

## ABSTRACT

Title of Thesis:                   IMPACT OF AGE AND EXPERIENCE ON  
PATTERN SEPARATION

Kelsey Leigh Canada, Master of Science, 2017

Thesis Directed By:           Associate Professor, Tracy L. Riggins,  
Department of Psychology

The ability to remember highly detailed events and discriminate between them is thought to be supported by two distinct but complementary neural computational processes: pattern completion and pattern separation. The current study focused on the process of pattern separation, in which similar memories are assigned distinct representations, thus reducing the overlap between similar inputs. This process is measured behaviorally by tasking individuals with mnemonically discriminating between similar stimuli. The present study addressed the contribution of age and experience, which are difficult to distinguish during development, to pattern separation in adults and 9- to 11-year-old children, in whom this process and its supporting neural substrates are still developing. We examined differences in participant's mnemonic discrimination of high-experience (e.g., own-race faces) and low-experience (e.g., other-race faces) stimuli. Results indicate better pattern separation overall in adults, and, that level of experience with a stimuli class may moderate age-related differences in pattern separation.

IMPACT OF AGE AND EXPERIENCE ON PATTERN SEPARATION

by

Kelsey Leigh Canada

Thesis submitted to the Faculty of the Graduate School of the  
University of Maryland, College Park, in partial fulfillment  
of the requirements for the degree of  
Master of Science  
2017

Advisory Committee:  
Professor Tracy Riggins, Chair  
Professor Elizabeth Redcay  
Professor Michael Dougherty

© Copyright by  
Kelsey Leigh Canada  
2017

## Acknowledgements

I am deeply grateful to my mentor and committee chair, Dr. Tracy Riggins, for her guidance and support throughout this project and my graduate training. I would also like to express my gratitude to my thesis committee members, Dr. Dougherty and Dr. Redcay, for their time and the invaluable feedback that improved my thesis. I also wish to thank the members of the University of Maryland Neurocognitive Development Lab for help with scheduling participants and all of the participants and families who gave their time to participate.

# Table of Contents

Acknowledgements.....	ii
Table of Contents.....	iii
List of Tables.....	iv
List of Figures.....	v
Chapter 1: Introduction.....	1
Age impacts mnemonic discrimination.....	3
Experience impacts mnemonic discrimination.....	4
Clarifying the roles of age and experience in mnemonic discrimination.....	5
Chapter 2: Method.....	7
Participants.....	7
Materials.....	8
Mnemonic Similarity Task (MST).....	8
Questionnaires.....	9
Procedure.....	10
Statistical Analysis.....	12
Chapter 3: Results.....	16
Preliminary Analyses.....	16
Main Analyses.....	16
Exploratory Analyses.....	21
Chapter 4: Discussion.....	24
Appendix A.....	29
Appendix B.....	39
References.....	42

## List of Tables

Table 1. Proportion of old/new responses to each stimuli condition by participant age group and stimuli race.....	17
Table 2. Summary of mnemonic discrimination performance, covariate measures, and item memory performance by age group and t-tests of assessing age group differences.....	17

## List of Figures

Figure 1. Example stimuli.....	9
Figure 2. Schematic representation of the MST.....	12
Figure 3. Mnemonic discrimination performance by Age Group.....	18
Figure 4. Mnemonic discrimination performance by Stimuli Race.....	19
Figure 5. Mnemonic discrimination performance by Stimuli Race and Age Group...20	
Figure 6. Item memory performance.....	21
Figure 7. Mnemonic discrimination performance by Stimuli Race, Age Group, and Experience Group.....	23

## Chapter 1: Introduction

Episodic memory is the ability to encode and retrieve specific details of life-experiences, including associations between people or objects, spatial relations of objects, and temporal information (Tulving, 1972, 1993; Rolls, 2016). These details are often recalled such that an individual can “mentally time travel” and re-experience a specific event (Tulving, 1972, 1993). For example, you may remember the last time you and your best friend went bowling at the local bowling alley. You both bowled on the leftmost lane and you used a red bowling ball while your friend chose a pink bowling ball. The time before that you both bowled on the center lane and each used a green bowling ball.

The ability to remember these episodic memories and discriminate between them is thought to be supported by two distinct, but complementary, neural computational processes: pattern completion and pattern separation (Bakker, Kirwan, Miller, & Stark, 2008; Norman, 2010). Pattern completion is the ability to retrieve full events using partial information. An example would be recalling the lane where you and your best friend bowled, which would bring to mind other details such as the color of the ball you used. Pattern separation is the ability to separately encode similar events by forming distinct representations in memory that minimize overlapping features (Stark, Yassa, Lacy, & Stark, 2013; Deuker, Doeller, Fell, & Axmacher, 2014). Although the experiences at the bowling alley are highly similar, each varies slightly in features such as the lane used and the color of each individual’s bowling ball. The process of pattern separation allows you to separate these highly

similar features and distinctly encode each event for later retrieval. While both pattern completion and pattern separation are important processes, the process of pattern separation was the focus of this study.

Pattern separation is a neural computational process dependent on the hippocampus, which makes it difficult to examine its contribution to episodic memory. In order to measure this process directly and determine if events have been distinctly encoded and stored for later retrieval, one would need to physically record neural firing patterns (Yassa & Stark, 2011). Such recordings are difficult/nearly impossible to obtain in vivo in humans. However, pattern separation can be investigated indirectly by examining behavior on tasks that require this process, such as mnemonic similarity tasks. These tasks require participants to engage in mnemonic discrimination, a process that requires individuals to discriminate between highly similar stimuli from memory (Stark et al., 2013). In order to discriminate between a remembered stimulus and a new stimulus that is highly similar, individuals must determine if differences exist between their memory representation of the original stimulus and the new highly similar stimulus. This requires an individual to overcome the interference from the shared elements of the representation of the original stimuli stored in memory and the new stimulus. For example, if an individual is shown a picture of a red bowling ball as the original stimulus, and is later shown a maroon bowling ball identical in all features except color at testing, successfully identifying the second maroon bowling ball as a new stimulus would reflect successful mnemonic discrimination. However, if the individual indicated that the second maroon bowling ball had been seen previously, the trial would be considered

unsuccessful and reflect a failure to mnemonically discriminate between the original and new stimuli. The degree to which an individual can discriminate between old stimuli and highly similar stimuli across trials provides an index of pattern separation ability. In short, successful mnemonic discrimination is the behavioral manifestation of successful pattern separation.

#### *Age impacts mnemonic discrimination*

Recent work examining the development of pattern separation ability, as measured by mnemonic discrimination, indicates that this ability improves during childhood (Keresztes et al., 2017; Ngo, Newcombe, & Olson, 2017). For example, in work by Ngo and colleagues (2017), 4- and 6-year-old children and adults were required to distinguish between previously viewed everyday items, items highly similar to the initial items (lures), and new items. Adults and older children performed better than younger children. However, despite the overall similar performance between adults and 6-year-olds, only adults reliably identified lure stimuli as “new,” indicating better mnemonic discrimination ability. Additionally, this group assessed the possibility that improvements in overall memory accounted for increases in mnemonic discrimination ability. While both memory for the original stimuli (i.e., item memory) and lure discrimination increased with age, increases in item memory did not fully account for age-related differences in mnemonic discrimination. This suggests pattern separation abilities develop across childhood.

The proposal that pattern separation develops across childhood is consistent with neuroanatomical data suggesting that the neural substrates supporting this ability (i.e., hippocampus) are also developing during this period. Specifically, pattern

separation is made possible in humans via two hippocampal subfields, the dentate gyrus (DG) and cornus ammonis 3 (CA3; Bakker et al., 2008; Lavenex & Banta Lavenex, 2013). Although literature within computational, animal, and adult research has characterized DG and CA3 as being important to pattern separation, little research has explored the process in children (see Appendix A). Recent structural MRI research in children shows CA3 and DG subfields mature between age 8 and 13 years (Krogsrud et al., 2014; Lee, Ekstrom, & Ghetti, 2014; Lavenex & Banta Lavenex, 2013; Tamnes et al., 2014). This suggests pattern separation, and subsequently, mnemonic discrimination, is likely not fully mature until after age 13.

#### *Experience impacts mnemonic discrimination*

Prior research also shows that experience impacts pattern separation as measured by mnemonic discrimination (Chang, Murray, & Yassa, 2015). For example, when Caucasian adults are tasked with mnemonically discriminating between stimuli they have ample experience with (e.g., faces of their own race) and stimuli with which they have less experience (e.g., faces of a different race), adults perform better when discriminating experienced stimuli. These findings suggest a role of experience in pattern separation, where details for experienced stimuli are more sharply represented and individuals can effectively generalize or discriminate within the class of experienced stimuli. Comparatively, for adults to successfully discriminate between stimuli with which they have less experience stimuli must be less similar since details are not as sharply represented and individuals are not able to generalize or discriminate as efficiently. This is consistent with work in adults that shows increased experience with a less experienced stimuli class (e.g., faces of another race), either through

naturally occurring experiences or in-lab training, improves the efficiency with which these stimuli are recognized (Bukach, Cottle, Ubiwa, & Miller, 2012; McGugin, Tanaka, Lebrecht, Tarr, & Gauthier 2011; Tanaka, Heptonstall, & Hagen, 2013; Wan, Crookes, Reynolds, Irons, & McKone, 2015). While Chang and colleagues (2015) did not control for participants' experience with individuals of the other race, they reported all subjects' interactions and experiences were more prevalent within their own race (i.e., Caucasian). This research argues that the ability to discriminate between highly similar stimuli differs as a function of experience with the stimuli (e.g. faces of one's own race versus another race), which suggests that in adults with mature pattern separation ability experience plays a role.

#### *Clarifying the roles of age and experience in mnemonic discrimination*

As indicated in the above research, age and experience have been shown to impact pattern separation ability, as measured by mnemonic discrimination. However, age and experience are difficult to distinguish during development because both contribute to memory improvement and are highly correlated (Fivush & Hudson, 1990). Previous work suggests that children, who may also have less experience with certain stimuli, are worse than adults in discriminating between highly similar stimuli (Ngo et al., 2017). However, it is an open question as to whether children with ample experience with stimuli show the same deficit when compared to adults.

The purpose of the current study was to examine the contribution of age and experience on pattern separation in three ways. First, it examined age-related differences in pattern separation via a mnemonic similarity task in Caucasian adults and 9- to 11-year-old children (Aim 1). This age group was selected because pattern

separation and its neural substrates are thought to be still developing. We hypothesized that adults would show better mnemonic discrimination than children. Second, it explored the role of experience on pattern separation via a mnemonic similarity task (Aim 2). Faces from different racial groups were selected as the task stimuli because previous research in adults shows an effect of experience in the ability to discriminate, from memory, between faces of one's own races versus another race. We hypothesized that both Caucasian adults and children would perform significantly better in discriminating between similar stimuli with which they have had ample experience compared to stimuli with which they have had less experience. Finally, we examined the interaction between age and experience on pattern separation via a mnemonic similarity task (Aim 3). We hypothesized that there would be an interaction between age and experience. Specifically, that Caucasian adults and children would comparably discriminate between similar stimuli with which they have had ample experience, as experience with the stimuli "boosts" children's performance to adult-like levels (Pezdek, Blandon-Gitlin, & Moore, 2003; Goodman et al., 2007); but, adults would discriminate between stimuli with which they have less experience better than children because neither group had extensive experience, thus age would play a role.

Addressing these questions will fill a gap in the memory literature and pave the way for future studies linking brain regions (e.g., hippocampal subfields) to pattern separation and experience in children.

## Chapter 2: Method

### Participants

A total of 32 9- to 11-year-old children recruited from the Baltimore-Washington area and 33 college-aged adults from the University of Maryland participated in the current study. Of these participants, 30 children (1 could not complete the task and 1 had a previously undisclosed diagnosis of autism) and 30 adults (3 did not meet the racial criterion for inclusion in the study) provided useable behavioral data. Of the 60 participants who provided useable behavioral data, 58 provided complete survey data (2 adults failed to complete the questionnaire). This resulted in complete data sets from 30 children ( $n_{\text{female}} = 19$ ) and 28 adults ( $n_{\text{female}} = 21$ ). Sample size was selected using previous literature examining the effect of experience on pattern separation (Chang et al., 2015). Children were recruited through the University Infant and Child Studies Consortium at the University of Maryland. Adults were recruited from the University of Maryland SONA system. To determine eligibility for the current study, all participants were screened for diagnoses for any neurological conditions, developmental delays, or disabilities. All participants in the current study were Caucasian to allow for questions regarding the impact of experience (i.e., greater amounts of experience with individuals of one's own race) to be examined. To ensure all participants could understand the instructions and complete the study effectively, participants had normal or corrected to normal vision and hearing and were fluent in English. For all child participants, parents or guardians provided informed consent. Children provided written assent to their participation. Adult undergraduate students gave informed consent prior to participation. Children

received a small gift and adults received course credit as compensation for their participation in the study.

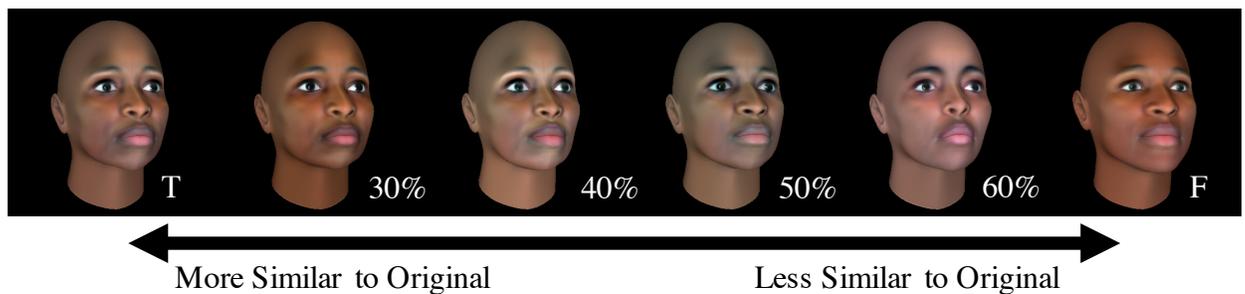
### Materials

Mnemonic Similarity Task (MST).

*Stimuli.* A total of 160 images of faces created using commercial software (FaceGen Modeler 3.1) and sampled from a prior study examining pattern separation and experience (Chang et al., 2015) were included in the current study. Fifty-two of these faces served as the original “target” stimuli and were morphed to create “lure” images that were highly similar, but not identical, to each of the original faces. Specifically, within FaceGen, a morphing function modified characteristics of each selected face by the specified percentage and output nine morphed faces from which one morphed stimulus was selected. For each of the initial 52 faces, 30%, 40%, 50%, and 60% morphs were created by Chang and colleagues (2015), with the 30% morph being the most similar to the original face and the 60% more being the least similar of the generated faces (see Figure 1 for example). While effects of interference level are not discussed in the current report, parametric stimuli manipulation is a recommended best practice in optimizing the validity of a MST by increasing the sensitivity to detect differences between original stimuli and highly similar stimuli (for reviews, see; Hunsaker and Kesner, 2013; Liu, Gould, Coulson, Ward, & Howard, 2015). Finally, the original 52 faces were morphed to 100% dissimilarity, resulting in 52 novel “foil” stimuli.

*Task.* Of the 160 faces, 52 faces divided evenly across gender and Black and Caucasian races were initially shown during encoding as the original faces. For the

current study, one morph for each original face was included at retrieval, with the exception of four faces. For these four faces, two morphs were included at different percentages to balance the number of lures at each morph level included for each stimuli race. This resulted in 56 lure faces shown at retrieval. In total, 52 original faces were shown at retrieval, 56 lures spread evenly across the morph percentages were shown at retrieval, and 52 novel foils were shown at retrieval. The task procedure will be described in detail below.



*Figure 1.* Example stimuli. Target stimuli (T) were identical to stimuli shown at encoding. Related lures varied from stimuli studied at encoding by 30%, 40%, 50%, or 60%. Novel foil stimuli (F) varied from studied stimuli by 100%.

Questionnaires. To allow for the possibility that some participants had varying levels of exposure and experience with individuals of the other stimuli race (i.e., Black), participants completed a questionnaire assessing both of these constructs. The questionnaire was based on Walker and Hewstone's (2006) Individuating Experience and Social Contact (IESC) questionnaire and included 10 items, 5 related to social contact and 5 related to individuating experience (see Appendix B). For items grouped into the social contact category, participants gave answers indicating their

relative exposure to individuals of the other stimuli race. All social contact items were scored on a 5-point response scale, with 1 indicating low contact and 5 indicating high contact (e.g., “I often spend time with Black people; 1: Strongly Disagree; 5: Strongly Agree). A social contact (SC) score was derived by taking the average of the 5 subgroup items.

For items grouped into the individuating experience category, participants were asked how often they engage in mutual helping, comforting, and inclusion activities with individuals of the other stimuli race. All individuating experience items were scored on a 5-point response scale, with 1 indicating low engagement and 5 indicating high engagement (e.g., “I have looked after or helped a Black friend when someone was causing them trouble or being mean to them”; 1: Never; 5: Very Often.) An individuating experience (IE) score was derived by taking the average of the 5 subgroup items.

An additional demographics questionnaire was completed by parents or guardians who provided written consent for child participants or by adult participants themselves. However, these data will not be discussed in this report.

### Procedure

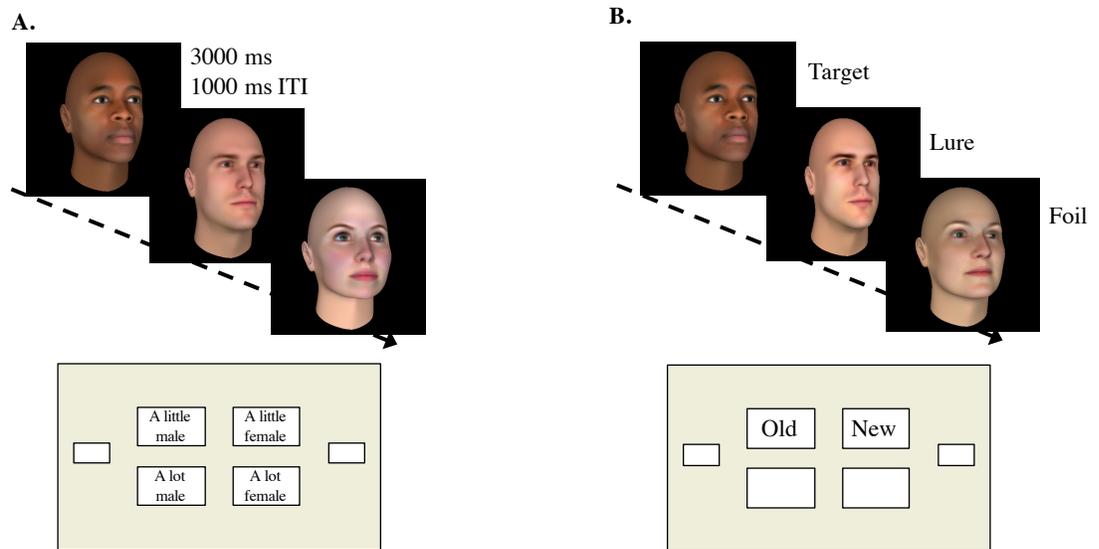
The procedures for child and adult participants were identical. Based on previous work examining both pattern separation and experience (Chang et al., 2015), participants first completed an incidental encoding task. During encoding, participants viewed 52 neutral computer-generated faces. Stimuli were presented on a black background for 3000 ms with a fixation-cross displayed for an inter-stimulus interval

of 1000 ms. Faces were presented in random order as determined by the presentation software, E-prime 2.0 (Psychology Software Tools, Pittsburgh, PA). To ensure deep encoding, participants made gender discrimination judgments (“What gender does this face look like?”) for each initial non-morphed face using a 4-choice button box to indicate if a face looked: “A lot like a male,” “A little bit like a male,” “A lot like a female,” or “A little bit like a female” (see Figure 2A for schematic representation). For both child and adult participants, the experimenter explained that the faces would differ in whether they looked more or less like a male or female. Participants were encouraged to spread their ratings across all possible options. Since the gender discrimination ratings were only used to ensure that participants attended to the stimuli during the encoding task, these judgments will not be addressed in the present report.

Following encoding, participants immediately completed a memory retrieval test. Participants made old/new judgments on 160 faces using a 2-choice button box with choices corresponding to “old” and “new.” The test included the 52 faces from encoding (target), 52 novel (foil) faces, and 56 morph faces similar but not identical to the original faces (lure). Stimuli were presented for 3000 ms with a fixation-cross displayed between trials at an inter-stimulus interval of 1000 ms and grouped into 4 trial blocks (see Figure 2B for schematic representation). Participants were instructed that in order for a face to be considered “old” it must be the same face from the encoding portion of the task. Participants were told that the task can be difficult because, in order for a face to be considered “old,” it has to be identical, or exactly the same, as a face from the first task involving gender discrimination.

To ensure any observed effects were not the result of the presentation order, all

160 possible stimuli were divided evenly by race for each stimuli type (i.e., lures at each morph level (30-60%), targets, and foils), with the resulting stimuli counterbalanced within each block. Each block was presented in random order. Following the completion of both the encoding session and memory test for the mnemonic similarity task, participants completed the IESC questionnaire.



*Figure 2.* Schematic representation of the MST. All faces were presented for 3000 ms with an inter-stimulus interval of 1000 ms. (A) The incidental encoding task. Participants made gender discrimination judgments on 52 faces (i.e., “What gender does this face look like?”) using a four-choice button box. (B) The memory test. Participants made mnemonic “old”/“new” judgements on 160 faces (52 targets, 56 lures, and 52 foils) using a two-choice button box.

### Statistical Analysis

IBM SPSS Statistics 20 (IBM Corp., Chicago, IL) was used for all statistical analyses. Results were additionally validated in R (R Core Team, 2017). Participants’ memory test data was excluded if they missed more than 10 trials (~20%) during the

incidental encoding task due to responses below 300 ms or above 3000 ms (Weidemann & Kahana, 2016; Wimmer, Braun, Daw, & Shohamy, 2014). Participants' trials from the memory test were excluded if response times were less than 300 ms or exceeded 3000 ms (Weidemann & Kahana, 2016). An alpha level of .05 was used for all statistical tests.

The goal of these analyses was to identify effects of age and experience on pattern separation in order to answer questions not yet considered in the field. Using only correct rejections of lures (i.e., the ability to identify highly similar stimuli as “new”) in the MST as a behavioral index of pattern separation does not account for the possible inclusion of correct rejections that result from insufficient/inattentive encoding of the original stimuli (i.e., misses, “new” target; Leal & Yassa, 2014). Consequently, mnemonic discrimination performance was assessed using the discrimination index  $d'$  (prime  $d'$ ) to identify how well participants differentiated between original (target) and highly similar (lure) stimuli (Stark, Stevenson, Wu, Rutledge, & Stark, 2015). While this measure of lure discrimination differs from that used in previous work examining pattern separation and experience (Chang et al., 2015), work examining the properties and assumptions of dependent measures commonly used in binary choice discrimination tasks identify  $d'$  as the ideal measure of lure discrimination (Rotello, Heit, & Dubé, 2015). We calculated  $d'(T, L)$  by subtracting the standardized hit rate (i.e., proportion of trials where the participant correctly identified target faces as “old”) from the standardized false alarm rate (i.e., proportion of trials where the participant incorrectly identified lure faces as “old”):  $d'(T, L) = z(\text{Target Hits}) - z(\text{Lure False Alarms})$ . The resulting number gave an

estimate of participants' ability to discriminate between old and highly similar items, with larger  $d'$  indicating better ability to differentiate between targets and lure. This measure corrects for response bias, or the possibility that participants are identifying all stimuli as "old" versus correctly rejecting lure stimuli and correctly identifying target stimuli.

To test for main effects of age and experience on mnemonic discrimination performance (Aims 1 and 2) and the interaction between age and experience on mnemonic discrimination performance (Aim 3), we performed a two-way repeated measures analysis of covariance (ANCOVA) with stimuli race (Caucasian, Black) as the within-subject factor, and age group of the participant (Adult, Child) as the between subject factor. To control for the possibility that participants had inconsistent exposure and experiences with individuals of the other race individuating experience and social contact sub scores from Walker and Hewstone's (2006) IESC Questionnaire were included as covariates.

To draw connections to previous literature assessing mnemonic discrimination performance between adults and children (e.g., Ngo et al., 2017), we assessed overall item memory using the discrimination index  $d'$  to identify how well participants differentiated between original (target) and novel (foil) stimuli, irrespective of their ability to discriminate between original stimuli (target) and stimuli highly similar to the originals (lure). Similar to our measure of lure discrimination, we calculated  $d'(T, F)$  by subtracting the standardized hit rate (i.e., proportion of trials where the participant correctly identified target faces as "old") from the standardized false alarm rate (i.e., proportion of trials where the participant incorrectly identified foil faces as "old"):  $d'(T,$

$F) = z(\text{Target Hits}) - z(\text{Foil False Alarms})$ . The resulting number gave an estimate of participants' ability to differentiate between old and novel items, with larger  $d'$  indicating better ability to differentiate between targets and foils. Potential differences between adult and child participants' hit rates and false alarm rates for target and foil items (i.e., measures utilized to calculate  $d'$ ) were also examined by conducting independent samples t-tests. This allowed us to explore what was driving differences in item memory ( $d'(T, F)$ ) between Age Groups if a difference was present (Lloyd, Doydum, & Newcombe, 2009).

## Chapter 3: Results

### Preliminary Analyses

All participants' mnemonic similarity task data was included ( $N = 58$ ). Participants provided responses for an average of 50.47 trials ( $SD = 1.89$ ) out of a possible 52 trials in the incidental encoding task. After excluding mnemonic similarity task trials with response times less than 300 ms or greater than 3000 ms, participants provided an average of 158.16 trials ( $SD = 2.54$ ) out of 160 possible total trials. Within each stimulus category participants provided, on average, 55.43 lure trials ( $SD = 0.99$ ), 51.21 foil trials ( $SD = 1.31$ ), and 51.52 target trials ( $SD = 0.73$ ). Overall, we excluded a total of 1.15% of total possible trials in the mnemonic similarity task.

### Main Analyses

Descriptive statistics of old/new responses for each stimulus condition (target, lure, foil) are shown by stimuli race, and collapsed across stimuli race, for each age group in Table 1. Descriptive statistics for item memory, lure discrimination (i.e., the ability to discriminate between similar stimuli), and covariate measures are shown in Table 2.

Table 1. Proportion of old/new responses to each stimuli condition by participant age group and stimuli race.

Trial Type Response	Targets		Lures		Foils	
	“Old”	“New”	“Old”	“New”	“Old”	“New”
Caucasian Stimuli						
Adult Mean (SD)	0.58 (0.14)	0.42 (0.14)	0.32 (0.13)	0.68(0.13)	0.42 (0.20)	0.58 (0.17)
Child Mean (SD)	0.56 (0.14)	0.44 (0.14)	0.33 (0.16)	0.67 (0.16)	0.48 (0.15)	0.52 (0.15)
Black Stimuli						
Adult Mean (SD)	0.65 (0.16)	0.35 (0.17)	0.34 (0.12)	0.66 (0.12)	0.33 (0.13)	0.67 (0.13)
Child Mean (SD)	0.57 (0.16)	0.43 (0.16)	0.38 (0.17)	0.62 (0.17)	0.43 (0.14)	0.57 0.14)
Combined						
Adult Mean (SD)	0.61 (0.11)	0.39 (0.11)	0.32 (0.10)	0.68 (0.10)	0.63 (0.12)	0.37 (0.12)
Child Mean (SD)	0.56 (0.13)	0.44 (0.13)	0.35 (0.15)	0.65 (0.15)	0.54 (0.12)	0.46 (0.12)

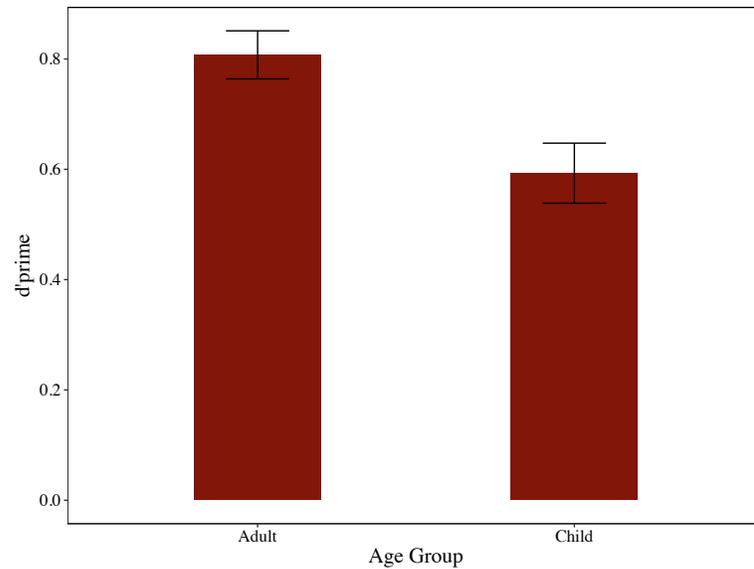
\*Note:  $N = 28$  for adult group; 30 for child group.

Table 2. Summary of mnemonic discrimination performance ( $d'$  T, L), covariate measures (IE and SC scores), and item memory performance ( $d'$  T, F) by age group and t-tests of assessing differences in each measure between age groups.

Measure	Age Group		Group Difference
	Adult	Child	
Overall $d'$ (T, L)	0.78 (0.21)	0.56 (0.34)	$t(56) = 2.92, p = .005$
$d'$ (T, L) Caucasian Stimuli	0.74 (0.30)	0.62 (0.38)	$t(56) = 1.33, p = .19$
$d'$ (T, L) Black Stimuli	0.87 (0.34)	0.56 (0.47)	$t(56) = 2.86, p = .005$
IE Score	3.23 (0.84)	3.17 (0.75)	$t(56) = 0.30, p = .76$
SC Score	2.68 (0.88)	2.77 (0.81)	$t(56) = -0.43, p = .67$
$d'$ (T, F)	0.66 (0.38)	0.29 (0.28)	$t(56) = 4.29, p < .001$

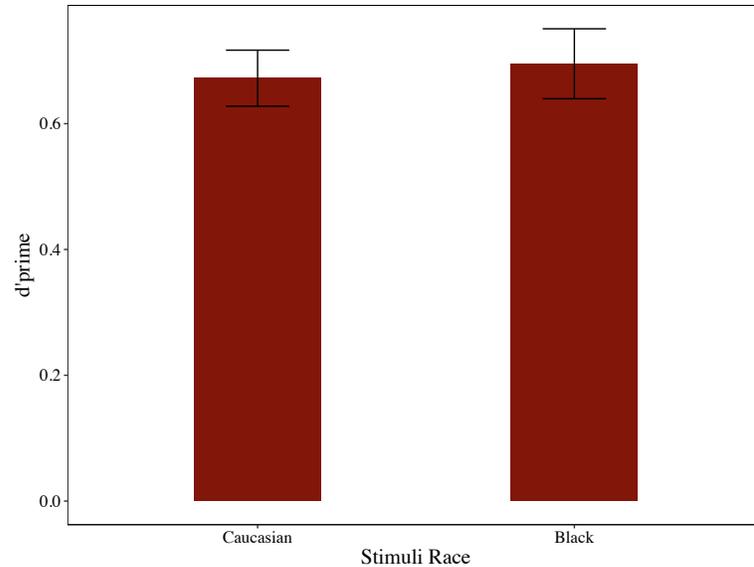
\*Note:  $N = 28$  for adult group; 30 for child group; 58 group comparisons.

Results indicated a significant difference in lure discrimination between adults and children across stimuli,  $F(1, 56) = 7.13, p = .009, \eta_p^2 = .076$  (see Figure 3). Adults showed better mnemonic discrimination compared to children. This suggests age-related differences in mnemonic discrimination.



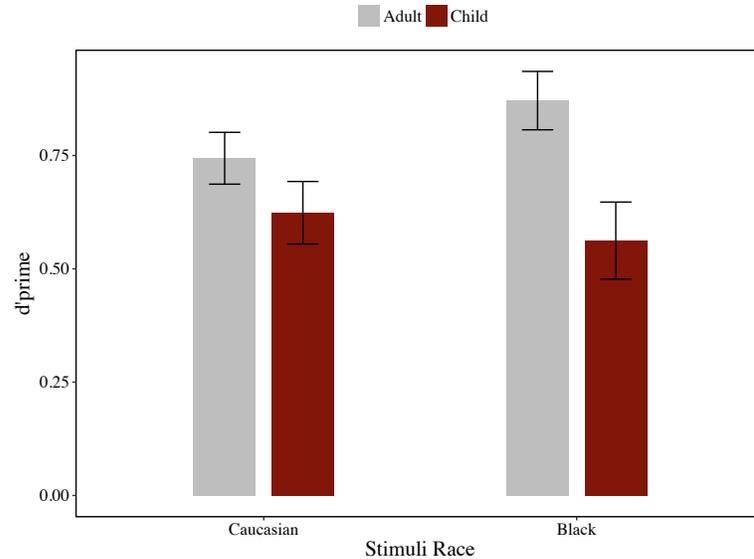
*Figure 3.* Mnemonic discrimination performance by Age Group. Adults showed overall better lure discrimination performance across all stimuli relative to children in mnemonic discrimination ability. A bias-corrected measure of lure discrimination,  $d'$ , was used,  $d'(T, L) = z(p(\text{“old”} | \text{target})) - z(p(\text{“old”} | \text{lure}))$ .

Results indicated no significant difference in lure discrimination between Black and Caucasian stimuli across participants,  $F(1, 56) = 0.15, p = .70, \eta_p^2 = .001$ , (Figure 4).



*Figure 4.* Mnemonic discrimination performance by Stimuli Race. No difference was observed across adults and children in lure discrimination performance between Caucasian and Black stimuli. A bias-corrected measure of lure discrimination,  $d'$ , was used,  $d'(T, L) = z(p(\text{“old”} | \text{target})) - z(p(\text{“old”} | \text{lure}))$ .

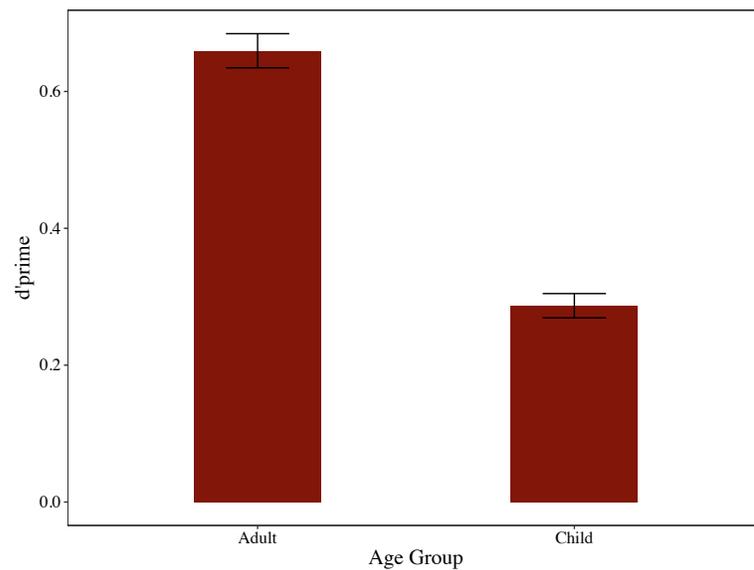
Finally, the interaction between Age Group and Stimuli Race was marginally significant,  $F(1, 56) = 2.51, p = .11, \eta_p^2 = .015$ . Adults and children discriminated between stimuli of their own race (Caucasian) similarly, whereas adults' lure discrimination of stimuli of the other race (Black) was greater than children's (Figure 5). This suggests age- and- experience interact to impact mnemonic discrimination.



*Figure 5.* Mnemonic discrimination performance by Stimuli Race and Age Group. Adults and children did not differ in lure discrimination performance for Caucasian stimuli (left). Adults showed better lure discrimination performance for Black stimuli relative to children (right). A bias-corrected measure of lure discrimination,  $d'$ , was used,  $d'(T, L) = z(p(\text{“old”} | \text{target})) - z(p(\text{“old”} | \text{lure}))$ .

To explore whether there were age-related differences in overall memory, we assessed item memory performance (i.e.,  $d'$ prime for targets and foils). Overall, adults ( $M = 0.67$ ,  $SD = 0.38$ ) showed better differentiation between target and foil stimuli than did children ( $M = 0.29$ ,  $SD = 0.28$ ),  $t(58) = 4.28$ ,  $p < .001$  (see Table 1, Figure 6). Age-related differences in item memory were mostly driven by children’s ( $M = 0.46$ ,  $SD = 0.12$ ) higher likelihood of incorrectly identifying unrelated foil stimuli as “old,” compared to adults ( $M = 0.37$ ,  $SD = 0.12$ ),  $t(56) = -2.58$ ,  $p = .012$ ). Adults ( $M = 0.61$ ,  $SD = 0.11$ ) and children ( $M = 0.56$ ,  $SD = 0.13$ ) did not reliably differ on overall hit rates,  $t(56) = 1.60$ ,  $p = .11$ . Adults ( $M = 0.46$ ,  $SD = 0.53$ )

differentiated between target and foils better than children ( $M = 0.21$ ,  $SD = 0.39$ ) for Caucasian stimuli,  $t(56) = 2.17$ ,  $p = .038$ ). Adults ( $M = 0.91$ ,  $SD = 0.43$ ) also differentiated between target and foils better than children ( $M = 0.38$ ,  $SD = 0.38$ ) for Black stimuli, ( $t(56) = 4.95$ ,  $p < .001$ ). Differences between age-groups in overall item memory reinforces our use of a bias-corrected measure of lure discrimination.



*Figure 6.* Item memory performance. Adults showed overall better item memory relative to children in item memory performance. Item memory was calculated using the discrimination index  $d'$  by subtracting the standardized false alarm rate from the standardized hit rate; i.e.,  $z(p(\text{“old”} | \text{target})) - z(p(\text{“old”} | \text{foil}))$ .

### Exploratory Analyses

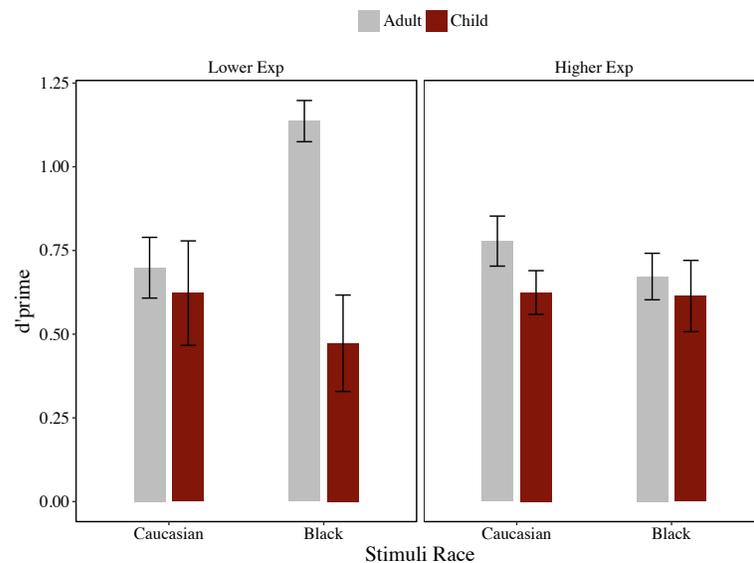
Given the high amounts of experience reported by participants on the IESC questionnaire and findings that overall Stimuli Race did not impact performance, exploratory analyses were conducted to further explore the possible role of

experience in a more fine-grained manner. High and low experience groups were created for adults and children using a median split on participants' IE score from Walker and Hewstone's (2006) IESC Questionnaire. We performed a three-way repeated measures analysis of covariance (ANCOVA) with stimuli race (Caucasian, Black) as a within-subject factor, and age group of the participant (Adult, Child) and level of experience (High, Low) as between subject factors. Amount of contact with individuals of the other race (SC score) was included as a covariate.

Similar to the above reported results, there was a significant difference in lure discrimination between adults and children across stimuli and experience groups,  $F(1, 54) = 7.09, p = .01, \eta_p^2 = .08$  (see Figure 3 for similar results). There was no significant difference in lure discrimination between Black and Caucasian stimuli across participants,  $F(1, 54) = 0.18, p = .67, \eta_p^2 = .005$ , (see Figure 4 for similar results); but there was a marginally significant interaction between Age Group and Stimuli Race,  $F(1, 54) = 2.58, p = .11, \eta_p^2 = .015$  (see Figure 5 for similar results).

The interaction between Age Group, Experience Group, and Stimuli Race was significant,  $F(1, 54) = 8.72, p = .004, \eta_p^2 = .05$ . Adults and children with high-levels of experience with other-race individuals discriminated between stimuli of their own race (Caucasian), and stimuli of the other race (Black) similarly (and these levels were similar across the age groups). In contrast, adults and children with low levels of experience with other-race individuals discriminated between stimuli of their own race (Caucasian) similarly, but, adults' discrimination for Black stimuli was greater than children's. Specifically, adults with low-experience levels discriminated between Black stimuli better than Caucasian stimuli, whereas children with low-experience

levels showed nominally worse performance for Black stimuli (Figure 7). These results suggest that interactions between age and experience are not consistent across levels of experience. Instead, different patterns of interaction were detected within high- and low-experience groups.



*Figure 7.* Mnemonic discrimination performance by Stimuli Race, Age Group, and Experience Group. High- and low-experience adults’ performance did not differ for Caucasian stimuli; low-experience adults outperformed high-experience adults for Black stimuli (left). High- and low-experience children’s performance did not differ for Caucasian stimuli or Black stimuli; high-experience children’s performance for Black stimuli trended toward better performance compared to low-experience children (right). A bias-corrected measure of lure discrimination,  $d'$ , was used,  $d'(T, L) = z(p(\text{“old”} | \text{target})) - z(p(\text{“old”} | \text{lure}))$ .

## Chapter 4: Discussion

The goal of the present study was to examine the impact of both age and experience on pattern separation. Results suggested age and experience interacted to impact performance. Consistent with our first hypothesis, age-related differences were observed in pattern separation ability. Adults showed better mnemonic discrimination across all stimuli compared to children. This is consistent with previous work showing age-related improvements in younger children compared to adults (i.e., Ngo et al., 2017), as well as with studies showing continual development of the neural substrates supporting this ability until around 13 years (Lee et al., 2014). Although adults also showed better item memory than children, we do not think this more general memory difference can account for the observed effects since our lure discrimination index accounted for degraded encoding of original stimuli and response bias.

We argue these findings may reflect age-related differences in pattern separation that are related to neural maturation (i.e., in the hippocampus). However, it is also possible that other developmental changes occurring during this period of childhood contributed to task performance. Work by Grill-Spector and colleagues (2006) has shown that, at least until the age of 11, cortical regions involved in the processes of faces (i.e., fusiform face area) continue to mature. Consequently, if the ability to process a stimuli class is still developing in children, it might also contribute to observed differences in lure discrimination. Future work would benefit in utilizing

a class of stimuli less limited by the protracted and concurrent development of other neural mechanisms.

Our second hypothesis was that experience would lead to better mnemonic discrimination for high experience stimuli (i.e., faces of one's own race) compared to low experience stimuli (i.e., faces of another race), based on the assumption that individuals would be spending the majority of their time with individuals of their own race. However, this prediction of a main effect of experience was not supported. Results instead showed no evidence of a difference between "high" versus "low" experience stimuli. This could be a result of participants' higher amounts of experience with individuals of the other race compared to the overall population of Caucasian individuals (as measured participants' IE scores). Both the University of Maryland and the Greater Baltimore-Washington area are diverse in their populations, and, it is likely our sample had more experience than anticipated with the low experience stimuli (i.e., faces of the other race).

The final hypothesis suggested age and experience would interact and was marginally supported. However, the pattern of the effect differed slightly from what was predicted. First, adults and children did not differ on "high" experience (i.e., Caucasian) stimuli. This was expected as we predicted no difference between children and adults when experience was high. In contrast, adults and children did differ on "low" experience stimuli. This was also expected, as we predicted adults, who have lived longer and have mature neural substrates supporting pattern separation, would show an age-related benefit in discriminating between other-race faces. The

surprising finding was that adults showed better mnemonic discrimination of other-race faces compared to same-race faces.

To explore possible explanations for this unexpected aspect of our finding, and that there was no difference in experience across participants, we conducted an exploratory analysis to compare performance between individuals with high- and low-experience with individuals of the other race. Our exploratory analysis suggested that experience may positively impact pattern separation ability (as hypothesized), as both adults and children with high-levels of experience showed similar performance for Caucasian and Black stimuli. However, the reverse (i.e., low experience is detrimental to performance) is not always the case, as adults (but not children) with low-experience with other-race individuals showed better performance on Black compared to White stimuli. This finding is surprising. Given the present data, we cannot conclude why this is the case. It may be that, contrary to findings, low-experience leads to even better pattern separation in adults, but not children. However, it may also be the case that adults with low-experience utilized different processing strategies (consciously or unconsciously) when viewing Black stimuli. Research has suggested that the other-race effect (i.e., better recognition for faces of one's own race) may occur because individuals process other-race faces using distinct features as opposed to holistically (Zhao, Hayward, & Bülhoff, 2014). This may have provided these participants an advantage in this specific task. Finally, children with low-experience may not have utilized such a different strategy for Black stimuli.

Although our exploratory analyses suggest an interaction in the contribution of both age and experience on pattern separation, the results raise many questions for

future investigations. One question is regarding the individuals in our study and their actual experience in the real world. Future studies could assess individual differences in experience directly (as opposed to only using as covariate) in a larger sample. Participants could be screened using Walker and Hewstone's IESC questionnaire before testing in order to create a priori high versus low level experience groups. Should this prove difficult given the diversity of the Greater Baltimore-Washington Area, subjects could be recruited from less diverse parts of the country. Another question is regarding the stimuli used in the present study. Although we implemented the recommended best practice of using parametrically manipulated stimuli (Liu et al., 2015), our stimuli (used previously to examine the impact of experience on pattern separation, Chang et al., 2015) were never normed for difficulty. It is possible that within our stimuli set, items parametrically manipulated to the same level of interference (i.e., the level of morph dissimilarity from the target), differed from one another in the level of mnemonic difference. In other words, perhaps parametric manipulations of stimuli overlap did not directly map onto the difficulty of resolving interference (i.e., stimuli were parametrically manipulated, difficulty was not). Whether morphometric differences in stimuli correspond to mnemonic differences remains unclear in the larger literature examining pattern separation through mnemonic discrimination (Hunsaker & Kesner, 2013; Wan et al., 2015; Liu et al., 2015; Leal & Yassa, 2014). Future work should strive to use both carefully manipulated and normed stimuli to provide clarity on the roles of age and experience on pattern separation.

Finally, a possible avenue of future research that would assist in our efforts to tease apart differential contributions of age and experience on pattern separation could utilize novel stimuli (versus faces) and have both a better operationalized definition of experience and more control over the amount of experience between participants. This might be accomplished by training both adults and children on stimuli of a novel class (then test on different members of that class). Research in adults suggest training participants' for as few as 10 hours (2 hours for 5 consecutive days) can benefit discrimination performance (McGugin, Tanaka, Lebrecht, Tarr, & Gauthier 2011; Tanaka, Heptonstall, & Hagen, 2013). Ideally, both adults and children would provide a baseline measure before a week of "experience," followed by a post-training mnemonic similarity task. Controlling the extent to which adults and children experience a novel class of items will better clarify the relations between age, experience, and pattern separation.

Despite the limitations noted, this study was the first, to our knowledge, to address questions of how age and experience impact pattern separation in the same study. Findings suggested an interaction between age and experience on pattern separation while also raising interesting questions about the nature of this interaction. This creates exciting opportunities for future studies that can further clarify differences in pattern separation across development.

## Appendix A.

Literature examining the relation of hippocampal subfields to pattern separation

### Computational models

In beginning to address the potential role of pattern separation in the improvement of episodic memory abilities, one can consider the literature characterizing the process and evidence for the role of hippocampal subfields. Computational models of pattern separation stress the role of the hippocampus and, more specifically, dentate gyrus (DG) and cornus ammonis 3 (CA3) subfields of the hippocampus. Theory predicts the perforant pathway, the neural connection from entorhinal cortex (EC) to all hippocampal subfields (Witter, 2007), acts as a competitive neuronal network where dentate granule cells (DGC) reduce redundant features from EC inputs to create outputs that are more easily differentiated (Marr, 1971; Rolls, 1996). Multiple mechanisms contribute to hippocampal pattern separation (O'Reilly & McClelland, 1994; Rolls, 2007, 2013). First, inputs from the environment project from regions of the neocortex to EC where patterns of activity represent inputs and connect from EC to DG via a feed-forward pathway. In the pathway from EC to DG, scattered firing activity by DGC creates a sparse orthogonalized representation of the input from the EC. (For clarification, sparse refers to a type of neural code in which an event is encoded by the strong activation of a small set of neurons.) Combined with the small number connections via mossy fibers from DGC to CA3 cells, DG produces a sparse signal and the mossy fibers project this representation to CA3. The signal from DG then transforms into sparse cell firing activity in CA3 by a threshold effect (O'Reilly & McClelland, 1994).

Consequently, sparse firing helps de-correlate different sets of CA3 cell firing, allowing distinctive memory storage in the CA3 network (Rolls, 2016).

Within this computational framework, pattern separation occurs when the output firing patterns from a set of neurons in CA3 are less similar to each other than the EC input firing patterns. When one input representation transforms to an output representation less similar than the input the hippocampus encodes different memories of similar events (Yassa & Stark, 2011). These models highlight DG and CA3 working together as necessary to store memories but not to recall them, highlighting the role of pattern separation during the encoding of memories (Deng, Aimone, & Gage, 2010).

Computational models of hippocampal pattern separation are not specific to one type of input and are equally relevant to both object and spatial pattern separation. However, this model of pattern separation function is specific to mammalian species (i.e. humans, rodents) and occurs differently in other species, such as birds. As previously mentioned, the hippocampus is considered necessary for episodic memory abilities in humans. However, in birds, the hippocampal structure lacks subregions with features corresponding to human DG, such as strong connections to EC and the avian neocortex, dorsal pallial derivative, and receives more limited input from the environment (Treves, Tashiro, Witter, & Moser, 2008). With DG's proposed necessity in mammalian pattern separation, research has proposed birds must engage other regions in the brain to facilitate the function and distinguish between different events (Rattenborg & Martinez-Gonzalez, 2011).

### Experimental

*Animal Models.* Neurophysiological research in rodents supports the computational models of pattern separation and suggests both DG and CA3 play roles in the pattern separation process. Jung and McNaughton (1993) utilized single-cell recordings and placed rats in a maze where they engaged in an eight-arm maze spatial memory task. Recordings revealed firing in DG specific to the direction and spatial orientation of the animal within the environment, and that these cells exhibited sparse and distributed firing related to CA3 cells. Work utilizing multi-unit recordings in rodents found that when rats were exposed to different environments with varying levels of similarity, CA3 neurons showed orthogonal activation patterns when small changes in the environment were present (Leutgeb et al., 2004; Leutgeb et al. 2007). This supports that CA3 is active in distinguishing between highly similar environments. cornus ammonis 1 (CA1), the subfield thought to facilitate pattern completion, did not display this pattern (Leutgeb et al., 2004).

Additional work examining rodent lesioning and aging effects on pattern separation also supports the role of DG and CA3 in pattern separation. Research utilizing lesioning found that, compared to non-lesioned rats, animals with damage to the DG showed impaired pattern separation abilities. In a task requiring rats to differentiate between a trained food well location covered by an object and a second food well location covered by an identical object, researchers varied the distance between the locations by 15 to 105 cm and tested rats' ability to identify the original location. Rats with lesions to the DG were unable to distinguish above chance between the original and second object locations when the spatial difference of the second location was smaller, at either 15 or 37.5 cm, supporting DG's role in

reducing interference between inputs, or spatial pattern separation (Gilbert, Kesner, & Lee, 2001). Work examining age-related changes in rats highlighted that behavioral performance and CA3 activity in older rats did not distinguish between two similar but different environments (Wilson et al., 2005). In other words, CA3 failed to engage in pattern separation. Instead, activity in CA3 displayed a shift toward pattern completion. Overall, work from rodents suggests both DG and CA3 play roles in the pattern separation process, with most of the underlying neural computations occurring in DG.

*Adult Humans.* Research utilizing behavioral assessments, structural neuroimaging, functional neuroimaging, and diffusion tensor imaging in humans supports the role of DG and CA3 in pattern separation. Unlike animal models where the brain can be actively recorded at a neural level or lesioned in specific regions, work in humans requires different methodologies to assess pattern separation. Typically, behavioral paradigms assess pattern separation within the visual modality by manipulating perceptual similarities of objects, although some paradigms have used object spatial location differences (e.g. Reagh & Yassa, 2014). Mnemonic similarity tasks using objects of varying degrees of similarity, as opposed to varying spatial features of the environment as in the rodent literature, are useful in human research as they are amenable to the scanning environment. Behavioral pattern separation tasks typically include an incidental encoding paradigm with pictures of objects and a contiguous recognition retrieval paradigm where each trial presents a previously seen object, slightly different object, or a new object. Objects shown previously would be targets to identify as old, similar objects (lures) are meant to tap

the ability to discriminate from the original object and would be identified as new, and new objects should not interfere with previous pictures and be labeled as new (e.g. Mnemonic Similarity Test; Stark, Yassa, Lacy, & Stark, 2013). Pattern separation is measured by comparing an individual's ability to distinguish between lures and targets.

When paired with fMRI, behavioral paradigms can utilize an effect found in blood-oxygen-level-dependent contrast imaging (BOLD) signals called repetition suppression where the BOLD signal decreases when viewing a previously view object, compared to the signal activity when viewing the object for the first time (Grill-Spector, Henson, & Martin, 2006). With fMRI, BOLD activity for lures can be compared to the activity for identical objects previously seen and novel items in order to assess pattern separation (Bakker et al., 2008). Pattern separation is indicated when brain activity in DG and CA3 for a lure object that is similar but not identical to a previously seen object does not show a suppressed signal and is treated more like a new object (Lacy, Yassa, Stark, Muftuler, & Stark, 2011). BOLD signals measured at retrieval during pattern separation paradigms serve as a proxy measure of the pattern separation process. As experimenters cannot directly measure the change in neural inputs and outputs in humans, brain activity measured at retrieval implicates the input encoding that took place. Additionally, due to resolution limitations, consistently and clearly distinguishing between DG and CA3 is difficult in fMRI, and the measured BOLD signal combines DG and CA3 subfield activity (Yassa & Stark, 2011).

Using this method, early fMRI studies identified both DG and CA3 as necessary for pattern separation (Bakker et al., 2008; Lacy et al., 2011). Subsequent

research has further clarified the role of the hippocampal subfields in pattern separation with a bias towards pattern separation observed in DG/CA3 and bias towards pattern completion observed in several medial temporal lobe (MTL) regions including CA1 (Doxey & Kirwan, 2015). Specifically, during a mnemonic similarity task, the observed pattern of activity in CA1 did not differentiate between repetitions of a target item, or between target repetitions and lure objects, whereas DG/CA3 showed different levels of activity for repeated targets versus lure objects, as mentioned previously (Lacy et al., 2011).

In a study assessing pattern separation in multiple facets of the visual modality, namely object, and location, researchers manipulated either the visual similarity of the object presented or the presentation location of an object (Reagh & Yassa, 2014). Participants had to make “old” and “new” judgments to discriminate either object appearance or object location similarities—the two manipulations were mutually exclusive. When comparing performance on the task to fMRI BOLD signals, the only region significantly more active during the correct rejection of lures was DG/CA3. This finding was consistent across both paradigms, with robust activation during lure discrimination limited to DG/CA3 during both object and spatial lure rejections (Reagh & Yassa, 2014). The activation during these paradigms is interesting as it shows DG/CA3 are active both in tasks requiring discrimination of similar stimuli and the discrimination of spatial locations of stimuli. When considering object and spatial manipulations separately, DG/CA3 engaged more during object lure versus spatial lure rejections. These findings are important as they mirror assessments of spatial pattern separation found in the rodent literature, and

provide further evidence for the involvement of DG/CA3 in both object and spatial pattern separation in adult humans.

Structural studies of the hippocampus also support DG and CA3 relations to pattern separation. With the proposed reliance on specific subfields of the hippocampus to facilitate pattern separation, one can consider the implications of damage occurring to this region of the brain. Fittingly, work examining behavioral pattern separation in individuals with brain damage limited to the hippocampus found that, compared to a neurotypical matched sample, patients with damage to the hippocampus showed impaired performance on a mnemonic similarity task meant to tax pattern separation (Duff et al., 2012; Kirwan et al., 2012). Additionally, work examining structural and functional correlates of behavioral pattern separation in the hippocampus found both age and volume of CA3 and DG predicted memory performance, with the volume of left DG/CA3 contributing to the successful discrimination of similar mnemonic representations more than other hippocampal subfields (Doxey & Kirwan, 2015).

Examining the effects of aging can also inform the role of DG and CA3 in pattern separation by comparing mnemonic discrimination ability and hippocampal subfield activity between young and non-demented older adults. This comparison is informative as it is well accepted that memory function declines with age, including the ability to encode new episodic memories ( Craik & Simon, 1980). Behavioral research investigating the effect of aging on pattern separation by comparing young and old adults found a shift in the tendency to engage in pattern completion in older adults, and age-related decline in pattern separation (Stark, Stevenson, Wu, Rutledge,

& Stark, 2015; Ally, Hussey, Ko, & Molitor, 2013; Stark et al., 2013; Yassa, Mattfeld, Stark, & Stark, 2011). This is similar to findings of a drift toward spatial pattern completion observed in aged rats (Wilson et al., 2005). Related to the behavioral impairment in pattern separation abilities for older adults, paired fMRI research found increased activity levels in DG/CA3 during a pattern separation inducing task, with older adults requiring more dissimilar inputs to be able to successfully encode inputs distinctly (Yassa et al., 2011). Additionally, high-resolution diffusion tensor imaging (hrDTI) has been used to assess the age-related decline in pattern separation ability. This technique allows for non-invasive investigation of white matter tracts in the human brain where the rate of molecular water diffusion identifies white matter microstructure integrity and position (Beaulieu, 2002; Le Bihan, 2003). Use of hrDTI to assess the connection of the MTL lobe (where the DG resides and receives input from EC) revealed an age-related decline in the perforant pathway integrity, and other paths in the MTL. After controlling for brain aging, better performance on a behavioral pattern separation task was associated with increased perforant path integrity thought to have higher connectivity with DG and other hippocampal subfields (Bennett & Stark, 2016). Overall, MRI studies in adults suggest specific subfields of the hippocampus, namely DG and CA3, work together to facilitate pattern separation.

*Children.* While, to date, behavioral assessments of pattern separation in childhood are very rare, it is important to consider pattern separation improvement, and the maturation of hippocampal subfields, as a possible mechanism in the development of episodic memory abilities. The limited work looking at spatial pattern separation

abilities in children has shown rapid improvement between the ages of 2 and 5 years of age (Ribordy, Jabès, Banta Lavenex, & Lavenex, 2013). In the existing study, researchers capitalized on allocentric spatial memory, or the memory for relations between locations in an environment thought to represent the “where” component of episodic memory (Ribordy et al., 2013). Basic allocentric spatial memory relies on CA3 to CA1 connections while the ability to discriminate between very close spatial locations relies on DG connections to CA3 (Gilbert et al., 2001). Because of the protracted development of CA3 and DG, the ability to distinguish between similar allocentric spatial memories is thought to run parallel with episodic memory abilities (Lavenex & Banta Lavenex, 2013). Children aged 18 months to 5 years were tested on two versions of a spatial memory test. In one version, children had to rely on local cues to locate a hidden reward, with a red cup hiding a reward, and intended to measure children’s ability to utilize a cue. The other condition required children to rely on relation cues to find the reward as all cups were white and an allocentric relational representation of the space was required to locate a reward. Children aged 24 months or younger successfully located rewards in the allocentric spatial condition only 30% of the time, whereas older children showed rapid improvements in locating the reward beyond 25 months of age, reaching 84% correct location trials. The improvement in allocentric spatial memory was related to increased spatial pattern separation ability resulting from DG and CA3 maturation (Lavenex & Banta Lavenex, 2013). These findings suggest performance improvement on the spatial task in children relates to increasing hippocampal maturation, specifically in DG and CA3, related to pattern separation function. Overall, pattern separation likely improves

during this period of development in the hippocampus and contributes to improvement in episodic memory abilities.

## Appendix B.

Individuating Experience and Social Contact (IESC) Adapted from Walker &

Hewstone (2006)

Social contact items:

1) *How many Black people do you know very well?*

1: Up to 2

2: Up to 5

3: Up to 8

4: Up to 12

5: More than 12

2) *I often spend time with Black people:*

1. Strongly Disagree

2. Somewhat Disagree

3. Don't Know

4. Somewhat Agree

5. Strongly Agree

3) *I spend a lot of my free time doing things with Black people.*

1. Strongly Disagree

2. Somewhat Disagree

3. Don't Know

4. Somewhat Agree

5. Strongly Agree

4) *I often go round to the houses of Black people*

1. Strongly Disagree
2. Somewhat Disagree
3. Don't Know
4. Somewhat Agree
5. Strongly Agree

5) *Black people often come around to my house*

1. Strongly Disagree
2. Somewhat Disagree
3. Don't Know
4. Somewhat Agree
5. Strongly Agree

Individuating experience items:

1) *I have looked after or helped a Black friend when someone was causing them trouble or being mean to them.*

1. Never
2. Hardly ever
3. Sometimes
4. Quiet Often
5. Very Often

2) *A Black person has looked after me or helped me when someone was causing me trouble or being mean to me*

1. Never
2. Hardly ever

3. Sometimes

4. Quiet Often

5. Very Often

3) *I have comforted a Black friend when they have been feeling sad*

1. Never

2. Hardly ever

3. Sometimes

4. Quiet Often

5. Very Often

4) *A Black person has comforted me when I have been feeling sad*

1. Never

2. Hardly ever

3. Sometimes

4. Quiet Often

5. Very Often

5) *I have asked a Black person to be on my team or in my group during sports or activities*

1. Never

2. Hardly ever

3. Sometimes

4. Quiet Often

5. Very Often

## References

- Ally, B. A., Hussey, E. P., Ko, P. C., & Molitor, R. J. (2013). Pattern separation and pattern completion in Alzheimer's disease: evidence of rapid forgetting in amnesic mild cognitive impairment. *Hippocampus*, *23*(12), 1246-1258.  
doi:10.1002/hipo.22162
- Angeli, A., Davidoff, J., & Valentine, T. (2008). Face familiarity, distinctiveness, and categorical perception. *Q J Exp Psychol*, *61*, 690–707.  
doi:10.1080/17470210701399305
- Bakker, A., Kirwan, C. B., Miller, M., & Stark, C. E. (2008). Pattern separation in the human hippocampal CA3 and dentate gyrus. *Science*, *319*(5870), 1640-1642.  
doi:10.1126/science.1152882
- Beaulieu, C. (2002). The basis of anisotropic water diffusion in the nervous system - a technical review. *NMR Biomed*, *15*(7-8), 435-455. doi:10.1002/nbm.782
- Bennett, I. J., & Stark, C. E. (2016). Mnemonic discrimination relates to perforant path integrity: An ultra-high-resolution diffusion tensor imaging study. *Neurobiol Learn Mem*, *129*, 107-112. doi:10.1016/j.nlm.2015.06.014
- Bukach, C. M., Cottle, J., Ubiwa, J., & Miller, J. (2012). Individuation experience predicts other-race effects in holistic processing for both Caucasian and Black participants. *Cognition*, *123*(2), 319-324. doi:10.1016/j.cognition.2012.02.007
- Brock Kirwan, C., Hartshorn, A., Stark, S., Goodrich-Hunsaker, N., Hopkins, R., & Stark, C. (2012). Pattern separation deficits following damage to the hippocampus. *Neuropsychologia*, *50*(10), 2408-2414.  
doi:10.1016/j.neuropsychologia.2012.06.011

- Chang, A., Murray, E., & Yassa, M. A. (2015). Mnemonic discrimination of similar face stimuli and a potential mechanism for the "other race" effect. *Behav Neurosci*, *129*(5), 666-672. doi:10.1037/bne0000090
- Craik, F.I.M., & Simon, E. (1980). Age differences in memory: The roles of attention and depth of processing. In L.W. Poon, J.L. Fozard, L.S. Cermak, D. Arenberg, & L.W. Thompson (Eds.), *New directions in memory and aging* (95-112). Hillsdale, NJ: Lawrence Erlbaum.
- Deng, W., Aimone, J. B., & Gage, F. H. (2010). New neurons and new memories: how does adult hippocampal neurogenesis affect learning and memory? *Nat Rev Neurosci*, *11*(5), 339-350. doi:10.1038/nrn2822
- Deuker, L., Doeller, C. F., Fell, J., & Axmacher, N. (2014). Human neuroimaging studies on the hippocampal CA3 region—integrating evidence for pattern separation and completion. *Front Cell Neurosci*, *8*. doi:10.3389/fncel.2014.00064.
- Doxey, C. R., & Kirwan, C. B. (2015). Structural and functional correlates of behavioral pattern separation in the hippocampus and medial temporal lobe. *Hippocampus*, *25*(4), 524-533. doi:10.1002/hipo.22389
- Duff, M. C., Warren, D. E., Gupta, R., Vidal, J. P., Tranel, D., & Cohen, N. J. (2012). Teasing apart tangrams: testing hippocampal pattern separation with a collaborative referencing paradigm. *Hippocampus*, *22*(5), 1087-1091. doi:10.1002/hipo.20967
- Fivush, R. & Hudson, J. (1990). *Knowing and remembering in young children*. Cambridge: Cambridge University Press.

- Gilbert, P., Kesner, R., & Lee, I. (2001). Dissociating hippocampal subregions: A double dissociation between dentate gyrus and CA1. *Hippocampus*, *11*(6), 626-636. doi:10.1002/hipo.1077
- Goodman, G., Sayfan, L., Lee, J., Sandhei, M., Walle-Olsen, A., & Magnussen, S. et al. (2007). The development of memory for own- and other-race faces. *J Exp Child Psychol*, *98*(4), 233-242. doi:10.1016/j.jecp.2007.08.004
- Grill-Spector, K., Henson, R., & Martin, A. (2006). Repetition and the brain: neural models of stimulus-specific effects. *Trends Cogn Sci*, *10*(1), 14-23. doi:10.1016/j.tics.2005.11.006
- Jacques, C., & Rossion, B. (2006). The speed of individual face categorization. *Psychological Science*, *17*, 485–492. doi:10.1111/j.1467-9280.2006.01733.x
- Jung, M. W. & McNaughton, B. L. (1993). Spatial selectivity of unit activity in the hippocampal granular layer. *Hippocampus*, *4*, 165–182. doi:10.1002/hipo.450030209
- Keresztes, A., Bender, A., Bodammer, N., Lindenberger, U., Shing, Y., & Werkle-Bergner, M. (2017). Hippocampal maturity promotes memory distinctiveness in childhood and adolescence. *Proc Natl Acad Sci USA*, *114*(34), 9212-9217. doi:0.1073/pnas.1710654114
- Krogsrud, S. K., Tamnes, C. K., Fjell, A. M., Amlie, I., Grydeland, H., Sultvedt, U., et al.. (2014). Development of hippocampal subfield volumes from 4 to 22 years. *Hum Brain Mapp*, *35*(11), 5646–5657. doi:10.1002/hbm.22576
- Lacy, J., Yassa, M., Stark, S., Muftuler, L., & Stark, C. (2011). Distinct pattern separation related transfer functions in human CA3/dentate and CA1 revealed

- using high-resolution fMRI and variable mnemonic similarity. *Learn Mem*, 18(1), 15-18. doi:10.1101/lm.1971111
- Lavenex, P., & Banta Lavenex, P. (2013). Building hippocampal circuits to learn and remember: insights into the development of human memory. *Behav Brain Res*, 254, 8-21. doi:10.1016/j.bbr.2013.02.007
- Leal, S. L., & Yassa, M. A. (2014). Effects of aging on mnemonic discrimination of emotional information. *Behav Neurosci*, 128(5), 539. doi:10.1037/bne0000011
- Le Bihan, D. (2003). Looking into the functional architecture of the brain with diffusion MRI. *Nat Rev Neurosci*, 4(6), 469-480. doi:10.1038/nrn1119
- Lee, J. K., Ekstrom, A. D., & Ghetti, S. (2014). Volume of hippocampal subfields and episodic memory in childhood and adolescence. *Neuroimage*, 94, 162-171. doi:10.1016/j.neuroimage.2014.03.019
- Leutgeb, J., Leutgeb, S., Moser, M., & Moser, E. (2007). Pattern Separation in the Dentate Gyrus and CA3 of the Hippocampus. *Science*, 315(5814), 961-966. doi:10.1126/science.1135801
- Leutgeb, S., Leutgeb, J., Treves, A., Moser, M., & Moser, E. (2004). Distinct Ensemble Codes in Hippocampal Areas CA3 and CA1. *Science*, 305(5688), 1295-1298. doi:10.1126/science.1100265
- Liu, K. Y., Gould, R. L., Coulson, M. C., Ward, E. V., & Howard, R. J. (2016). Tests of pattern separation and pattern completion in humans—A systematic review. *Hippocampus*, 26(6), 705-717. doi:10.1002/hipo.22561.

- Lloyd, M. E., Doydum, A. O., & Newcombe, N. S. (2009). Memory binding in early childhood: Evidence for a retrieval deficit. *Child Dev*, 80(5), 1321-1328.  
doi:10.1111/j.1467-8624.2009.01353.x.
- Marr, D. (1971). Simple Memory: A Theory for Archicortex. *Philos Trans R Soc Lond B Biol Sci*, 262(841), 23-81. doi:10.1098/rstb.1971.0078
- McGugin, R. W., Tanaka, J. W., Lebrecht, S., Tarr, M. J., & Gauthier, I. (2011). Race-specific perceptual discrimination improvement following short individuation training with faces. *Cogn Sci*, 35(2), 330-347.  
doi:10.1111/j.1551-6709.2010.01148.x
- Ngo, C. T., Newcombe, N. S., & Olson, I. R. (2017). The ontogeny of relational memory and pattern separation: Abrupt change in performance between ages 4 and 6. *Dev Sci*. doi:10.1111/desc.12556.
- Norman, K. A. (2010). How hippocampus and cortex contribute to recognition memory: revisiting the complementary learning systems model. *Hippocampus*, 20(11), 1217-1227. doi:10.1002/hipo.20855
- O'Reilly, R. C. & McClelland, J. L. (1994), Hippocampal conjunctive encoding, storage, and recall: Avoiding a trade-off. *Hippocampus*, 4, 661-682.  
doi:10.1002/hipo.450040605
- Pezdek, K., Blandon-Gitlin, I., & Moore, C. (2003). Children's face recognition memory: More evidence for the cross-race effect. *J Appl Psychol*, 88(4), 760-763. doi:10.1037/0021-9010.88.4.760

- R Core Team (2017). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- Rattenborg, N. C., & Martinez-Gonzalez, D. (2011). A bird-brain view of episodic memory. *Behav Brain Res*, 222(1), 236-245. doi:10.1016/j.bbr.2011.03.030
- Reagh, Z. M., & Yassa, M. A. (2014). Object and spatial mnemonic interference differentially engage lateral and medial entorhinal cortex in humans. *Proc Natl Acad Sci USA*, 111(40), E4264-4273. doi:10.1073/pnas.1411250111
- Ribordy, F., Jabes, A., Banta Lavenex, P., & Lavenex, P. (2013). Development of allocentric spatial memory abilities in children from 18 months to 5 years of age. *Cogn Psychol*, 66(1), 1-29. doi:10.1016/j.cogpsych.2012.08.001
- Rolls, E. T. (2007). An attractor network in the hippocampus: theory and neurophysiology. *Learn Mem*, 14(11), 714-731. doi:10.1101/lm.631207
- Rolls, E. T. (2013). The mechanisms for pattern completion and pattern separation in the hippocampus. *Front Syst Neurosci*, 7, 74. doi:10.3389/fnsys.2013.00074
- Rolls, E.T. (1996). A theory of hippocampal function in memory. *Hippocampus*, 6(6), 601-620. doi:10.1002/(sici)1098-1063(1996)6:6<601::aid-hipo5>3.0.co;2-j
- Rolls, E.T. (2016). Pattern separation, completion, and categorisation in the hippocampus and neocortex. *Neurobiol Learn Mem.*, 129, 4-28. doi:10.1016/j.nlm.2015.07.008
- Rotello, C. M., Heit, E., & Dubé, C. (2015). When more data steer us wrong: Replications with the wrong dependent measure perpetuate erroneous

conclusions. *Psychon Bull Rev*, 22(4), 944-954. doi:10.3758/s13423-014-0759-2

Stark, S. M., Stevenson, R., Wu, C., Rutledge, S., & Stark, C. E. (2015). Stability of age-related deficits in the mnemonic similarity task across task variations.

*Behav Neurosci*, 129(3), 257-268. doi:10.1037/bne0000055

Stark, S. M., Yassa, M. A., Lacy, J. W., & Stark, C. E. (2013). A task to assess behavioral pattern separation (BPS) in humans: Data from healthy aging and mild cognitive impairment. *Neuropsychologia*, 51(12), 2442-2449.

doi:10.1016/j.neuropsychologia.2012.12.014

Tanaka, J. W., Heptonstall, B., & Hagen, S. (2013). Perceptual expertise and the plasticity of other-race face recognition. *Vis Cogn*, 21(9-10), 1183-1201.

doi:10.1080/13506285.2013.826315

Tamnes, C., Walhovd, K., Engvig, A., Grydeland, H., Krogsrud, S., & Østby, Y. et al. (2014). Regional Hippocampal Volumes and Development Predict Learning and Memory. *Dev Neurosci*, 36(3-4), 161-174. doi:10.1159/000362445

Treves, A., Tashiro, A., Witter, M. P., & Moser, E. I. (2008). What is the mammalian dentate gyrus good for? *Neuroscience*, 154(4), 1155-1172.

doi:10.1016/j.neuroscience.2008.04.073

Tulving, E. (1993). What Is Episodic Memory?. *Curr Dir Psychol Sci*, 2(3), 67-70.

doi:10.1111/1467-8721.ep10770899

Walker, P. M., & Hewstone, M. (2006). A perceptual discrimination investigation of the own-race effect and intergroup experience. *Appl Cogn Psychol*, 20(4),

461-475. doi:10.1002/acp.1191

- Wan, L., Crookes, K., Reynolds, K. J., Irons, J. L., & McKone, E. (2015). A cultural setting where the other-race effect on face recognition has no social-motivational component and derives entirely from lifetime perceptual experience. *Cognition*, 144, 91-115. doi:10.1016/j.cognition.2015.07.011
- Weidemann, C. T., & Kahana, M. J. (2016). Assessing recognition memory using confidence ratings and response times. *Royal Soc Open Sci*, 3(4), 150670. doi:10.1098/rsos.150670
- Wilson, I. A., Ikonen, S., Gallagher, M., Eichenbaum, H., & Tanila, H. (2005). Age-associated alterations of hippocampal place cells are subregion specific. *J Neurosci*, 25(29), 6877-6886. doi:10.1523/JNEUROSCI.1744-05.2005
- Wimmer, G. E., Braun, E. K., Daw, N. D., & Shohamy, D. (2014). Episodic Memory Encoding Interferes with Reward Learning and Decreases Striatal Prediction Errors. *J Neurosci*, 34(45), 14901–14912. doi:10.1523/JNEUROSCI.0204-14.2014
- Witter, M. P. (2007). Intrinsic and extrinsic wiring of CA3: indications for connectional heterogeneity. *Learn Mem*, 14(11), 705-713. doi:10.1101/lm.725207
- Yassa, M. A., & Stark, C. E. (2011). Pattern separation in the hippocampus. *Trends Neurosci*, 34(10), 515-525. doi:10.1016/j.tins.2011.06.006
- Yassa, M. A., Lacy, J. W., Stark, S. M., Albert, M. S., Gallagher, M., & Stark, C. E. (2011). Pattern separation deficits associated with increased hippocampal CA3 and dentate gyrus activity in non-demented older adults. *Hippocampus*, 21(9), 968-979. doi:10.1002/hipo.20808

- Yassa, M. A., Mattfeld, A. T., Stark, S. M., & Stark, C. E. (2011). Age-related memory deficits linked to circuit-specific disruptions in the hippocampus. *Proc Natl Acad Sci USA*, 108, 8873–8878. doi:10.1073/pnas.1101567108
- Zhao, M., Hayward, W. G., & Bühlhoff, I. (2014). Holistic processing, contact, and the other-race effect in face recognition. *Vision Res*, 105, 61-69. doi:10.1016/j.visres.2014.09.006.