

Neurobiological Contributions of Pubertal Development, Top-down control of Emotional Arousal, and Reward Processing on Mnemonic Performance

PROPOSAL FOR DISSERTATION
DOCTOR OF PHILOSOPHY IN COGNITIVE NEUROSCIENCE, PSYCHOLOGY
COLLEGE OF ARTS, SCIENCES AND EDUCATION

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08/11/2022

I propose to Major Professor (Aaron T. Mattfeld, PhD) and Committee Members (Timothy Allen, PhD, Dana McMakin, PhD, and Matthew DeGennaro, PhD), a functional magnetic resonance imaging and behavior study to be conducted in fulfillment of requirements for Doctor of Philosophy in Psychology with an emphasis in Cognitive Neuroscience.

Background and Significance

The hippocampus is a structure that plays a crucial role in forming and retrieving episodic memories, which are memories for the what, when, and where of an event. One possible explanation for how episodic memories are formed and stored is through the processes of pattern separation and completion, which characterizes how a new event may be stored orthogonally to (pattern separation) or together with (pattern completion) previous contextual information [1]. The hippocampus, with its multiple distinct subregions, appears particularly suited for the operations of pattern separation and completion. The dentate gyrus (DG), with its strong excitatory granule cells and sparse connections is thought to play an important role in pattern separation [2, 3, 4, 5], while the CA1 [6, 7, 8, 9] and CA3 [10, 11] receive multiple sources of input and likely play important roles in pattern completion. These processes are often assessed in humans by using mnemonic similarity tasks (MST), that examine what are thought to be behavioral correlates of pattern separation and completion: mnemonic discrimination and generalization.

The hippocampus also shares connectivity with numerous systems in the brain including those for reward [12, 13] and arousal [14, 15]. Despite these known patterns of regional connectivity, little work has been done across the literature demonstrating how these connections impact mnemonic generalization in humans.

Research Objectives and Questions

In this dissertation, I outline two objectives to investigate how pubertal development and reward processing contribute to mnemonic performance.

Aim 1: *Characterize changes in memory discrimination/generalization for valenced information related to medial temporal lobe development.*

Aim 2: *Examine how reward and loss relate to mnemonic discrimination and generalization.*

Experimental Design, Hypotheses, and Preliminary Data

AIM 1: Characterize changes in memory discrimination/generalization for valenced information related to medial temporal lobe development.

Memory increases in specificity, driven by maturation of key neurobiological substrate taking root around the onset of puberty and continuing into adolescence [16, 17, 18, 19]. Whether these specificity-supporting neurobiological mechanisms are similarly employed across different stimulus valences (e.g., emotional versus neutral) remains unknown. Around the same developmental window, the prevalence of anxiety disorders increases [20]. Together, understanding how developmental differences in memory specificity interact with emotional salience of stimuli may provide important insight into our understanding of negative overgeneralization, a characteristic symptom of anxiety where individuals generalize negative associations to similar events [21]. In pursuit of Aim 2, we seek to understand the relation between cross-sectional indices of neurobiological maturation around the onset of adolescence and measures of behavioral discrimination and generalization to stimuli with emotional valence. Data from a two-session magnetic resonance imaging (MRI) study in which participants completed the study and test sessions of an emotional mnemonic similarity

task with a twelve-hour delay between sessions was analyzed. In this analysis, I sought to examine how the level of pubertal maturity in the hippocampus predicted mnemonic generalization and completion for negative and neutral images. To answer this question, I examined how emotional valence and hippocampal pubertal maturation interacted to predict lure discrimination (LDI) and generalization (LGI) performance. I expected to observe an increase in neutral lure discrimination performance (LDI) with increasing hippocampal pubertal maturity index (PMI), with neutral lure generalization (LGI) remaining relatively stable. We also expected the relationship between negative LDI and LGI to differ for negative stimuli. We also expect that any relationships between PMI and mnemonic performance will be localized to the hippocampal formation (HF), rather than other MTL regions such as the rhinal cortices or amygdala (AMY).

Regional Volumetric and Connective Pubertal Maturity Index: PMI

To calculate regional maturity scores partial least squares correlation (PLSC) was conducted to produce regional maturity for the HF (DG/CA2/CA3/CA4, CA1, subiculum, posterolateral and anteromedial entorhinal cortices), rhinal (RHI) cortices (perirhinal cortex and parahippocampal cortex), and amygdala (AMY) (resulting k-means clusters determined by probabilistic tractography) according to an approach first outlined by [22]. Due to the nature of our sample, and the strong effects of pubertal status on development within our age range, the Pubertal Development Scale (PDS) was used in lieu of age in construction of maturity scores. The PDS was scored so that the value obtained roughly equivocated Tanner staging [23]. A correlation matrix was produced by PDS-Shirtcliff and volumetric measures for each ROI. The resultant matrix was then decomposed via singular value decomposition (SVD). Resultant weights for each ROI were then multiplied by each subject's vector of ROI volumes to produce a singular regional maturity score. This process was completed for the HF, RHI and AMY to produce Hippocampal, Amygdala, and Rhinal PMI, respectively. This PLSC analysis was conducted using NumPy (1.19.4) [24] in Python 3.8.3. PLSC was also used to compute connectivity maturity metrics between regions. A correlation matrix was constructed using total PDS score and the median number of random walks between the seed and target regions. This matrix was decomposed via SVD and the resultant weights were multiplied by the median connection strength to produce a connectivity maturity score. This was conducted for the following connections: Amygdala to HF, HF to Rhinal Cortices, and HF to mPFC. These formed the basis of our Amy-HF connectivity, HF-RHI connectivity, and HF-mPFC connectivity PMI scores respectively.

Emotional Mnemonic Similarity Task: eMST.

Participants took part in an emotional similarity task that consisted of an incidental encoding session and a followup test session approximately 12 hours later. During the incidental encoding session, participants were asked to rate scene images as negative, neutral or positively valenced. Participants returned 12 hours later and completed a recognition memory task that asked them to rate images as old (they saw during encoding) or new (they did not see the images during encoding), with the caveat that some of these images would be similar, but not the same as images during encoding. Performance on these similar images, referred to as lures, was used to calculate LDI and LGI performance. For more information, see [25] and Fig. 1A.

Data Analysis.

Structural magnetic resonance imaging (sMRI) and diffusion magnetic resonance imaging (dMRI) were used along with clinical measures of pubertal maturity to produce volumetric and connective estimates of PMI to address the following research questions:

1. Determine if increasing volumetric PMI in the HF is associated with increased lure discrimination performance for neutral images, and if this relationship holds for negative images; *examine the results of two mixed effects linear models predicting LGI and LDI, with age, gender, image valence, HF volumetric PMI, and image valence X HF volumetric PMI as predictors. Prediction:* The interaction between image valence X HF volumetric PMI will be a significant predictor of LGI and LDI performance
2. Determine if this relationship between volumetric PMI is unique to the hippocampus; *examine the results of several mixed effects linear models predicting LGI and LDI, with age, gender, image valence, RHI/AMY volumetric PMI, and image valence X RHI/AMY volumetric PMI as predictors. Prediction:* The interaction between image valence X RHI/AMY volumetric PMI will not be a significant predictor of LGI and LDI performance.
3. Explore if similar interactions occur when PMI is examined based on diffusion-based regional connectivity (AMY to HF, HF to RHI, HF to mPFC), rather than volumetric PMI; *examine the results of several mixed effects linear models predicting LGI and LDI, with age, gender, image valence, AMY to HF/HF to RHI/HF to mPFC connectivity PMI, and image valence X AMY to HF/HF to RHI/HF to mPFC volumetric PMI as predictors. Prediction:* There will be an interaction between image X regional connectivity PMI for the examined connections (AMY to HF, HF to RHI, HF to mPFC)

Results.

1. As predicted, we identified a significant interaction between HF volumetric PMI and stimulus valence predicting LDI and LGI. ([Fig. 1B](#)). We observed that HF volumetric PMI was associated with greater discrimination of neutral images, and limited or minimally reduced discrimination of negative images. We found enhanced generalization of negative images associated with greater HF volumetric PMI, while neutral generalization remained steady or decreased slightly as a function of HF volumetric PMI ([Fig. 1B](#)).
2. Divergent patterns were not observed in discrimination (LDI) across PMI and image valence in the rhinal cortices or the amygdala. Rhinal volumetric PMI significantly interacted with stimulus valence when predicting LGI, while amygdala maturity did not. As rhinal maturity increased, LGI decreased for negative images, and increased for neutral images.
3. We did not identify an interaction between AMY-HF connectivity PMI and stimulus valence predicting LDI, or LGI. We did not identify an interaction between HF-RHI connectivity PMI and stimulus valence predicting LDI or LGI. When comparing discrimination across image valence (negative and neutral) and our HF-mPFC connectivity PMI we observed a trend towards differential discrimination following corrections for multiple comparisons. Negative image discrimination was reduced with elevated HF-mPFC connectivity PMI, while greater neutral image discrimination was evident with greater HF-mPFC connectivity PMI. Generalization exhibited a significant relationship with valence in the opposite pattern, with greater HF-mPFC

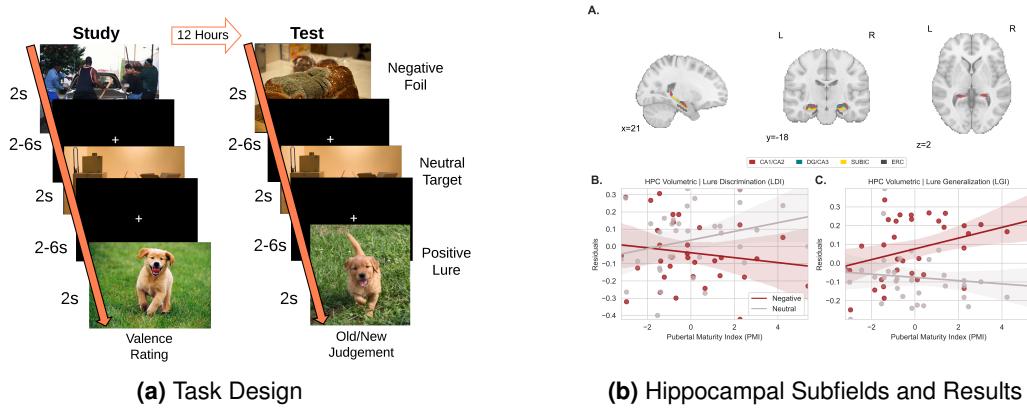


Figure 1. Aim 1 Task Progression

connectivity PMI associated with greater negative image generalization, and reduced neutral image generalization.

Aim 1 is complete, and the resulting manuscript is currently under review at Learning & Memory as of Summer 2022

AIM 2: Examine how avoided loss and unexpected loss impact mnemonic discrimination and generalization using a performance-based behavioral paradigm.

Manipulating dopaminergic reward-based pathways has long been the domain of classical conditioning paradigms, which have consistently shown VTA neurons responding to cues of reward anticipation [26]. DA from the VTA in responses to reward has been shown to produce long-term potentiation based protein synthesis in the CA1 subfield of the hippocampus, providing more evidence that DA is potentially biasing the system toward pattern completion [27]. In human fMRI research regional co-activation between the VTA, ventral striatum, and hippocampus has been shown to predict superior memory performance [28]. This finding, however, comes with the caveat that memory specificity was not tested, and this improved memory performance may come at the cost of a more generalized memory representation. Other studies have found that these same regions are active during reward and loss learning preceding improved memory performance during recognition memory tasks [29]. DA impacts memory performance by promoting pattern completion processes in the CA1 region of the hippocampus [13], with disruptions in DA signaling leading to poorer performance when given degraded memory cues [30]. Thus, modulation of DA in the hippocampus through reward based manipulations appears to bias the system toward pattern completion.

Within functional neuroimaging paradigms, reward responses often take the form of changes in signal within the ventral striatum. This “reward prediction error” (RPE) signal results in increased signal in the ventral striatum following a trial that was successfully rewarded [31, 32]. Models examining RPE have found that rather than total information influencing received reward, an event is rewarding based on the gap between expected and received reward [33]. Additionally, these hippocampal signal also changes in response to RPEs [34]. These signals are likely due to the

excitation induced by DA neurons following a reward. While these paradigms often examine RPE in response to reward and loss within a task, very few studies examine the effect of averted losses (trials that were expected to be a loss, but were avoided), which should have a similar impact to reward.

For Aim 2, I will examine how loss and reward impact memory performance, expanding the current literature by examining the impact of averted loss and gain, and using a novel performance-based reward paradigm. Participants completed a performance-based loss aversion task consisting of two sessions, Study and Test, with the study session taking place in an MRI scanner. In this experiment, I sought to determine how loss and reward, as well as averted loss and reward influence memory performance. I expect that trials that were rewarded would be better recognized, and that trials where loss was averted would show similar memory performance. I also expect that lure generalization will be higher for these rewarded or loss-averted trials compared to neutral trials.

Loss Aversion Assessment Task: LAVA.

The task consisted of two sessions, an incidental encoding session in the MRI scanner and a behavioral-only recognition memory test 24 hours later. During the encoding session participants were shown object images and were instructed to endorse whether the object was more typically found indoors or outdoors. Each object image was accompanied by a cue in the form of a box in one of three colors indicating whether the participant would gain (green; 72 images), lose (red; 72 images), or maintain (gray; 72 images) arbitrary points on the given trial. Participants were instructed that they would be given points for each correct answer on gain trials, would lose a point for each incorrect answer on loss trials, and would neither gain nor lose on maintain trials. Importantly, they were informed that scoring 25 or more points on the task would reward them with an additional twenty dollars. For each encoding trial, the cue + stimulus pair was presented for 2000ms. This was followed by an interstimulus interval (ISI) of 2000–6000ms. Then, a Go! Prompt was given for 500ms indicating the participant should give their indoor or outdoor rating. This response window was followed by another 2000–6000ms ISI, then a Feedback window showing whether the response was correct or incorrect and how many points were gained or lost on the trial. After completing the task, participants returned 24 hours later for a surprise recognition memory task. During the recognition memory task, participants were shown object images that were either presented during encoding (targets; 108 images), were similar to those during encoding (lures; 108 images), or were completely new (foils; 108 images) and were asked to rate the images as Old or New. This task was self-paced.

Neuroimaging data collection and preprocessing.

Magnetic resonance imaging data was collected on a Siemens Magnetom Prisma 3T scanner with a 32-channel head coil at the Center for Imaging Science at Florida International University (Miami, FL). Functional data was obtained using T2*-sensitive gradient echo pulse sequence (66 interleaved axial slices, slice thickness = 2.0 mm, TR = 1760 ms, TE = 35 ms, flip angle = 52°, field of view (FOV) = 200 mm, voxel size = $2.0 \times 2.0 \times 2.0\text{mm}^3$). Four hundred and seventy-seven whole-brain images were collected per experimental run. To ensure stabilization of magnetic resonance signal, acquisition of data began after the fourth volume. For purposes of coregistration and registration, high-resolution three-dimensional magnetization-prepared rapid gradient echo sequence collected (MP-RAGE: 176 axial slices, slice thickness = 1.0 mm, TR = 2500 ms, TE = 2.9 ms, flip angle = 8°,

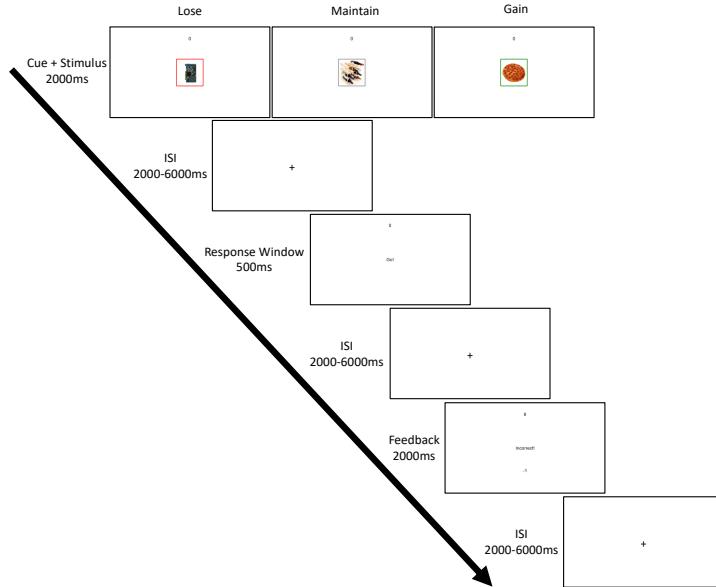


Figure 2. Hippocampal Pubertal Maturity is associated with increased discrimination of neutral images and increased generalization of negative images

FOV = 256 mm, voxel size = $1.0 \times 1.0 \times 1.0 \text{ mm}^3$). Functional Neuroimaging data are preprocessed using standard methods using fMRIPrep [35].

Data Analysis.

Functional magnetic resonance imaging (fMRI) using anatomical regions of interest (ROI) will be conducted to address the following research questions

1. Determine the impact of reward and averted loss on subsequent memory performance for targets and lures; *examine the results of three mixed effects linear models predicting LGI, LDI, and recognition memory performance with age, gender, and trial-type as predictors.* **Prediction:** Trial-type will be a significant predictor of LGI, LDI, and recognition memory performance. Further, I expect post-hoc tests to reveal that this difference is driven by higher recognition memory and LGI for rewarded and loss-averted trials compared to maintain trials. These findings will provide evidence that loss-averted trials have similar impact on memory as loss and reward themselves.
2. ROI analysis examining hippocampus and ventral tegmental area (VTA) for reward and loss-averted trials; *differences in fMRI based activation in the VTA and HPC ROI defined using FreeSurfer parcellation and segmentation (aparc+aseg) [36] between reward versus maintain trials and loss-averted versus maintain trials.* **Prediction:** Higher levels of activation in the VTA for reward and loss-averted trials relative to maintain trials. This provides evidence that VTA activation at time of encoding differs depending on type of trial, and potentially impacts subsequent memory encoding.

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