons within the ROI, and ODI quantifies the branching and bending of the neurons. These two metrics together, in addition to MD, can provide the field with a richer understanding of the minute changes within complex structures such as the hippocampus throughout development.

NODDI and Memory

To the author's knowledge, no studies have investigated the relation between NODDI metrics in the hippocampus and mnemonic discrimination in either adults or children. However, several studies have found relations with other measures of memory. In one study, neurite density in the CA1 and the CA3/DG was negatively associated with delayed memory on a word memorization task in adults, even after regressing out the effect of age on subfield integrity (Radhakrishnan et al., 2020). In another study in older adults with and without mild cognitive impairment, lower NDI and lower ODI values were associated with worse memory performance on two standardized memory assessments (Pillai et al., 2025). This study did not investigate group differences or the effect of age on the NODDI-memory relation, however, so it is possible that mild cognitive impairment or age may have contributed to the opposite findings regarding

the direction of the relation. Only one study was found to use NODDI metrics in a developmental population. In this study, greater neurite density in the left hippocampus was associated with better learning on an eyeblink conditioning task in preschoolers (Vieites et al., 2024). Few studies have used NDI and ODI to examine hippocampal microstructure and memory because NODDI is a relatively new technique (circa 2012) and requires multi-shell dMRI rather than traditional single-shell data (which MD and FA can be estimated from), which can create logistical and technical barriers for research groups. However, the lack of research on this topic highlights an important gap in our knowledge on hippocampal microstructure and pattern separation, a process that occurs within the hippocampus. Because NDI and ODI have been shown to be more precise than traditional diffusion metrics within the hippocampus, they offer a promising and informative way to examine the hippocampus' relation with memory.

The Present Study

Given that there have been no published studies in early childhood exploring relations between mnemonic discrimination, sleep, and hippocampal microstructure, the following thesis addresses the following research questions in a study of habitually napping children between the ages of three and six years. First, the present work aims to identify associations between age and mnemonic discrimination performance, as well as between age and three metrics of hippocampal microstructure (MD, ODI, NDI). Then, we will determine whether napping or being kept awake during the expected nap time impacts mnemonic discrimination performance. Additionally, the relation between hippocampal microstructure and mnemonic discrimination performance will be

assessed. Finally, an exploratory analysis will be conducted to attempt to mitigate the limitations of the proposed main analysis.

Hypotheses

The research questions addressed in the present study yield several hypotheses. First, we hypothesize that age, mnemonic discrimination and the three dMRI metrics will be positively associated. Additionally, because all participating children are habitual nappers, we expect that sleep will impact mnemonic discrimination scores, such that napping will result in worse mnemonic discrimination performance compared to being kept awake, in line with the findings from Dunstan et al. (2024). Second, we hypothesize that MD will be negatively related to mnemonic discrimination, NDI will be negatively related to mnemonic discrimination, and ODI will be positively related to mnemonic discrimination. Finally, we expect that both sleep and dMRI will be significant predictors of mnemonic discrimination ability such that a) napping will be associated with worse mnemonic discrimination performance compared to being kept awake when controlling for the impact of microstructure on memory performance and b) microstructure will be associated with mnemonic discrimination even when controlling for the impact of sleep on mnemonic discrimination. Regarding the latter hypothesis, we expect that the directions of this association will be the same as the associations outlined above between the dMRI metrics and mnemonic discrimination.

Chapter 2: Methods

Participants

Participants are part of an ongoing longitudinal study looking at the relations between sleep, memory, and hippocampal development in habitually napping preschoolers between the ages of three and six years. In this study, a habitual napping child is defined as a child who naps at least five times a week. Participants are recruited through the respective local communities through online advertisements, community outreach events, and email listservs. Participants were compensated monetarily for their participation in the study. Exclusion criteria included known sleep or neurological disorders, communicative and language delays, and prior completion of the memory task. This study is a collaboration between the University of Maryland, College Park (UMD) and the University of Massachusetts Amherst (UMass).

Data Selection

Participants complete up to three timepoints across a 12-month span, with each timepoint 6 months apart. The procedures outlined in the sections below are identical for all three timepoints. Habitual nappers who had at least one wave of both usable dMRI and memory data were included in the study (for an explanation of data exclusion criteria, please see the sub-sections *Mnemonic Similarity Task* and *Magnetic Resonance Imaging*). For participants who completed multiple waves, one wave was randomly selected. This approach was used to maximize data quality, as data from participants' first wave is typically of lower quality than data from subsequent waves. This difference in quality includes the quality of the MRI images

themselves, which cannot be accounted for by statistically controlling for age in analyses. Subjects that had values outside 3 standard deviations above or below the mean on at least one variable of interest were excluded. This procedure yielded a final sample of 63 children (M_{age} = 3.96 years, *SD* = 0.67, 35 females).

Procedure

All methods used in the current study were approved by the University of Maryland Institutional Review Board. Participants were sent an electronic copy of the consent form and MRI screening form prior to the first study visit.

Mnemonic Similarity Task

Children completed the Mnemonic Similarity Task (MST; Stark et al., 2019), a behavioral measure of mnemonic discrimination that targets hippocampal-dependent pattern separation processes. The administration of this task is identical across the two sites. In this task, children were shown pictures of objects and then tested on their ability to recall those items among completely novel objects and similar lures, which serve as distractors. During encoding, children were shown 60 pictures of everyday objects sequentially and asked if each picture belongs "Inside" or "Outside"; "*Did you see this exact picture in the Inside/Outside game?"* (See Figure 1).

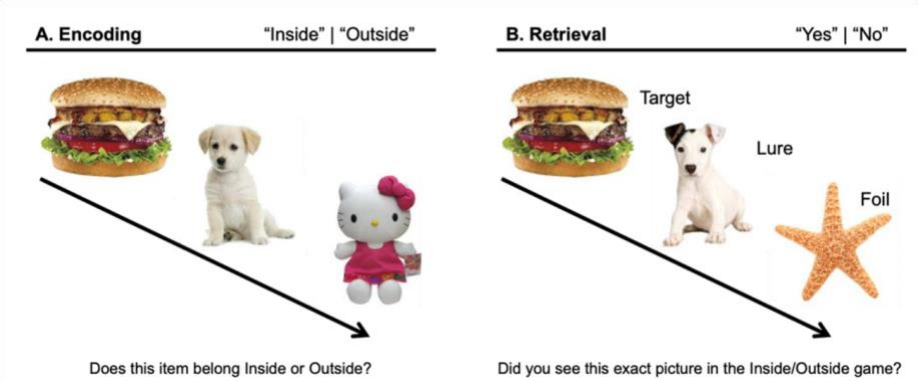


Figure 1. Depiction of the MST task. Encoding (A), in which the participants were shown pictures of objects and were asked if the picture belongs "Inside" or "Outside". During the retrieval portion of the task (B), the participants were shown pictures, some old (targets), some similar (lures), and some new (foils) and were asked if they had seen the picture previously in Encoding (referred to as the "Inside/Outside game").

The purpose of the Inside/Outside judgement during encoding was to ensure the child was attending to each image. Following encoding, the children were presented with a retrieval task in which they were shown 45 pictures in random order: 15 old (*targets*), 15 similar (*lures*), and 15 new (*foils*). At each picture, children were asked if they had been shown that picture in the Inside/Outside game (accepted responses are "Yes" or "No").

The retrieval task was repeated twice: once immediately after encoding (immediate retrieval) and again after the child's nap or a similar period spent awake (delayed retrieval) (see Figure 2). During the similar period spent awake, the child played with the researchers; activities included, but were not limited to, coloring, Play-Do, playing with toys, puzzles, or board games.

Activities that included other memory games, TV, or a fair amount of physical activity were not allowed. The nap/wake condition was counter-balanced across two weeks and across subjects, such that each child received both conditions one week apart. Children received one of three versions of this task, which differ only in the pictures shown; the order was counter-balanced across subjects.

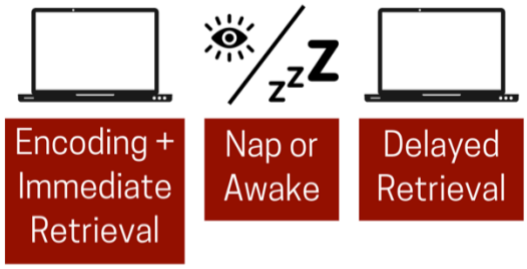


Figure 2. Flowchart of MST task protocol. First, the child did the MST encoding task, then the immediate retrieval task. Then, the child either napped or spent the same period awake. Then, the child completed the delayed retrieval task. Sleep conditions were within-subject and counterbalanced across subjects.

A Lure Discrimination Index (LDI) was calculated by taking the percentage of incorrect lures from the percentage of correct targets, which measures how well participants can discriminate between similar pictures (targets and lures). Retrieval sessions in which the child answered entirely "Yes" or "No" were excluded. Additionally, sessions in which the child had demonstrated alternating answer bias on at least 41 sequential trials out of the 45 total (91.1%) were excluded.

Magnetic Resonance Imaging

Neuroimaging data were collected approximately one week after the last memory session (M_{days} = 25.88, *SD* = 17.76). The MRI acquisition protocols were the same across sites. Children first participated in a mock scan to get them comfortable with the scanning environment and practiced staying still during the scan. Following the mock scan, children completed the actual brain scan. Padding is placed around the child's head to minimize head movement. Children watch a movie of their choice throughout the structural sequences to prevent boredom that may contribute to head and body movement. Real time motion during the scans is monitored using FIRMM at the UMD site, and visual observation by the researchers at both sites; children are given reminders to remain still if excess or chronic movement was detected.

Images were acquired using a Siemens 3.0 T scanner (MAGNETOM Prisma Fit and MAGNETOM XQ Numaris at the UMD and UMass sites, respectively) with a 32-channel head coil. Images acquired included a high-resolution T1-weighted MPRAGE sequence (TR/TE = 2500/29 ms, FOV = 256 mm, 176 sagittal slices, spatial resolution = 1.0 mm^3). T1 images were rated for quality after acquisition; if the images are deemed to be low quality, the scan was repeated in the same scanning session. Diffusion images were collected with multi-shell spin-echo Echo Planar Imaging sequence with a Simultaneous Multi-Slice acceleration. The diffusion scheme consisted of Multidirectional Diffusion Weighted (MDDW) acquisitions collected in 64 orthogonal directions for both gradient values b = 1500 s/mm^2 and b = 3000 s/mm^2. The first acquisition and the last five acquisitions had no diffusion weighting (b = 0). This yielded a total of 128 diffusion-weighted images and 6 non-diffusion-weighted images (UMD: TR/TE =

3500/102 ms, FOV = 218 x 218 mm, 72 axial slices, 1.73^3 mm spatial resolution; UMASS: TR/TE = 3500/132 ms, FOV = 240 x 240 mm, 72 axial slices, 2.0 mm^3 spatial resolution).

T1 images were pre-processed using Freesurfer 7.4's recon-all pipeline and were visually inspected for quality. For the scans deemed to be of acceptable quality, a binary ROI mask was created for the total hippocampus for each subject using Freesurfer. The dMRI data was corrected for motion, eddy current-induced distortions, and b0 inhomogeneities using Mrtrix3 (Tournier et al., 2019). Diffusion images from both sites were upsampled to 1.0 mm isotropic to maximize data quality. Participants were excluded for excessive head motion (total outliers > 3%) as indicated by MRtrix3's quality control algorithm, eddyQC. As dMRI was collected across two sites, the diffusion data was harmonized using the methods outlined in Cetin-Karayumak et al. (2024) which uses rotation invariant spherical harmonics (RISH). This technique has been shown to minimize inter-site effects better than popular harmonization methods such as ComBat (Fortin et al., 2017).

The tensor model was fit using MRtrix3 and NODDI was fit using AMICO (Daducci et al., 2015) in harmonized diffusion space. Each subject's b0 images were averaged and then registered to their T1 image using ANTs SyNQuick (Tustison et al., 2021). Inverse transforms were then applied to the NODDI and tensor images and the mask was regridded to the transformed NODDI and tensor images. The alignment of the mask to the diffusion images were visually inspected for quality, and no subjects were excluded for poor alignment. Finally, average MD, NDI, and ODI were obtained across the hippocampus in left and right hemispheres.

Because MD is on a 10^{-4} scale, values were multiplied by 1,000 for ease of readability and estimation in the statistical analyses.

Analytic Plan

All statistical analyses were carried out in R. First, we inspected histograms and QQ plots on all variables of interest. Bivariate Pearson's correlations were conducted across all metrics of interest. Next, we tested sex differences in each of the variables of interest using paired t-tests. A two-way repeated-measures analysis of variance (ANOVA) was conducted on differences in mnemonic discrimination between the retrieval tasks (immediate, delayed) and sleep conditions (nap, wake), to identify the role of sleep on mnemonic discrimination. A composite LDI score was then calculated for each subject by averaging their LDI scores across all sessions. Three multiple linear regressions were run in which average mnemonic discrimination ability was regressed on each of the diffusion metrics (MD, NDI, ODI) and age.

Finally, a hierarchical probit regression model that utilized a Bayesian signal detection framework was used to address several limitations present in the analyses outlined above. One limitation is that although the data was cleaned to exclude sessions in which subjects answered only "Yes" or only "No" on every trial, it was not possible to establish a reliable threshold for excluding response bias across all subjects, since each subject may naturally tend to favor one response over the other (Kellen et al., 2021). Another limitation is that partial data was deleted listwise to compare mnemonic discrimination performance within conditions. Finally, the linear regressions utilized averaged data, which assumes that homogenous response certainty across trials. For example, a correct response on 3 out of 4 trials reflects higher certainty than correctly responding 30 out of 40 trials, yet both yield the same hit rate. This results in a metric that

doesn't account for variation in uncertainty across trials. Thus, a more complex analysis that accounts for these limitations is preferred.

Signal detection theory (SDT) is a popular framework in recognition memory analysis, as it accounts for the subject's natural response bias as well as the subject's ability to distinguish between old and new stimuli (termed *discriminability*), both of which contribute to subject's answers on the retrieval task. In SDT, it is assumed there are two underlying distributions across the memory task; *signal*, which represents target trials in which a previously seen picture is presented, and *noise*, which represents lure trials that the subject has not previously seen (Kellen et al., 2021). Hierarchical regressions allow for partial data, which provides greater power to test these interactions while still accounting for the shared within-person variance between repeated measures. Finally, the Bayesian signal detection theory framework allows us to capture the degree of uncertainty across trials by integrating all the subjects' trial data into the model to create estimates. (Dennis et al., 2008).

In this model, *c* is the intercept coefficient and *d'* is the slope coefficient (Vuorre, 2017). Means and standard deviations of *d'* (M = 0.47, SD = 0.42) and *c* (M = -0.33, SD = 0.51) were hand-calculated for the sample data to set informative priors. For the models that included age as a covariate or interaction term, informative priors for age were used as well:

$$\begin{aligned} d' &\sim N(0.5, 0.5) \\ c &\sim N(-0.5, 0.5) \\ age &\sim N(0, 0.5) \end{aligned} \tag{1}$$

Priors were confirmed to be informative using the method outlined in Gelman et. al (2017). Models were run in RStudio using the package brms. The chain was run for 10,000 iterations with the first 500 for burn-in. The co-predictors of interest were added to the base model to mirror the tests run using the frequentist approaches (e.g. age, retrieval condition, sleep condition, age & diffusion). The primary aim of the hierarchical Bayesian models was to confirm the findings of the frequentist methods, while accounting for noise, outliers, and uncertainty.

Chapter 3: Results

Descriptive Statistics

Participants were 63 habitually napping children between the ages of 3 and 6 years (M_{age} = 3.96, *SD* = 0.67, 35 F). Both sites recruited participants from their surrounding metropolitan areas. The participants from which the sample was drawn from was predominately White, non-Hispanic/Latino and moderate-to-high income across both sites.

Associations between mnemonic discrimination performance, metrics of hippocampal microstructure, and age

Pearson's correlations were run on the variables of interest, including age, LDI, and hippocampal MD, NDI and ODI (see Table 1).

Variable	*M*	*SD*	1	2	3	4	5
1. Age	3.97	0.66	-				
2. Aggregated LDI$^{\lozenge}$	15.00	13.11	0.43**	-			
3. Total Hippocampal MD$^{\oplus}$	0.88	0.04	-0.11	-0.17	-		
4. Total Hippocampal NDI	0.29	0.04	0.20	0.10	0.35*	-	
5. Total Hippocampal ODI	0.31	0.02	0.14	0.28*	0.08	0.31*	-

Table 1. Descriptive statistics and correlations for study variables

Notes: $^{\lozenge}$ Lure Discrimination Index averaged across all available sessions for each subject

$^{\oplus}$ Values were multiplied by 1,000 for readability

* $p < .05$, ** $p < .001$

Subjects' LDI scores were aggregated across sessions for interpretability. Results showed that age was moderately positively correlated with average memory performance. Contrary to

our hypotheses, age was not correlated with the three hippocampal microstructure metrics of interest. Furthermore, only ODI was correlated with average memory performance. Among the brain measures, MD and NDI were positively correlated, as were NDI and ODI. MD and ODI were not significantly correlated.

Differences in mnemonic discrimination between experimental conditions

Our first research question asked whether mnemonic discrimination performance differed between the nap and the awake conditions to determine the impact of sleep on mnemonic discrimination. The difference between immediate and delayed retrieval was also tested to determine if memory decayed during the delay between the two tasks. LDI scores were subjected to a two-way repeated measures analysis of variance by having two levels of retrieval (immediate, delayed) and two levels of sleep condition (nap, wake). There were no significant main effects of retrieval, $F(1, 56) = 0.22$, $p = 0.639$, nor sleep condition, $F(1, 56) = 0.27$, $p = 0.609$. Additionally, the interaction was non-significant, $F(1, 56) = 0.60$, $p = 0.442$. Given the results of the ANOVA (see Figure 3), LDI was aggregated across all experimental conditions to yield each subject's average LDI score. This aggregated LDI score was used for the following regressions.

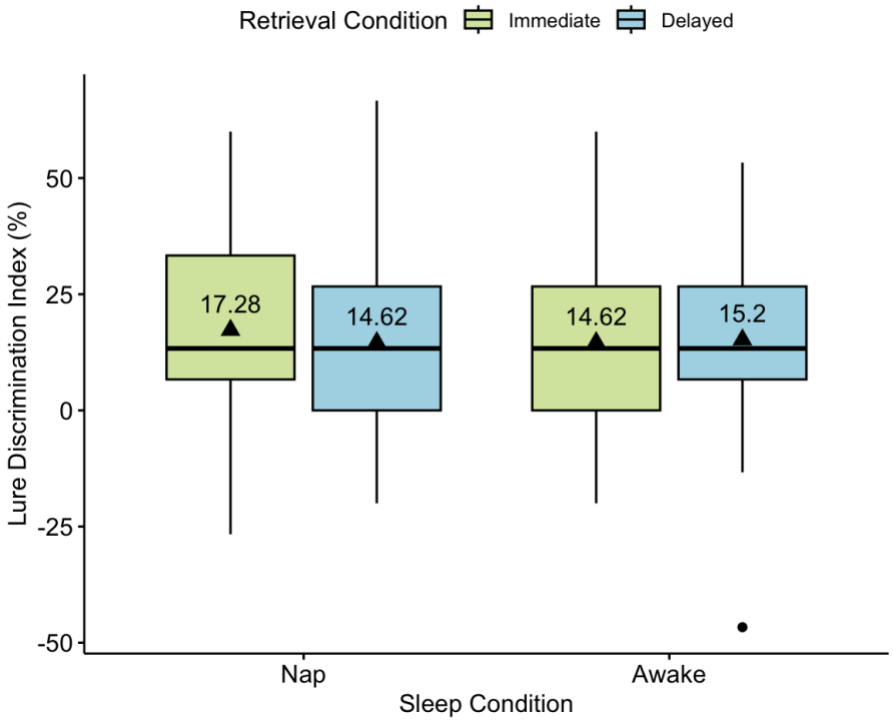


Figure 3. Boxplot of LDI by experimental conditions.

Relations between mnemonic discrimination and total hippocampal microstructure

Our second research question asked if mnemonic discrimination was related to three metrics of hippocampal microstructure (MD, NDI, ODI). A series of three multiple linear regressions were run, regressing average memory performance on age and each of the three metrics of hippocampal microstructure (see Table 2).

Model 1: Average Mnemonic Discrimination Performance Regressed on Age and Total Hippocampal Mean Diffusivity

Variable	*b*	SE	95% CI		*t*	*p*
			LL	*UL*		
Intercept	20.16	37.28	-54.42	94.73	0.54	.591
Age**	8.14	2.27	5.3.61	12.67	3.59	< .001
Total Hippocampal MD⊕	-42.26	2.39.83	-121.93	37.41	-1.06	.293

Notes. $R^2 = 0.20$
*$p < .05$, **$p < .001$
⊕ Values were multiplied by 1,000 for readability
CI = Confidence Interval; *LL* = Lower Limit; *UL* = Upper Limit

Model 2: Average Mnemonic Discrimination Performance Regressed on Age and Total Hippocampal Neurite Density

Variable	*b*	SE	95% CI		*t*	*p*
			LL	*UL*		
Intercept	-19.32	13.94	-47.19	8.56	-1.39	.17
Age**	8.34	2.32	3.70	12.99	3.59	< .001
Total Hippocampal NDI	4.39	42.21	-80.03	88.82	0.10	.917

Notes. $R^2 = 0.19$
*$p < .05$, **$p < .001$
CI = Confidence Interval; *LL* = Lower Limit; *UL* = Upper Limit

Model 3: Average Mnemonic Discrimination Performance Regressed on Age and Total Hippocampal Orientation Dispersion

Variable	*b*	SE	95% CI		*t*	*p*
			LL	*UL*		
Intercept*	-53.96	20.18	-94.32	-13.60	-2.67	.010
Age**	7.77	2.23	3.32	12.23	3.49	< .001
Total Hippocampal ODI	124.26	63.05	-1.86	250.39	1.97	.053

Notes. $R^2 = 0.34$
*$p < .05$, **$p < .001$
CI = Confidence Interval; *LL* = Lower Limit; *UL* = Upper Limit

Table 2. Results from linear regressions

First, we tested whether total hippocampal mean diffusivity and age predicted memory performance. Age significantly predicted average mnemonic discrimination performance, but total hippocampal mean diffusivity did not. Then, we regressed memory performance on total hippocampal neurite density, which was not a significant predictor of average memory performance, but age was. Finally, memory performance was regressed on total hippocampal orientation dispersion and age. Total hippocampal orientation dispersion was a marginally significant predictor of average memory performance and age was a significant predictor. Overall, the linear regressions did not find a significant relation between hippocampal microstructure and mnemonic discrimination performance.

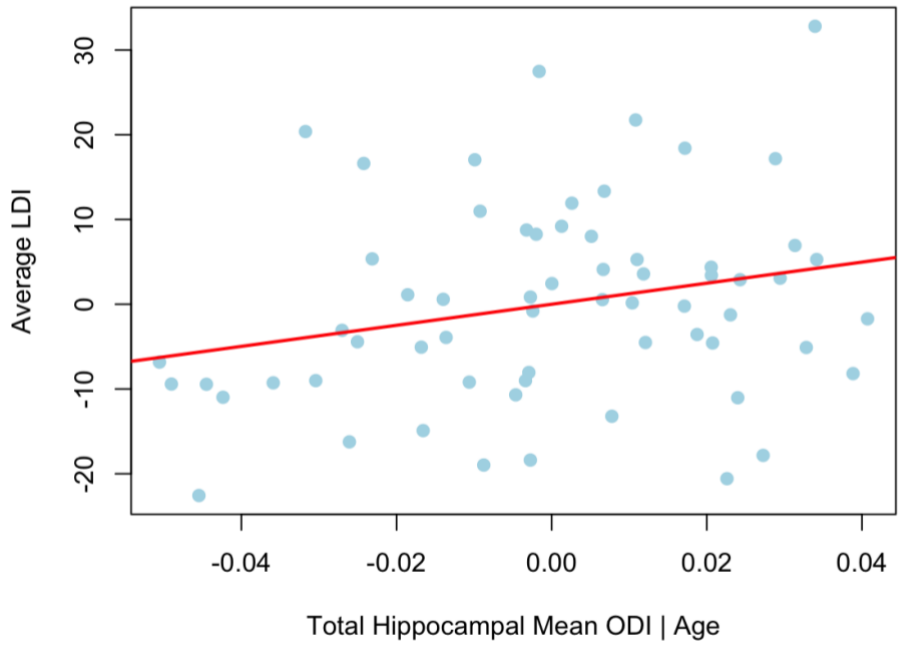


Figure 4. Partial plot of average LDI regressed on total hippocampal ODI when controlling for age

Results of the Hierarchical Probit Regression Models

A series of Bayesian models using the signal detection theory framework was run to critically test the findings of the frequentist models, which were limited in their ability to account for noise present in the dataset. All models yielded good convergence, as assessed by R-hat values and trace plots, $\hat{R} = 1.0$. Posterior predictive checks revealed that all models yielded good fit, meaning the model predicted values that mirrored the observed subject responses well. The first hierarchical Bayesian model regressed subjects' responses on the correct answers using informative priors based on the sample's mean and standard deviation of *d'* and *c*.

The analysis revealed that children were able to discriminate between targets and lures, $M_{d'} = 0.46$, 95% HDI [0.36, 0.57], $p_{MAP} < .001$. Additionally, the results suggest that although it is likely that the children had a slight "No" response bias overall, the possibility that there was no response bias cannot be ruled out, $M_c = 0.10$, 95% HDI [-0.03, 0.24], $p_{MAP} = .313$ (See Figure 5).

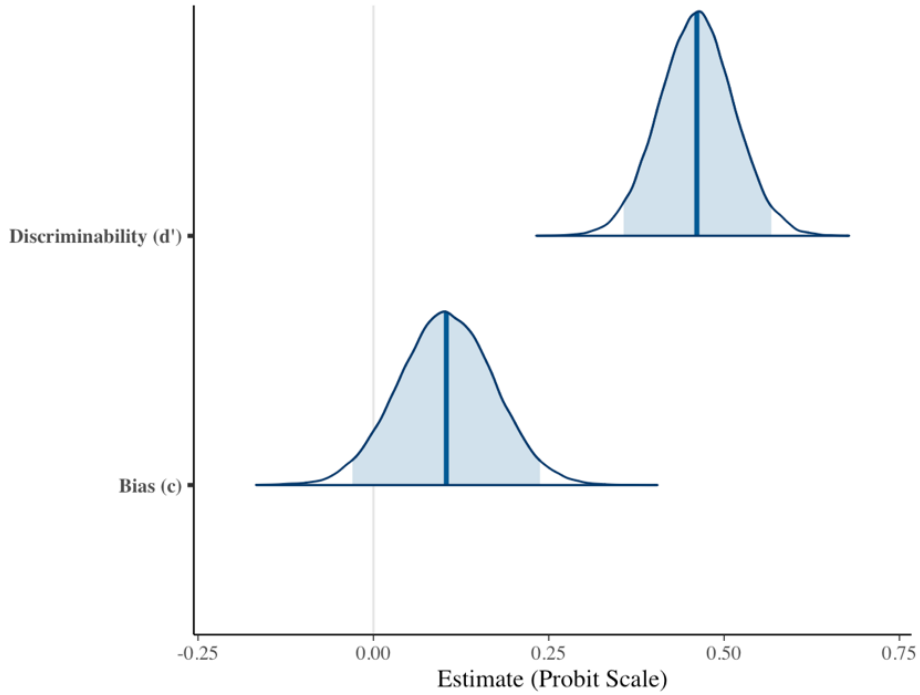


Figure 5. Posterior predictive draws density plots for *d'* and *c*

Next, the interaction between age and discriminability was tested. Equivalence testing revealed a positive and significant effect of age on discriminability, such that discriminability improved as age increased (see Figure 6), $M_{d'}$ | Age = 0.22, 95% HDI [0.09, 0.34], p_{MAP} = .004. As such, age was included as a covariate for the following models.

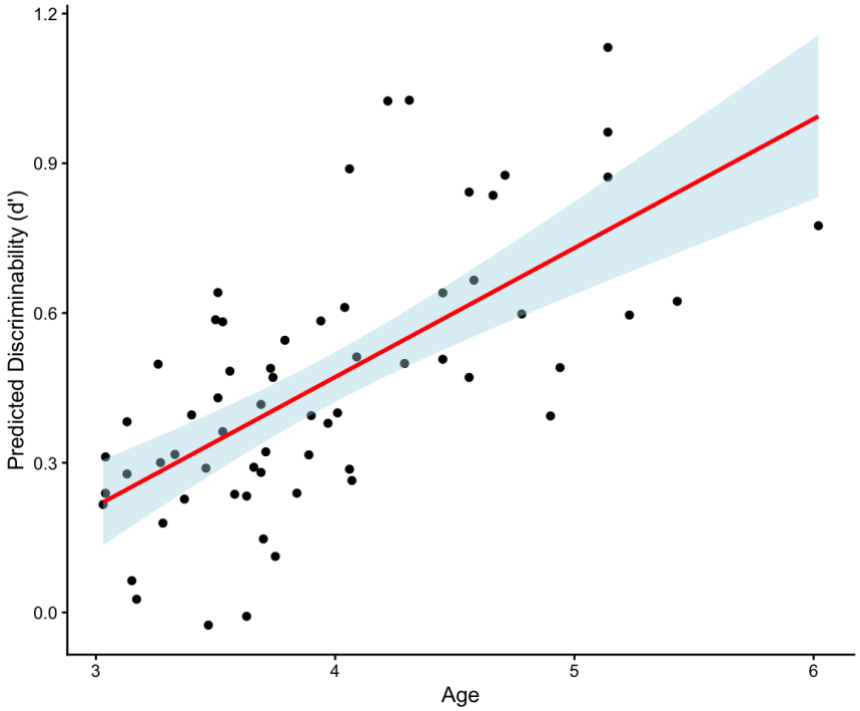


Figure 6. Plot of predicted discriminability versus age

Then, the interaction of the retrieval conditions (immediate, delayed) and discriminability when controlling for age was tested. Examination of the posterior predictive plots found negligible evidence of an interaction, $M_{d'}$ | Age = 0.06, 95% HDI [-0.06, 0.18], p_{MAP} = .661. Additionally, the interaction of the sleep conditions (nap, awake) and discriminability was tested, controlling for age. Again, the model demonstrated negligible evidence of an interaction between sleep or wake and discriminability, $M_{d'}$ | Age = 0.01, 95% HDI [-0.11, 0.14], p_{MAP} = .984. Therefore, the subsequent series of regressions using the hippocampal diffusion metrics did not include the experimental conditions as covariates.

Finally, a series of regressions testing the interaction of total hippocampal diffusion metrics (MD, NDI, ODI) on discriminability controlling for age were conducted. The interaction between mean diffusivity and discriminability when controlling for age yielded a posterior mean

of $M_{d'}$ | Age = -0.31 with a 95% HDI of [-1.33, 0.72]. Because this interval contains zero, it is likely that total hippocampal mean diffusivity did not affect mnemonic discrimination performance, $p_{MAP} = .858$. Similarly, it was found to be likely that neurite density did not affect discriminability, $M_{d'}$ | Age = 0.48, 95% HDI [-1.68, 2.63], $p_{MAP} = .887$. Finally, it was found to be likely that neurite orientation and dispersion in the hippocampus did not affect discriminability when controlling for age, $M_{d'}$ | Age = 1.66, 95% HDI [-0.99, 4.27], $p_{MAP} = .439$. The results of the Bayesian analyses reveal that the relations between hippocampal microstructure and mnemonic discrimination were not statistically detectable after controlling for age.

Chapter 4: Discussion

This study sought to understand the relations between sleep, mnemonic discrimination, and hippocampal microstructure in habitually napping children. We hypothesized that children would do worse on the delayed retrieval task after taking their nap, in line with previous findings (Dunstan et al., 2024). Contrary to our hypotheses, there were no differences in mnemonic discrimination performance between the experimental conditions. Performance between immediate and delayed retrieval was comparable, suggesting the delay between tasks did not decay the memory traces enough to be statistically detectable. Additionally, there was no difference was detected between the nap and wake conditions, suggesting that the nap had an insignificant impact on mnemonic discrimination performance. Assessments of the relation of hippocampal microstructure and mnemonic discrimination performance were also non-significant. The linear regression indicated a marginal finding of a positive relation between neurite orientation and dispersion and mnemonic discrimination ability when controlling for age, suggesting that as the hippocampal structure becomes more complex, mnemonic discrimination ability improves. However, these findings were not supported by the Bayesian analysis, which is assumed to be more precise as the models remove the noise contributed to the memory data by subjects' criterion and uncertainty.

There were several factors that likely contributed to a lack of significance of effects. The first, is that the study had a small sample size and was thus underpowered. A power analysis revealed that the multiple linear regressions would require a sample size of at least 96 participants to detect a small effect (Cohen's $d = 0.10$) at a power of 0.80 at the $\alpha = .05$ significance level. This finding is encouraging for future research, as data collection for the

larger longitudinal study, of which this thesis used data from, is still ongoing. Another possible explanation for the failure to reach significance could be the heavy hand age plays in developmental data. Age effects were found by both the Frequentist and Bayesian regressions, suggesting that memory performance did increase with age. However, hippocampal microstructure was not consistently correlated with age, suggesting that microstructure is variable throughout early childhood. This could be due to microstructural changes that occur in development such as synaptogenesis, synaptic pruning, and myelination; these changes have been shown to drive cognitive development (Lebel et al., 2019; Lebel & Deoni, 2018; Tamnes et al., 2018). It is likely that age was heavily driving variability in memory performance, and some of the variance in hippocampal microstructure, and the removal of the effect of age on the other two variables caused the remaining relation to not reach significance. Herein lies the greatest limitation of cross-sectional study designs in developmental populations: age predicts much of other variables of interest, and by controlling for the effect of age in a developing population, the variance shrinks considerably. Future studies should focus on longitudinal analyses, which look at the trajectory of change across age, as opposed to removing the effect of age on variables that are dependent on age (Callow et al., 2020).

Despite the failure to reach significance, the present study still provides important information for the larger field. First, it demonstrates the utility in Bayesian signal detection theory models in mnemonic discrimination research, as they provide distributions predicted from observed data, which allows us to determine the probability of the null and alternative hypotheses (Fornacon-Wood et al., 2022). Additionally, signal detection theory provides an alternate metric (i.e. discriminability, *d'*) to the traditional Lure Discrimination Index, which is

not robust to response bias or uncertainty across trials. Furthermore, this study makes use of burgeoning techniques for assessing hippocampal microstructure. Literature utilizing these techniques in early childhood for memory research is sparse, so the study did not have strong hypotheses or expectations for the results of the analyses. Future studies should consider NODDI when assessing hippocampal microstructure in early childhood to further our understanding of its development and relation to memory.

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