PRIORITIZED MEMORY CONSOLIDATION OVER SLEEP: DO PSYCHOLOGICAL AND PHYSIOLOGICAL MARKERS AT ENCODING SET THE STAGE?

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Abstract

Emotion enhances memory longevity and vividness. Perceiving an experience as emotional, as well as the autonomic and functional brain responses involved in initially encoding an emotional experience, have been theorized to "tag" these memories. Tagged memories may then be prioritized for consolidation during sleep. However, direct evidence supporting this theory is sparse. The aim of the present study was to determine which encoding-related indicators of memory tagging interact with post-encoding sleep oscillations to promote emotional memory retention and vividness. To test this, participants incidentally encoded positive, neutral and negative multisensory stimuli during 3T fMRI scanning with concurrent heart rate monitoring. Participants provided emotional intensity ratings after each stimulus presentation. Following a 120-min post-encoding nap opportunity recorded with polysomnography, participants completed a surprise memory test. Memory for emotional and neutral stimuli was equivalent, though emotional stimuli tended to be remembered more vividly. Perceived emotional intensity, but not heart rate deceleration (HRD) magnitude or functional brain activity, was diagnostic of later successful retrieval of emotional, but not neutral stimuli. Higher REM sleep theta power during the nap was associated with a greater emotional intensity (EI) subsequent memory effect (i.e., higher EI for later remembered compared to forgotten stimuli) for positive stimuli, which were also remembered more vividly. Higher NREM spindle density was associated with a *greater* EI subsequent memory effect for neutral stimuli and *lesser* EI subsequent memory effect for negative stimuli. Lastly, higher numbers of NREM spindle-slow oscillation coupling events predicted a negative relationship between perceived emotional intensity at encoding and memory vividness for negative stimuli. Taken together, the present findings suggest that subjective, rather than objective, encoding-related arousal responses acted as emotion "tags". How subjective arousal impacted later memory varied as a function of the memory's emotion category and REM and NREM-specific oscillations. Future work is needed to clarify the underlying mechanisms for these observed effects.

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INTRODUCTION

Emotional memories are more resistant to forgetting than neutral memories across time (LaBar & Cabeza, 2006; Yonelinas & Ritchey, 2015). Evidence has strongly linked emotional memory consolidation, and resulting brain plasticity, to increased encoding-related arousal (McGaugh, 2018). Preliminary evidence also supports a role for sleep preferentially strengthening memories "tagged" by emotion during encoding (Kim & Payne, 2020; Payne & Kensinger, 2018).

Emotional Arousal at Encoding Supports Memory Consolidation

Emotional memories are more enduring (Kleinsmith & Kaplan, 1963; Park, 2005; Yonelinas & Ritchey, 2015) and remembered more vividly (Kensinger & Schacter, 2008; Phelps & Sharot, 2008) than non-emotional memories. This process begins at encoding, where emotional content captures (Bennion et al., 2015; Herten et al., 2017; Pourtois et al., 2013; Talmi, 2013) and narrows (Easterbrook, 1959; Loftus et al., 1987) attention, increases subjective (e.g., Bradley et al., 1992; Lang et al., 1993) and autonomic arousal (e.g., Abercrombie et al., 2008; Bradley et al., 2001, 2008; Buchanan et al., 2006; Lang et al., 1993; Palomba et al., 1997), and strongly engages regions of our brain responsible for sensory and emotion processing as well as memory formation (Bowen et al., 2018; Dahlgren et al., 2020; Murty et al., 2010). The present discussion will focus on the latter

factors thought to influence emotional memory consolidation (i.e., emotion-enhanced subjective arousal, autonomic reactivity and functional brain activity).

Compared to viewing neutral material, viewing emotional material (i.e., negative and positive) increases subjective ratings of emotional arousal (e.g., Bradley et al., 1992; Lang et al., 1993) as well as autonomic nervous system responses (Bradley et al., 2008; Lang et al., 1993; Tambini et al., 2017) and greater heart rate deceleration (HRD) responses in particular (Abercrombie et al., 2008; Cunningham et al., 2014; Palomba et al., 1997). HRD is one component of the "orienting response" (Cook & Turpin, 1997) which results in increased allocation of attention to, and cognitive processing of, salient stimuli. Greater HRD responses are elicited when participants view emotional compared to neutral stimuli including pictures (Abercrombie et al., 2008; Anttonen & Surakka, 2005; Ashton et al., 2019; Cunningham et al., 2014; Groch et al., 2011; Palomba et al., 1997), sounds (e.g., Anttonen & Surakka, 2005; Bradley & Lang, 2000) and picture-sound combinations (Anttonen & Surakka, 2005).

Greater subjective ratings of emotional arousal (e.g., Bradley et al., 1992) and elevated HRD responses at encoding (Abercrombie et al., 2008; Mather & Sutherland, 2011; Palomba et al., 1997) have also been linked to successful memory retrieval. For example, picture stimuli rated as more emotionally arousing were better remembered than non-arousing picture stimuli up to one year later (Bradley et al., 1992). Palomba et al. (1997) showed that HRD responses were greatest for negative pictures, which were also more likely to be later remembered. Abercrombie et al. (2008) reported that HRD magnitude was greater for subsequently remembered than subsequently forgotten picture stimuli, irrespective of emotion-category. Therefore, subjective ratings of stimulus

emotionality and elevated HRD responses at encoding may serve as indicators of emotional memory tagging.

Consolidation of emotional memories also critically depends on enhanced encoding-related activity in both medial temporal lobe (MTL) and neocortical structures. For example, elevated encoding-related activity in MTL structures, including the amygdala and hippocampus, is diagnostic of emotional memory retrieval (Dahlgren et al., 2020; Murty et al., 2010). Functional connectivity between the amygdala and hippocampus is enhanced during the encoding of emotional relative to neutral content (Fastenrath et al., 2014). Further, connectivity between the amygdala and other memory-promoting MTL regions (i.e., parahippocampal gyrus) has been shown to predict long-term emotional memory enhancement (Ritchey et al., 2008). These findings are broadly consistent with rodent work showing that emotional experiences enhance arousal-related neuromodulators and amygdala activity, directly influencing hippocampal plasticity (de Quervain et al., 2007; H. Hu et al., 2007; Joëls et al., 2011; Schwabe et al., 2012). In rodents, emotion also promotes the formation of memory engrams, lasting cellular memory traces, in, among other regions, the amygdala and hippocampus (Kitamura et al., 2017). In humans, successful emotional memory retrieval depends on enhanced encoding in visual (Bowen et al., 2018; Dahlgren et al., 2020; Murty et al., 2010; Todd et al., 2020) and auditory (Grosso et al., 2015) sensory processing regions in the brain, corresponding to stimulus modality (i.e., visual or auditory stimuli, respectively). Recent work from our lab has also demonstrated that connectivity between the amygdala and visuo-sensory cortex, coupled with high autonomic reactivity, during encoding facilitates the vivid retrieval of negative memories (Kark & Kensinger, 2019b).

Sleep-Dependent Memory Consolidation

Sleep has been shown to play a critical role in memory processing (Rasch & Born, 2013). An abundance of studies have demonstrated that episodic memories are better retained across delays including sleep compared to delays including continued wakefulness (Rasch & Born, 2013). Rather than passive protection from memory interference (though see Yonelinas et al., 2019 for an alternative account), sleep may actively promote systems-level consolidation of episodic memories (Born & Wilhelm, 2012; Diekelmann & Born, 2010), whereby labile memory traces encoded in the hippocampus are redistributed to the neocortex, where they are incorporated into existing memory structures (Cairney et al., 2018; Klinzing et al., 2019; Roscow et al., 2021; Sterpenich et al., 2021). This process is theorized to be initiated during deep, non-rapid eye-movement (NREM) sleep, and NREM stage 3 (N3; also known as "slow wave sleep") specifically, by spontaneous reactivation of hippocampal traces and coordinated coupling of hippocampal sharp-wave ripples (~80 hz), thalamocortical sleep spindles (~12-15 Hz) and cortical slow oscillations (<1 Hz; Klinzing et al., 2019). A number of human studies have supported a memory benefitting role of sleep spindles, slow oscillations, and, to a lesser extent, spindle-slow oscillation coupling. For example, spontaneous memory reactivation during slow wave sleep (SWS), as assessed by EEG decoding, was associated with episodic memory retrieval (Schönauer et al., 2017). Reactivating memories experimentally by presenting encoding-associated sensory cues during SWS has been shown to increase sleep spindle activity (Cairney et al., 2018), hippocampal functional brain activity (Rasch et al., 2007) and promote memory retention compared to non-cued memories (Hu et al., 2020). Provoking slow oscillations

with non-invasive brain stimulation has also been demonstrated to enhance episodic memory (Wunderlin et al., 2021).

Emotional memories are theorized to be selectively strengthened by REM sleep via emotional memory replay (phenomenologically captured in emotional dream content; Foulkes, 1962; Stickgold, 2001) and reactivation of emotional memory networks (Dang-Vu et al., 2010; Kim & Payne, 2020; van der Helm & Walker, 2009). Theta oscillations, which arise from synchronized activation of the neocortex, hippocampus and amygdala (Paré et al., 2002), have also been theorized to be particularly important for REM sleep-dependent emotional memory consolidation (Hutchison & Rathore, 2015), possibly signifying emotional memory replay (Genzel et al., 2015). In rodents, REM sleep theta coherence in the neocortex, hippocampus and amygdala predicts retention of fear memories (Popa et al., 2010), while REM sleep theta suppression impairs fear recall (Boyce et al., 2016). In human studies, associations between REM sleep physiology and emotional memory retention have been inconsistent. While some studies have shown that REM sleep and/or REM sleep theta oscillations support retention of negative (Groch et al., 2013; Nishida et al., 2009; Payne et al., 2012; Sopp et al., 2017) and positive (Kim et al., 2019) memories, other large-scale studies have found no such associations (Ackermann et al., 2015). Further, human studies that have attempted to modulate emotional memory effects by depriving participants of REM sleep (Morgenthaler et al., 2014) or enhancing (Harrington et al., 2021) or suppressing (Johnson & Durrant, 2018) REM sleep theta power have been unsuccessful. It therefore remains an open question under what conditions REM sleep physiology might play a role in the selective strengthening of emotional memories.

Interestingly, recent work in rodents has demonstrated that emotional memories benefit from oscillatory phase coupling of cortical slow oscillations, thalamocortical sleep spindles, and hippocampal sharp-wave ripples (Latchoumane et al., 2017) and that sharp-wave ripples co-occur with replay of encoding-related single cell recording patterns of emotional experiences (Girardeau et al., 2017). In humans, SWS sleep (Alger et al., 2018; Cairney et al., 2014; Payne et al., 2015), sleep spindle activity (Alger et al., 2018; Cairney et al., 2014; Kaestner et al., 2013) and NREM delta power (1-4Hz; Payne et al., 2015) has been shown to enhance emotional memory retrieval, though only one study to date has examined spindle-slow oscillation coupling and found an inverse relationship between coupling and emotional memory retention under conditions of high baseline stress (Denis, Kim, et al., 2021). While findings are still equivocal, theories support REM and NREM sleep playing independent (Ekstrand, 1972) or complementary roles (Giuditta, 2014; Kim & Payne, 2020) in the consolidation of emotional memories.

Despite converging evidence for a beneficial effect of sleep on emotional memory consolidation, two recent meta-analyses (Lipinska et al., 2019; Schäfer et al., 2020) and a comprehensive review (Davidson et al., 2021) found a lack of behavioral evidence for sleep's beneficial role on emotional memory consolidation compared to continued wake. While several experiment characteristics influenced observed effects (Lipinska et al., 2019), including method of encoding (explicit vs. incidental), test-retest schedule (delayed memory test only vs. immediate and delayed memory tests) and memory test type (recognition vs. recall), additional psychological and physiological factors, such as encoding-related emotional arousal (Payne & Kensinger, 2018) and sensory-focused encoding (Bowen et al., 2018), as well as post-encoding sleep oscillatory dynamics (Kim

& Payne, 2020), were not accounted for in the meta-analyses. These factors may be critical in the process of selecting which memories are "tagged" for selective consolidation across sleep.

Emotion Tags Memories to be Consolidated Across Sleep

The idea that emotion "tags" certain memories for consolidation originated from work in rodent models (Richter-Levin & Akirav, 2003). As discussed above, emotional experiences evoke the release of arousal-related neuromodulators that, in turn, enhance communication between the amygdala and hippocampus and promote hippocampal plasticity (McGaugh, 2018). This is theorized to occur when arousal-related neuromodulators, such as norepinephrine and corticosterone (the rodent equivalent to cortisol in humans), increase the availability of plasticity-related proteins available for capture by newly formed (i.e., "tagged") hippocampal synaptic connections. These tagged synapses are then selectively strengthened (i.e., consolidated; Richter-Levin & Akirav, 2003).

A burgeoning body of research in humans has conceptually confirmed the importance of arousal-related biomarkers around the time of encoding in the selective retention of emotional information (e.g., Cunningham et al., 2014, 2018, 2021; Shields et al., 2017) and further, have implicated a role for sleep in the selective consolidation of memories "tagged" by emotion (Kim and Payne, 2018; Payne and Kensinger, 2018; though see Ackermann et al., 2019). For example, Cunningham et al. (2014) showed that stronger encoding-related HRD responses to emotional stimuli was associated with better retrieval of these stimuli when participants slept after encoding, but not when they remained awake.

In a separate study, Bennion et al. (2015) showed that higher cortisol levels during memory encoding were associated with enhanced retrieval of negative, but not neutral, content when participants slept after encoding, but not when they remained awake. Kim et al. (2019) also demonstrated that post-encoding REM sleep theta power was positively associated with emotional, and specifically positive, memory performance, but only in participants mounting a high cortisol response to a pre-encoding psychosocial stress test. Using the same dataset as Kim et al. (2019), Denis et al. (2021) observed that better memory for emotional and neutral stimuli was associated with increased SWS in the same group of high stress responders. Interestingly, however, sleep spindle-slow oscillation coupling during SWS, which, as mentioned earlier, is thought to aid memory consolidation, was, in fact, negatively associated with emotional performance (Denis, Kim, et al., 2021).

Like autonomic and arousal-related neuromodulator activity, encoding-related functional brain activity has also been demonstrated to interact with sleep to promote memory consolidation and emotional memory consolidation specifically. For example, Rauchs et al. (2011) found that hippocampal subsequent memory effects (i.e., higher encoding-related activity for later remembered items compared to later forgotten items) were only observed in a group that obtained a full night of sleep after encoding, but not a group that was deprived of sleep. Neural activity associated with the encoding of neutral (Jegou et al., 2019) or emotional memories (i.e., memories of reward; Sterpenich et al., 2021) has also been shown to be preferentially replayed during NREM sleep. Further, sleep has been demonstrated to promote connectivity between limbic and cortical regions to support emotional memory retrieval (Payne & Kensinger, 2011).

The Present Study

As discussed above, convergent evidence supports an interactive role of encoding-related emotional reactivity and post-encoding sleep on emotional memory consolidation. However, whether subjective and objective markers of tagging at encoding interact with post-encoding sleep physiology to promote emotional memory retention has not been directly tested in a single study. Here, I aimed to address this knowledge gap. To do so, I used a more ecologically valid, multisensory emotional memory task and assessed both memory quantity and quality, the latter of which has received little attention in sleep and emotional memory research.

I hypothesized that encoding-related autonomic reactivity (as measured by HRD) and MTL activity in the amygdala and hippocampus would be the strongest indicators of memory tagging and would interact with REM sleep theta power and/or NREM sleep physiology (spindles, delta power, or spindle-slow oscillation coupling) to selectively strengthen emotional memories. I additionally explored the novel idea that individual differences in sleep physiology would moderate the relationship between stronger sensory-focused encoding and memory performance and vividness for emotional stimuli.

1.0 METHODS

1.1 PARTICIPANTS

Forty-five healthy young adults (age 19-38 years), recruited from Boston College and the greater Boston area, participated in the study (see **Table 1** for participant demographics). Participants had normal or corrected-to-normal vision, were fluent in English, had no history of major medical, neurological, psychiatric or sleep disorders, were not taking any psychoactive medications at the time of study participation, and did not have any MRI contraindications. Participants provided written informed consent prior to study participation and were paid for their participation. All procedures were approved by the Boston College institutional review board.

Table 1. Participant Demographics.

	Value	%
Sample Size	45	-
Age		
M	25	-
SD	4.7	-
Range	19 – 38	-
Sex		
Female	27	60.0%
Male	18	40.0%
Ethnicity		
Hispanic	8	17.8%
Non-Hispanic	37	82.2%
Race		
African American, Black	4	8.9%
Asian	19	42.2%
Caucasian, White	18	40.0%
Other	4	8.9%
Marital Status		
Married	1	2.2%
Single	44	97.8%
Eduction (Years)		
M	16.7	-
SD	2.1	-
Range	12 – 22	-

Note. M, Mean; SD, Standard Deviation

1.2 EXPERIMENTAL PROCEDURES

A schematic of the experimental protocol is presented in **Figure 1**. Briefly, participants completed demographic, psychometric and sleep questionnaires (see **Appendix** for additional details), then underwent 3T fMRI scanning that included a functional localizer task and an incidental encoding task with concurrent heart rate

monitoring. Following the scan, participants were given a 2-hour nap opportunity monitored with polysomnography. Following the nap, participants completed a second scan that included a memory retrieval test.

Figure 1. Experimental Timeline. Scanning and nap time was held constant across all participants to minimize time-of-day confounds in task performance and circadian fluctuations in sleep drive.

1.3 BEHAVIORAL TESTING

1.3.1 Study Stimuli

Real-life emotional experiences are inherently multisensory (Klasen et al., 2012, 2014; Robins et al., 2009), though the majority of emotional memory studies to date have used only visual stimuli. Therefore, to increase the ecological validity of the present study, I chose to use multisensory stimuli. Encoding stimuli were 300 emotional and neutral pictures paired with neutral verbal labels drawn from a previous study (Ford et al., 2014) paired with semantically-related audio clips that matched the emotion category (i.e., negative, neutral or positive) of the picture. Audio clips were selected from the International Affective Digital Sounds database (IADS; Bradley & Lang, 2007) and online databases of Creative Commons Licensed sounds (Freesound.org and YouTube.com). Pictures were matched for low-level visual features and audio clips for

frequency and amplitude characteristics across emotion categories (see **Appendix** for additional details). Previously studied and novel neutral verbal labels served as cues during the memory retrieval test.

1.3.2 Functional Localizer Task

The functional localizer task was administered to determine the specific brain regions that responded to visual or auditory stimuli in the current participant sample (Saxe et al., 2006). This task consisted of three rounds of viewing emotional (negative and positive) and neutral pictures, listening to emotional and neutral sounds or viewing a fixation cross. Each round consisted of participants viewing one block of 7 pictures for 3 s each, one block of listening to 7, 3s audio clips and one block containing a 21-second fixation cross (see **Figure 2**). Pictures and audio clips were obtained from the same databases as the "study stimuli", but never used in the incidental encoding task.

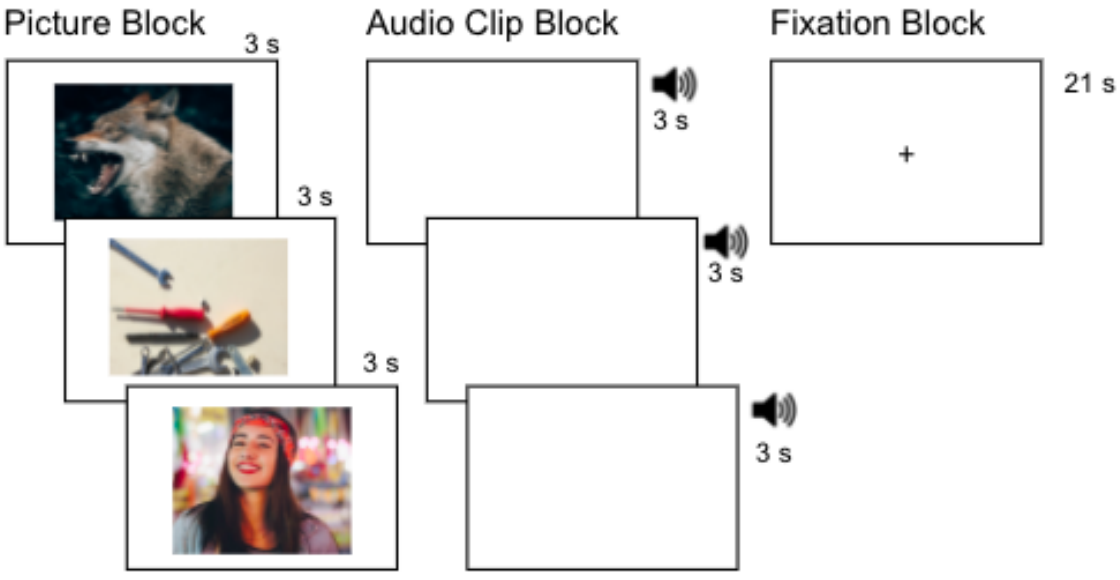

Figure 2. Functional localizer task. Participants completed 3 rounds of picture only, sound only and fixation blocks. Each round consisted of viewing 7 emotional and neutral images

(3 seconds each), listening to 7 emotional and neutral sounds (3 seconds each) and viewing a fixation cross (21 seconds). Images above were obtained from unsplash.com, but not used in the actual task.

1.3.3 Incidental Encoding

During incidental encoding, participants viewed a subset of 150 multisensory stimuli that each included an emotional (i.e., negative or positive) or neutral picture paired with a semantically-related neutral verbal label and semantically-related and emotion category-matched audio clip. Five blocks of 30 stimuli were presented during 3T fMRI scanning and concurrent heart rate monitoring. Each block contained 10 negative, 10 neutral and 10 positive multisensory stimuli, ordered pseudo-randomly such that stimuli of a particular emotion category appeared no more than twice in a row. Stimuli were presented for 3 s each and followed by a rating screen in which participants were given an additional 3 s to rate the stimulus' emotional intensity on a 5-point scale, ranging from 0 (not emotional) to 4 (very emotional), using an MRI-safe button box. Participants were informed that "emotional intensity" referred to the "instant feeling" the stimulus had on them personally, irrespective of whether the feeling was negative, neutral or positive and that the experimenters were interested in the participant's personal reaction, not how they thought other people in general should feel. Thus, emotional intensity ratings closely resembled the construct of emotional arousal. Further, participants were not informed that their memory for these stimuli would later be tested, thus encoding was incidental. Stimuli were separated by a 6-12 s jittered fixation cross (see **Figure 3**). Emotional intensity ratings were averaged for items that were later remembered or items that were later forgotten for each emotion category. To minimize the chance of order effects, four versions of the encoding task were created and

counterbalanced across participants. A practice version of the encoding task was administered outside of the scanner prior to the first scan.

1.3.4 Memory Retrieval Test

During the memory retrieval test, which occurred 3 hours after the incidental encoding task, participants viewed 150 verbal labels from the incidental encoding phase and 150 unstudied labels. Five blocks of 60 stimuli were presented during 3T fMRI scanning. Labels were presented for 3 s each and followed by a rating screen in which participants were given an additional 3 s to rate how vividly they remembered the picture-audio clip pair that originally accompanied the label. Using an MRI-safe button box, participants selected either "no memory" (i.e., did not remember seeing the label and/or could not recall its associated picture-audio clip pairing), "somewhat vivid", "vivid", or "extremely vivid" (see **Figure 3**). Participants were informed that memory vividness ratings could be based on how vividly they remembered the details of the picture-audio clip pair and/or how vividly they remembered their reaction or thoughts about the picture-audio clip pair. Memory vividness responses were numerically coded from 0 ("no memory") to 3 ("extremely vivid"). Stimuli were presented in immediate succession or separated by a 1.5 - 6 s jittered fixation cross. Consistent with signal detection theory (Hautus et al., 2021), previously encoded labels given a memory vividness rating of 0 (i.e., "no memory") were counted as "misses" and labels given a rating of 1-3 as "hits". Unstudied labels given a memory vividness rating of 0 were counted as "correct rejections" and labels given a rating of 1-3 as "false alarms". Memory performance for each emotion category was calculated using d', which is the subtraction

of the z-score transformed false alarm rate from hit rate (Hautus et al., 2021; Snodgrass & Corwin, 1988). Memory vividness ratings were averaged separately for each emotion category. To minimize the chance of order effects, two versions of the retrieval task were created and counterbalanced across participants. A practice version of the memory retrieval test was administered outside of the scanner following the nap.

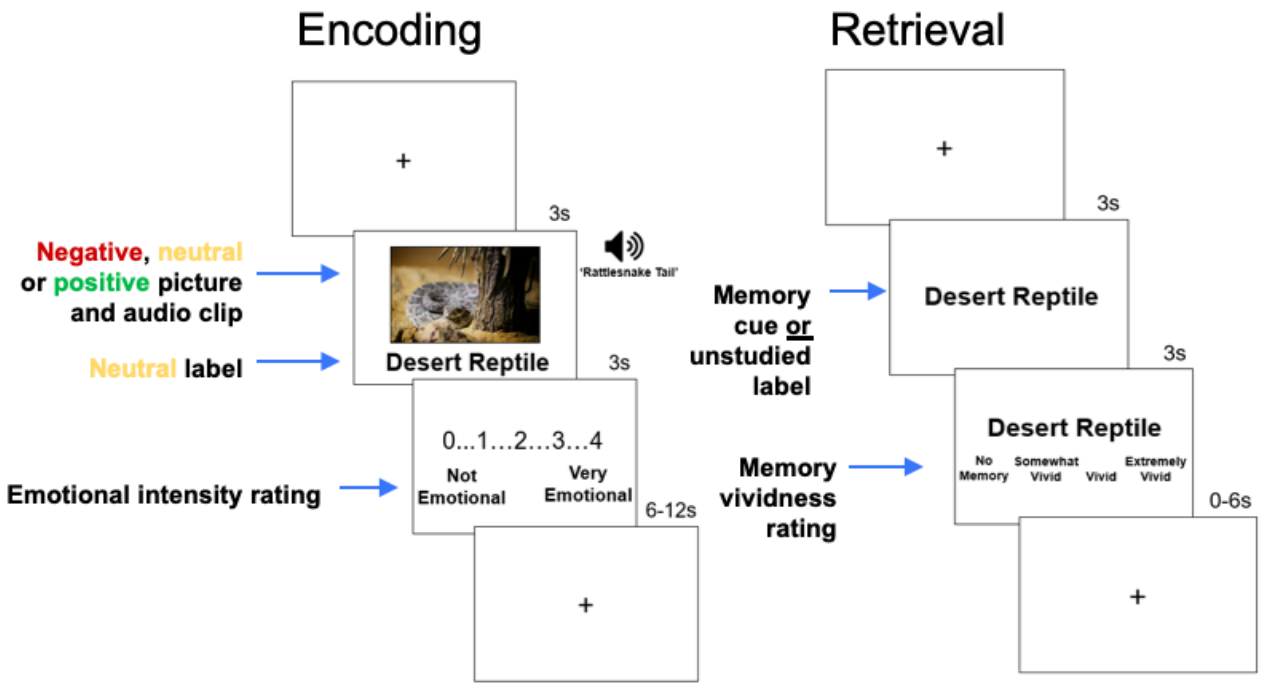

Figure 3. Memory Task. **(A)** During *Encoding*, participants were presented with 150 multisensory (picture-label-sound) stimuli, immediately rated each stimulus' emotional intensity on a 5-point scale from 0 (not emotional) to 4 (very emotional). Participants were not informed that their memory would later be tested, thus encoding was incidental. **(B)** During *Retrieval*, participants viewed 150 "old" (i.e., previously accompanied with a picture and sound at *Encoding*) labels interspersed with 150 "new" (i.e., not presented during *Encoding*) labels. While viewing the labels, participants were to bring back to mind its picture-sound pairing and then rated the vividness of their memory for this pair. Figure adapted from Thakral, Bottary and Kensinger (2022).

1.4 PHYSIOLOGICAL MONITORING

1.4.1 Heart Rate Data Acquisition, Preprocessing, and Analysis

HR was monitored and recorded during the encoding phase MRI scan with an MRI-compatible pulse oximeter (Model 7500FO Fiber-Optic Pulse Oximeter, Nonin Medical, Inc) attached to the participant's left index finger. HR data were sampled at 1000 Hz using the BIOPAC System MP150 module and AcqKnowledge software (BIOPAC Systems Inc., Goleta, CA), which was time-locked to MRI scan onset for each run. In AcqKnowledge, stimulus onsets were marked in an event channel. Participants were additionally outfitted with a respiratory belt and two galvanic skin conductance monitoring electrodes (data not presented here).

Event-related heart rate deceleration (HRD) was determined using custom Matlab scripts developed by Dr. Sarah M. Kark (Kark & Kensinger, 2019b). Prior to pre-processing, raw HR values (in beats per minute) were adjusted for the ~ 4 second lag in HR change post-stimulus onset. To minimize high-frequency fMRI noise, HR time series data were smoothed (moving median window = 1.5 seconds), linearly detrended, z-scored and averaged in 0.5 second time-bins. HR artifacts (e.g., supraphysiological values, such as HRs exceeding 200 beats per minute) were visually-inspected and removed. Event-related HRD was defined as the minimum HR occurring 1-7 seconds after stimulus onset compared to the 1 second prior to stimulus onset (see **Figure 4**). The sign of the HRD value was then inverted such that a more positive value corresponded to a greater HRD response. Note that the minimum HR window spanned the rating's screen and subsequent fixation cross. However, these screens were inherently neutral and thus should not have influenced the HRD response. Importantly, HRDs at the category and stimulus-level did

not correlate with subjective ratings of emotional intensity and therefore served as an independent marker of encoding-related emotional arousal (see **Appendix** for additional details).

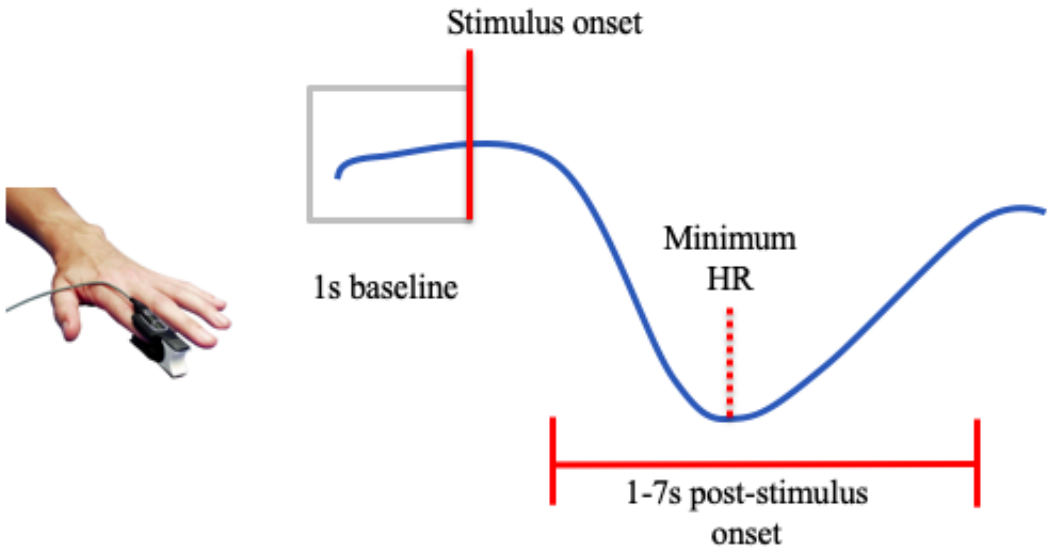

Figure 4. Heart rate deceleration (HRD) schematic. HRD response was calculated as the minimum heart rate 1 - 7 s following stimulus onset compared to a 1 s pre-stimulus baseline.

1.4.2 Sleep Recording and Scoring

Sleep was monitored with polysomnography, which included 6-channel scalp electroencephalography (EEG) positioned at frontal (F3 and F4), central (C3 and C4) and occipital (O1 and O2) locations, bilateral electrooculography and chin electromyography. EEG electrodes were referenced to contralateral mastoid electrodes (M1 and M2). Signals were acquired with a Grass Aura PSG amplifier and TWin recording software (sampling rate: 200Hz, high- and low-pass filter 0.1 and 35 Hz, respectively, 60Hz notch filter). PSG recordings were visually scored for NREM sleep (N1, N2 and N3), REM sleep and wake using standard criteria (Iber et al., 2007) by an experienced research technician who

was blind to participants' demographic and experimental data. Epochs containing EEG artifacts (e.g., muscle, cardiac and eye-movement artifacts) were visually detected and excluded from quantitative EEG analyses (detailed below). Due to experimenter error, PSG data from one participant was not collected.

1.4.2.1 Spectral Analysis

Power spectral density (PSD) was estimated at frontal (F3 and F4) and central (C3 and C4) electrodes for all artifact-free sleep epochs. PSD was estimated using Welch's method (*pwelch* function in Matlab; Hamming windows = 5-s with 50% overlap). To minimize the typical 1/f scaling of the power spectrum, estimates were obtained from the temporal derivative of the EEG time series (Cox et al., 2017). Given that signal amplitude is at least partly driven by individual differences such as skull thickness and gyrul folding (Cox & Fell, 2020), we then normalized, within subject, each electrode's 0-30Hz power spectrum by dividing power at each frequency by that electrodes' average 0-30Hz power (e.g., Denis, Bottary, et al., 2021).

1.4.2.2 Sleep Spindle and Slow Oscillation Detection

Sleep spindles were automatically detected at frontal (F3 and F4) and central (C3 and C4) electrodes for all artifact-free NREM sleep epochs using a wavelet-based detector (Denis, Mylonas, et al., 2021; Mylonas et al., 2019; Wamsley et al., 2012). Sleep spindles were detected by subjecting raw NREM (N2+N3) EEG signal to a time-frequency transformation using complex Morlet wavelets (peak frequency = 13.5 Hz, full-width half-max wavelet bandwidth = 3 Hz corresponding to 12-15 Hz spindle

detection range). Spindles were detected by a wavelet scale thresholding algorithm whenever the wavelet scale exceeded six times the median signal amplitude for a minimum of 400ms (Denis, Mylonas, et al., 2021). Spindle density was then calculated as the number of spindles per minute of NREM sleep.

Slow oscillations were automatically detected at frontal (F3 and F4) and central (C3 and C4) electrodes for all artifact-free NREM sleep epochs. Data were first band-pass filtered between 0.5-4Hz using the EEGLAB *pop_eegfiltnew* function. All positive-to-negative zero crossings in the filtered time series were then identified. Candidate slow oscillations were marked if two such consecutive zero crossings fell .8 - 2 s apart (corresponding to a frequency of 0.5-1.25Hz). Peak-to-peak amplitudes were determined for all candidate slow oscillations and oscillations in the top quartile (i.e. with the highest amplitudes) at each electrode were retained as slow oscillations (Denis, Kim, et al., 2021; Helfrich et al., 2018; Staresina et al., 2015).

1.4.2.3 Sleep Spindle - Slow Oscillation Coupling

Slow oscillation-spindle couplings were identified at frontal (F3 and F4) and central (C3 and C4) electrodes for all artifact-free NREM sleep epochs. Data were first bandpass filtered in the delta (0.5-4 Hz) and spindle (12-15 Hz) bands using the EEGLAB *pop_eegfiltnew* function. The Hilbert transform was then applied to extract the instantaneous phase of the delta-frequency-filtered signal and the instantaneous amplitude of the spindle-frequency-filtered signal and then the peak amplitude of each spindle was detected. Coupled events occurred when the peak spindle amplitude

occurred during the slow oscillation (i.e., between two positive-to-negative zero crossings). The number of coupled events was then determined at each electrode.

Sleep scoring and quantitative sleep EEG analyses were performed using the Danalyzer toolbox (Denis, Mylonas, et al., 2021; github.com/ddenis73/danalyzer) implemented in Matlab (MathWorks, Inc., MA). In the present study, the following sleep variables were selected for analysis based on their previously observed role in sleep-dependent memory consolidation: total sleep time (mins), REM amount (mins and %), N3 amount (mins and %), REM theta power (4–7 Hz), NREM delta power (1–4 Hz), NREM sleep spindle density (number per min), NREM sleep spindle - slow oscillation coupling (total number of coupling events). Final values for quantitative EEG analyses (i.e., power spectral density, sleep spindles, slow oscillations) were averaged across frontal and central electrodes. REM theta power was not calculated for 12 participants (27.2%) that did not obtain at least 5 mins of REM sleep during the nap.

1.5 FUNCTIONAL MAGNETIC RESONANCE IMAGING (FMRI) ANALYSIS

1.5.1 Image Acquisition

Imaging data were collected with a Siemens Magnetom Prisma Fit scanner using a 32-channel head coil. Whole-brain anatomical images were acquired with a single-shot interleaved multi-slice T1-weighted structural scan (3D MEMPRAGE, Sagittal Slices = 176, Slice Thickness = 1 mm, Voxel Size = 1 mm^3, Field of View [FOV] = 256 mm, TR = 2530ms, TE1 = 1.69ms, TE2 = 3.55ms, TE3 = 5.41ms, TE4 = 7.27ms, TI = 1100ms, Flip Angle = 7°, Base Resolution = 256, Echo Spacing = 9.8ms, Bandwidths 1-4 = 650

Hz/Px, Averages = 1, Concatenations = 1). Functional images were acquired using an interleaved multi-slice EPI sequence (Coronal Slices = 69, Thickness = 2mm, Voxel Size = 2 mm^3, FOV = 208 mm, TR = 1500ms, TE = 28ms, Flip Angle = 75°, Base Resolution = 104, Bandwidth = 1718 Hz/PZ, Echo Spacing = .67ms).

1.5.2 Preprocessing

All fMRI data were preprocessed and analyzed using SPM12 (Wellcome Department of Cognitive Neurology, London, UK) via MATLAB version R2017a (The Mathworks Inc.). Structural and functional images were aligned to the anterior commissure. Functional scans were realigned using a least squares approach and 6 parameter rigid body spatial transformation, and motion information was used for unwarping, with all images set to match the mean image. Images were then co-registered to the structural scan. Finally, images were normalized to the MNI template (written at 2mm voxels) using a two-step process that first segmented and normalized the structural scans and then applied those normalization parameters to the functional images. Functional images were smoothed with a full-width at half-maximum 4mm^3 Gaussian kernel. Participants were excluded if their linear motion parameters (x, y, z) or rotational motion parameters (pitch, roll, yaw) extended beyond 5mm or 3 degrees respectively.

1.5.3 Encoding-Related Activity

For each participant, a general linear model (GLM) was created using encoding data concatenated across the 5 scanning runs. The GLM contained 6 event regressors of interest (negative subsequent hits, negative subsequent misses, neutral subsequent hits,

neutral subsequent misses, positive subsequent hits and positive subsequent misses) and 7 regressors of no interest (6 motion regressors: x, y, z, pitch, roll, yaw, and a linear drift regressor). Events were modeled with a 3 s boxcar function beginning at each stimulus onset. Contrast analyses then compared each task-related regressor of interest to baseline activity. At the second level, t-contrasts (event>baseline) for each emotion category and memory combination were inclusively masked with bilateral amygdala, hippocampal or functional localizer-defined visual or auditory processing region masks (additional details about region-of-interest definition detailed below). Region-of-interest (ROI) selection for the present study was based on prior work demonstrating that successful retrieval of emotional memories is supported by enhanced encoding-related activity in the medial temporal lobe as well as stimulus modality-specific sensory processing regions (Dahlgren et al., 2020; Murty et al., 2010). Parameter estimates for each masked contrast were then extracted for each participant.

1.5.4 Region-of-Interest Definition

Bilateral amygdala and hippocampal ROIs were drawn from a maximum probability atlas of the human brain (Hammers et al., 2003; see **Figure 5**) To define visual and auditory processing ROIs, the functional localizer scan was analyzed in a blocked design, with each visual and auditory block modeled with a 21-second boxcar function. The associated blood-oxygen-level-dependent (BOLD) response was modeled via convolution with a canonical hemodynamic response function yielding regressors in a GLM that modeled the BOLD response for each block. Two contrasts were modeled: sound > picture blocks (i.e., visual processing region activity) and picture > sound blocks

(i.e., auditory processing region activity). To conform with the analysis approach used in recent study using data from the current study (Thakral et al., 2022), visual and auditory processing region masks were thresholded at $p < 0.005$ with a cluster extent threshold of 28 voxels to yield a threshold corrected for multiple comparisons of $p < 0.05$ (Slotnick, 2017; Slotnick & Schacter, 2004).

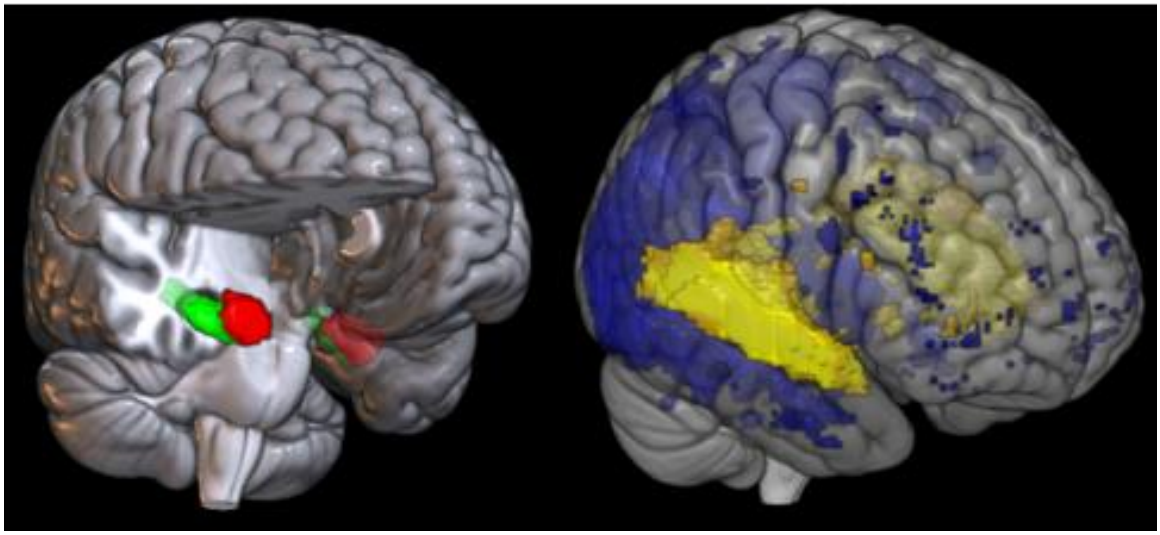

Figure 5. Medial Temporal Lobe and Functional Localizer Defined Regions-of-Interest. Left, amygdala (red) and hippocampal (green) regions-of-interest (ROIs) drawn from a maximum probability map of the human brain (Hammers et al., 2003). Right, visual (blue) and auditory (yellow) processing ROIs based on results of the functional localization. Images were created using MRIcroGL (nitrc.org/projects/mricrogl).

1.6 STATISTICAL ANALYSIS

Emotion category-specific memory performance (d') and memory vividness was determined using analysis of variance (ANOVA) with the factor Emotion (negative, neutral and positive). Emotion category-specific subsequent memory effects for

emotional intensity ratings, HRD and fMRI activity (amygdala, hippocampus and visual and auditory processing regions) at encoding were determined with an Emotion x Memory (subsequently remembered and subsequently forgotten) ANOVA. Moderating effects of nap physiology (i.e., REM mins/%, SWS mins/%, TST mins, REM theta power, NREM delta power, NREM spindle density and NREM coupling number) on subsequent memory was determined using separate Emotion x Memory analysis of covariance (ANCOVA) for each nap physiology variable. Simple correlations between encoding-related variables and sleep on emotion category-specific d' and memory vividness were conducted using Spearman's Rho. Finally, the interactive effects of encoding-related variables and sleep on emotion category-specific d' and memory vividness was assessed using multiple regression models. Values exceeding 2 standard deviations from the mean were excluded from analyses on a pairwise basis. ANOVA and ANCOVA models were Greenhouse-Geisser corrected and post-hoc tests were corrected using the Tukey method. Within-subject correlation coefficients were compared using Meng's Z and exploratory correlations were Bonferroni-corrected.

2.0 RESULTS

2.1 Emotion Category-Related Differences in Psychological and Physiological Measures at Encoding

The results of this analysis are summarized in **Table 2**. Emotion Category main effects were observed in ANOVA models for emotional intensity ratings, $F(1.75, 57.76) = 158.02$, $p < .001$, $\eta 2p = .827$, heart rate deceleration responses, $F(1.81, 52.57) = 9.00$, $p < .001$, $\eta 2p = .237$, amygdala reactivity, $F(1.97, 51.23) = 7.94$, $p = .001$, $\eta 2p = .234$, and functional localizer-defined visual, $F(1.89, 58.68) = 4.72$, $p = .014$, $\eta 2p = .132$, and auditory, $F(1.82, 56.42) = 20.18$, $p < .001$, $\eta 2p = .394$, processing regions, but not in the hippocampus, $F(1.99, 53.65) = .931$, $p = .40$, $\eta 2p = .033$. Negative stimuli, relative to neutral stimuli, were rated as more emotionally intense, $t(33) = 17.48$, $p_{Tukey} < .001$, $d = 3.065$, produced larger HRD responses, $t(29) = 4.93$, $p_{Tukey} < .001$, $d = .925$, and evoked greater encoding-related functional brain activity in the amygdala, $t(26) = 4.23$, $p < .001$, $d = .842$, and visual, $t(31) = 2.78$, $p_{Tukey} = .024$, $d = .491$, and auditory, $t(31) = 5.84$, $p < .001$, $d = 1.03$, processing regions. Positive stimuli, relative to neutral stimuli, were rated as more emotionally intense, $t(33) = -14.70$, $p_{Tukey} < .001$, $d = 2.592$, and evoked stronger encoding-related functional brain activity in auditory processing regions, $t(31) = -4.45$, $p < .001$, $d = .816$. However, positive and neutral stimuli produced similar HRD responses, $t(29) = -2.07$, $p_{Tukey} = .114$, $d = .347$, and encoding-related functional brain activity in the amygdala, $t(26) = -2.23$, $p = .085$, $d = .500$, and visual processing regions, $t(31) = 1.95$, $p_{Tukey} = .142$, $d = 3.74$. Negative stimuli, relative to positive stimuli, were rated as more

emotionally intense, $t(33) = 4.48$, $p_{Tukey} < .001$, $d = .719$. However, negative and positive stimuli produced similar HRD responses, $t(29) = 1.91$, $p_{Tukey} = .154$, $d = .393$, and encoding-related functional brain activity in the amygdala, $t(26) = 1.62$, $p = .265$, $d = .332$, and visual, $t(31) = 1.17$, $p_{Tukey} = .480$, $d = .207$, and auditory, $t(31) = 1.05$, $p_{Tukey} = .553$, $d = .177$, processing regions.

Table 2. Emotion Category-Related Differences in Psychological and Physiological Measures at encoding

			Post-hoc comparisons		
		Emotion Main Effect?	Negative > Neutral	Positive > Neutral	Negative > Positive
Subjective	Emotional Intensity Ratings	Yes	**p < .001**	**p < .001**	**p < .001**
Objective	Heart Rate Deceleration Response	Yes	**p < .001**	p = .11	p = .15
	Amygdala Activity	Yes	**p < .001**	p = .09	p = .26
	Hippocampal Activity	No	p = .40	p = .69	p = .85
	Visual Processing Regions Activity	Yes	**p = .02**	p = .14	p = .48
	Auditory Processing Regions Activity	Yes	**p < .001**	**p < .001**	p = .55

2.2 Emotion Category-Related Differences in Memory Performance (d') and Vividness

An Emotion Category main effect was observed for memory performance (i.e., d'), $F(1.98, 75.30) = 3.52$, $p = .035$, $\eta 2p = .085$ (see **Figure 6)**. Positive stimuli were better remembered than negative stimuli, $t(38) = 2.56$, $p_{Tukey} = .038$, $d = .433$. However,

memory for negative, t(38) = 1.88, p_{Tukey} = .159, d = .301, and positive, t(38) = .590, p_{Tukey} = .827, d = .084, stimuli was similar to that of neutral stimuli. An Emotion Category main effect was also observed for memory vividness, F(1.67, 65.05) = 3.79, p = .035, η2p = .088 (see **Figure 6**). Negative, t(39) = 2.247, p_{Tukey} = .076, d = .388, and positive, t(39) = 2.224, p_{Tukey} = .08, d = .332, stimuli tended to be remembered more vividly than neutral items, though this difference was not statistically significant. Negative and positive stimuli were remembered with similar vividness, t(39) = .900, p_{Tukey} = .644, d = .142.

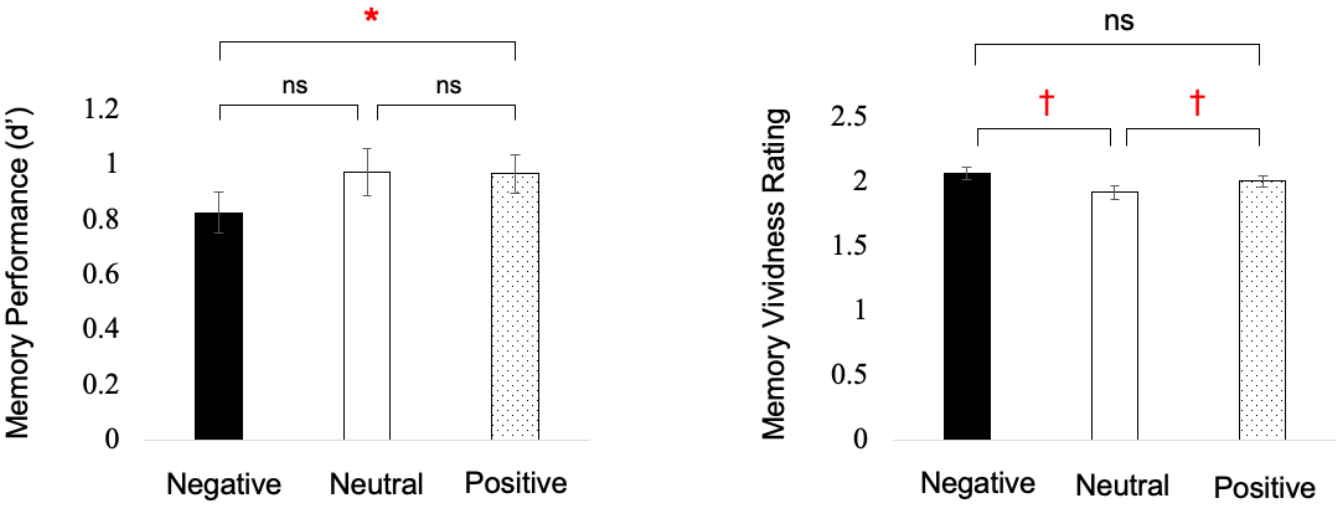

Figure 6. Memory Results. Left, emotion category-related differences in memory performance (d'); Right, emotion category-related differences in memory vividness. *, p < .05; †, p < .10; ns, non-significant.

2.3 Relationship Between Psychological and Physiological Measures at Encoding and Subsequent Memory

A main effect of Memory was observed for emotional intensity ratings, F(1.00, 33.00) = 22.77, p < .001 , η2p = .408, suggesting that subsequently remembered stimuli were rated as more emotionally intense at encoding than subsequently forgotten stimuli

(i.e., a subsequent memory effect). Although the Emotion x Memory interaction for emotional intensity ratings was not significant, $F(1.84, 60.57) = 2.56$, $p = .09$, $\eta 2p = .072$, multiple comparisons-corrected post-hoc tests revealed that the observed subsequent memory effect was significant for negative, $t(33) = 3.11$, $p_{Tukey} = .041$, $d = .438$, and positive, $t(33) = 3.90$, $p_{Tukey} = .005$, $d = .684$, but not neutral, $t(33) =$, $p_{Tukey} = .693$, $d = .235$, stimuli (see **Figure 7**). Emotional intensity ratings were not associated with memory performance for emotional (negative $r = -.218$, $p = .194$; positive $r = -.138$, $p = .414$) or neutral, $r = -.165$, $p = .314$, stimuli, but were correlated with memory vividness for positive, $r_s = .416$, $p = .01$, but not negative, $r = .063$, $p = .709$, or neutral, $r = .156$, $p = .337$, stimuli (see **Figure 7**).

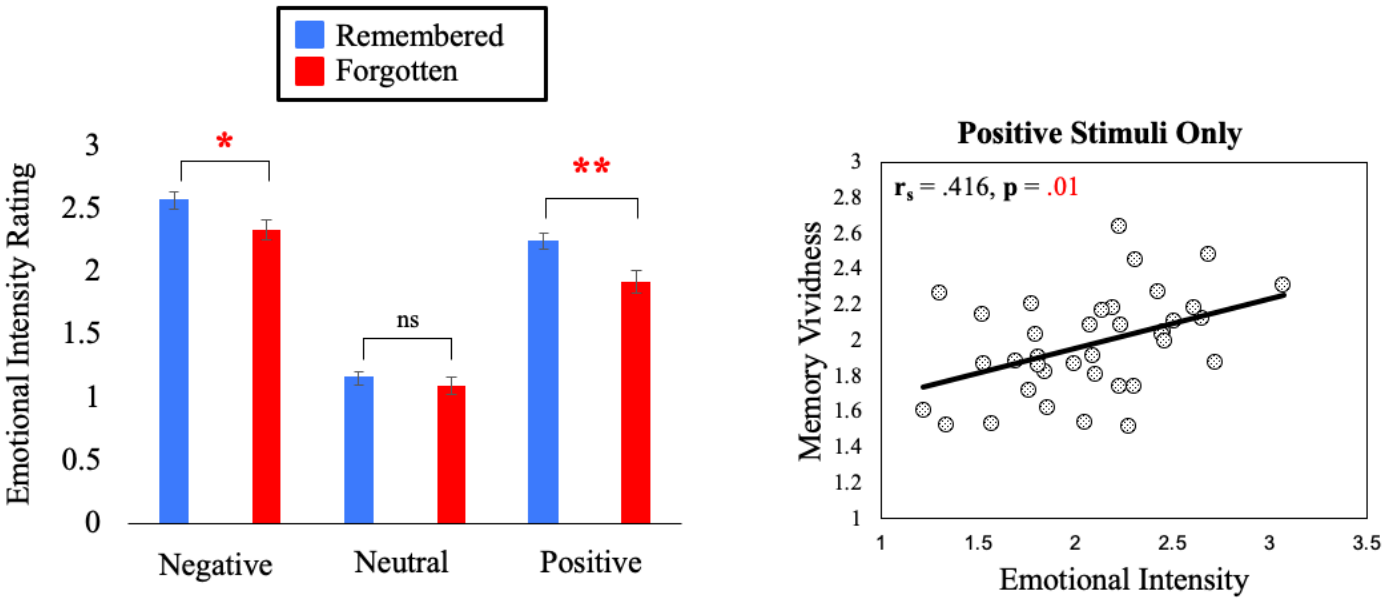

Figure 7. Effects of emotional intensity ratings at encoding on memory retrieval and vividness. Left, emotion category-specific emotional intensity rating subsequent memory effects. Right, emotional intensity ratings for positive stimuli predicted greater memory vividness for these stimuli. *p < .05, **p < .01

No main effect of Memory, $F(1, 29) = .412$, $p = .526$, $\eta 2p = .014$, or Emotion x Memory interaction, $F(1.99, 57.73) = .050$, $p = .951$, $\eta 2p = .002$, was observed for HRD responses. This suggests that HRD responses were similar for subsequently remembered and subsequently forgotten stimuli across each emotion category. However, HRD responses to negative stimuli were positively correlated with negative memory performance (d'), $r_s = .361$, $p = .043$. No other significant correlations between HRD and memory performance or vividness were observed (all ps > .07).

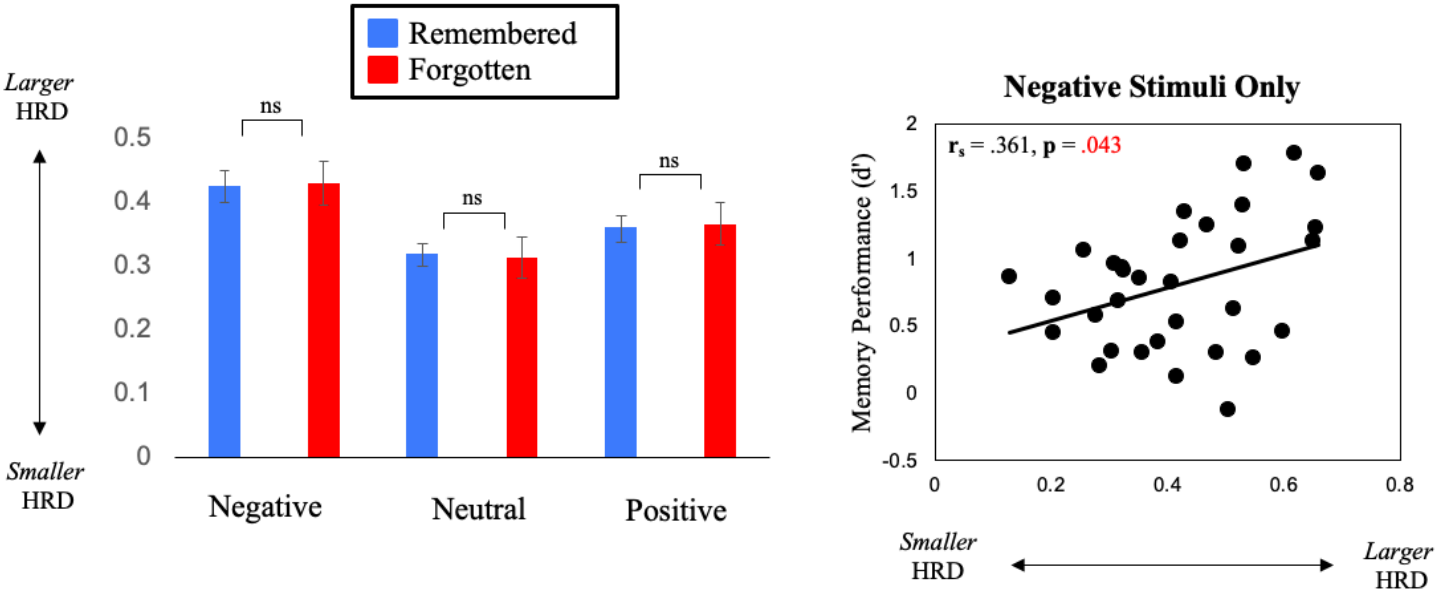

Figure 8. Effects of heart rate deceleration (HRD) responses at encoding on memory retrieval. Left, emotion category-specific heart rate deceleration (HRD) response subsequent memory effects. Right, greater HRD responses to negative stimuli predicted better memory performance for these stimuli.

No significant Memory main effects were observed for functional brain activity in any of the investigated regions (i.e., amygdala, hippocampus and visual and auditory processing regions), suggesting the activity levels were similar for subsequently remembered and subsequently forgotten stimuli (see **Table 3**). Similarly, no significant

Memory x Emotion interactions were observed for functional brain activity in the amygdala, hippocampus, or visual processing regions (see **Table 3**). However, a Memory x Emotion interaction was observed in auditory processing regions, driven by greater functional brain activity for neutral stimuli that were subsequently forgotten compared to those that were subsequently remembered, t(34) = -2.37, p = .023, d = -.401. Functional brain activity was similar for subsequently remembered and subsequently forgotten negative, t(34) = 1.13, p = .268, d = .190, and positive, t(34) = -.90, p = .374, d = -.152, stimuli. No significant correlations between encoding-related functional brain activity and memory performance (d') or vividness were observed (all *p*s > .05).

Table 3. Functional brain activity ANOVA results.

	Memory			Memory x Emotion		
	F	p	η2p	F	p	η2p
Amygdala	2.44	.13	.09	1.17	.32	.04
Hippocampus	.66	.42	.02	.31	.72	.01
Visual Processing Regions	3.07	.09	.09	.01	.99	< .001
Auditory Processing Regions	.30	.59	.01	4.26	.03	.12

Note. Significant values in red text for emphasis.

2.4 Direct and Indirect Roles of Nap Physiology on Memory

Nap composition is reported in **Table 4**. All participants slept during the nap opportunity and obtained stages N1, N2 and N3. Twelve participants did not obtain REM

sleep. Importantly, subjective sleep quality prior to encoding and sleepiness ratings during the study visit did not predict nap composition or memory performance (see **Appendix** for additional information). Therefore, the following analyses focused on the direct and moderating effects of nap physiology on memory.

Table 4. Nap composition.

	TST	N1 (mins)	N1 (%)	N2 (mins)	N2 (%)	N3 (mins)	N3 (%)	REM (mins)	REM (%)	Sleep latency mins	WASO mins	Sleep efficiency %
N	44	44	44	44	44	44	44	32	32	44	44	44
Mean (SD)	85.5 (27.2)	4.0 (3.1)	6.1 (6.6)	36.6 (15.7)	43.9 (15.4)	31.9 (15.9)	37.1 (15.1)	13.0 (12.5)	12.8 (11.7)	14.9 (8.83)	12.5 (13.7)	74.2 (17.5)
Min	19.5	1	0.9	9.0	18.4	2.0	7.0	0	0	5	1	23.8
Max	116	18.5	33	78.5	86.7	59.0	65.1	43.5	41.4	54	53	93.7

Note. TST, total sleep time; WASO, wake after sleep onset.

2.4.1 Direct Effects of Nap Physiology on Memory Performance and Vividness

Simple correlations revealed that REM theta power was significantly correlated with positive, $r_s = .40$, $p = .036$, but not negative, $r_s = .214$, $p = .273$, or neutral, $r_s = .334$, $p = .076$, memory performance (d'). REM sleep percentage was positively correlated with neutral, $r_s = .326$, $p = .043$, but not negative, $r_s = .192$, $p = .243$, or positive, $r_s = .222$, $p = .181$, memory vividness. However, the magnitude of these correlations did not differ by emotion category for REM theta power (negative-neutral: $z = -.95$, $p = .83$; positive-neutral: $z = .62$, $p = .27$; negative-positive: $z = -1.33$, $p = .91$) or REM sleep percentage (negative-neutral: $z = -.81$, $p = .79$; positive-neutral: $z = -.93$, $p = .82$; negative-positive: $z = -.22$, $p = .59$)

2.4.2 Nap Physiology as a Moderator of Subsequent Memory Effects

For emotional intensity ratings, Emotion x Memory x REM theta power, $F(1.98, 41.62) = 3.41$, $p = .043$, $\eta 2p = .140$, and Emotion x Memory x NREM spindle density, $F(1.84, 56.94) = 7.06$, $p = .002$, $\eta 2p = .186$, interactions were observed. The Emotion x Memory x REM theta power interaction was driven by a trending positive association between the magnitude of the emotional intensity subsequent memory effect (i.e., emotional intensity for remembered compared to forgotten stimuli) for positive stimuli and REM sleep theta power, $r_s = .368$, $p = .06$ (**Figure 9**). This suggests that retrieval was shifted toward positive stimuli rated as more emotionally intense at encoding in participants with higher amounts of REM sleep theta power. The Emotion x Memory x NREM spindle density interaction was driven by a significant positive association for neutral stimuli, $r_s = .555$, $p < .001$, and negative association for negative stimuli, $r_s = -.362$, $p = .029$, between the magnitude of the emotional intensity subsequent memory effect and NREM spindle density. This suggests that while retrieval was shifted toward neutral stimuli rated as more emotionally intense at encoding in participants with higher amounts of NREM spindle density, the opposite was true for negative stimuli (see **Figure 9**). No other nap physiology measures moderated emotional intensity subsequent memory effects (all *p*s > .05).

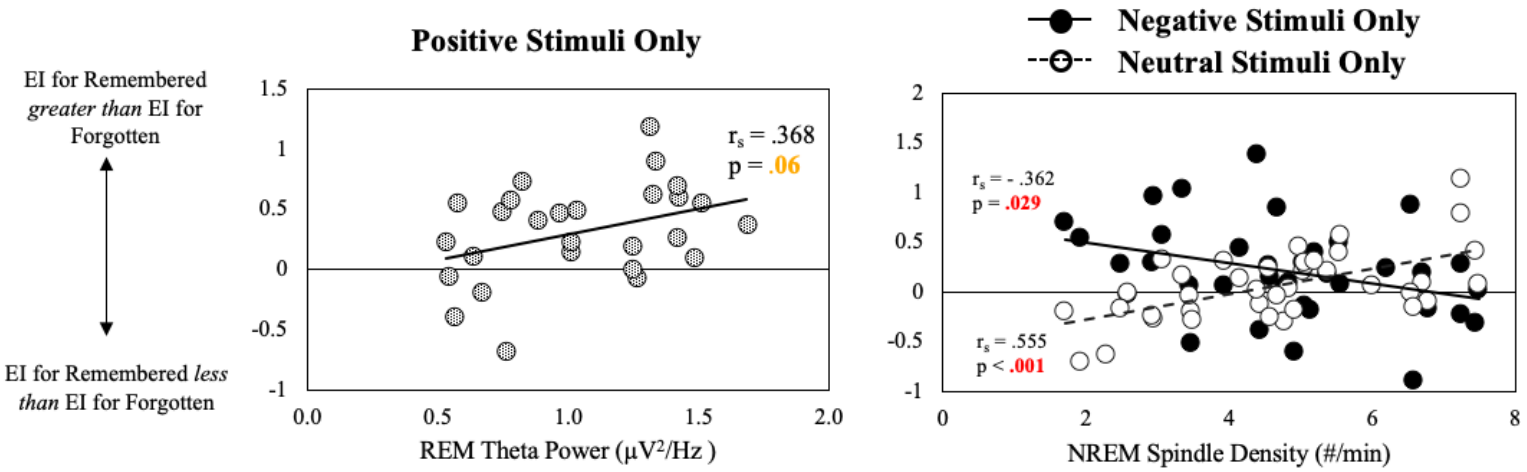

Figure 9. Moderating effects of nap physiology on emotional intensity (EI) subsequent memory effects**.** Left, greater emotional intensity subsequent memory effect for positive stimuli was associated with greater REM theta power. Right, NREM sleep spindle density was positively associated with an emotional intensity subsequent memory effect for neutral stimuli and negatively associated with an emotional intensity subsequent memory effect for negative stimuli.

Nap physiology did not moderate subsequent memory effects in HRD responses or functional brain activity in the hippocampus and visual or auditory processing regions (all ps > .05). However, a significant Memory x NREM spindle density interaction was observed for amygdala activity, $F(1,25) = 5.39$, $p = .029$, $\eta 2p = .177$. This interaction was driven by a negative, albeit non-significant, association between the magnitude of the amygdala subsequent memory effect and NREM spindle density, $r_s = -.342$, $p = .081$. This suggests that retrieval was shifted toward stimuli that evoked lower amygdala activity at encoding in participants with greater NREM spindle density. No other nap physiology measures moderated amygdala subsequent memory effects (all *p*s > .05).

2.4.3 Interactions Between Psychological and Physiological Measures at Encoding and Nap Physiology on Memory Performance and Vividness

Multiple regression models revealed that negative emotional intensity ratings at encoding and NREM sleep coupling number interacted significantly to predict negative memory vividness, B = -.014, t(31) = - 2.09, .045, η2p = .123. Simple slopes analysis revealed that the effect of negative emotional intensity on negative memory vividness was positive, but non-significant, with low numbers of NREM coupling events, B = .312, t(31) = 1.66, p = .108, and negative, but similarly non-significant, with high number of NREM coupling events, B = - .172, t(31) = -1.06, p = .297. The average effect of negative emotional intensity on negative memory vividness was non-significant, B = .070, t(31) = .53, p = .601. No other multiple regression analyses produced significant interactions between psychological and physiological measures at encoding and nap physiology on memory performance (d') or memory vividness (all *p*s > .05).

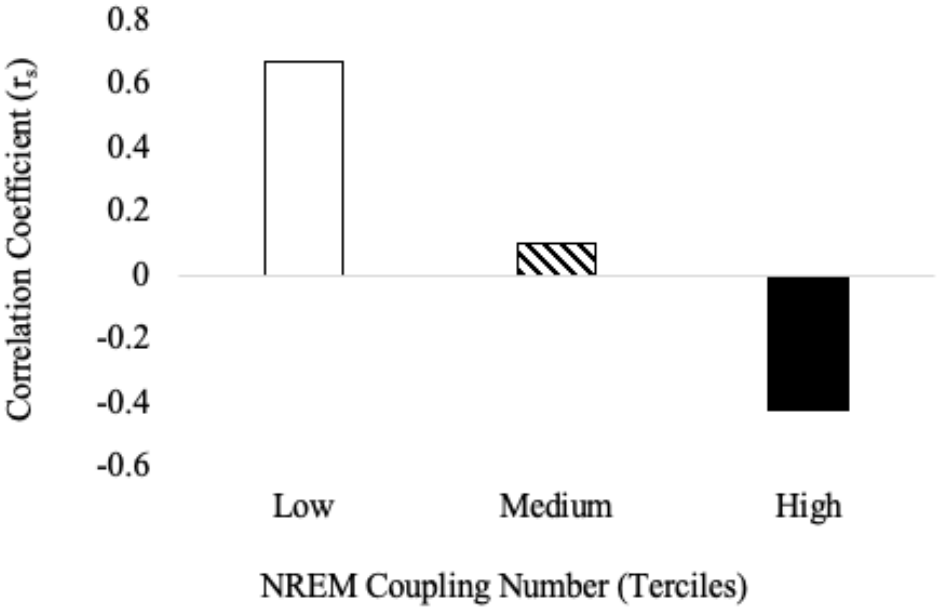

Figure 10. Interactive effect of subjective emotional intensity at encoding and NREM coupling on memory vividness for negative stimuli. The correlation coefficient (r_s) represents the correlation between average emotional intensity rating and average memory vividness for negative stimuli only.

3.0 DISCUSSION

3.1 BEHAVIORAL RESULTS

Previous work has shown that emotional memories tend to be remembered better than, and with more vividness than, neutral ones across short (Talmi, 2013) and longer (e.g. 24 hours and beyond; Yonelinas & Ritchey, 2015) retention delays. In the present study, I did not observe and emotional enhancement of memory effect (i.e., positive or negative stimuli being better remembered than neutral stimuli), though positive stimuli were better remembered than negative stimuli. This differs from two previous studies using similar neutral label-cued memory retrieval paradigms, with one showing no emotion category-related differences in picture memory performance (Ford et al., 2014) and the other showing an emotional enhancement for negative compared to positive and neutral scenes (Bowen & Kensinger, 2017). While it is not entirely clear why these behavioral differences existed between the current study and prior work, the design of the present study differed from these two prior studies by pairing audio clips with studied visual stimuli. It has been theorized that negative emotion narrows attention, while positive emotion broadens attention (Fredrickson, 2004) which, in turn, may potentially impact holistic encoding of a multimodal stimulus. Additionally, preliminary evidence suggests that visual-audio stimuli evoke stronger physiological reactivity (skin conductance, heart rate responses) compared to visual or auditory stimuli alone (Heffer et al., 2021). This prior work may suggest that, in the present study, holistic encoding of stimuli (i.e., equivalent allocation of cognitive resources to visual-auditory stimuli and paired neutral verbal labels) was uniquely

influenced by the stimuli's emotional category. Enhanced emotional reactivity by paired audio clips may have exaggerated attentional effects during encoding, narrowing attention to negative scenes at the expense of their paired neutral labels and broadening attention such that positive scenes and labels were strongly encoded. While this explanation is only speculative, it may explain why, in the present study, negative and positive stimuli were remembered with similar levels of vividness above that of neutral items; memories for key stimulus elements (i.e., picture-audio clip pairings) may have been similarly retained for negative and positive stimuli, but this effect may have been obscured by differences in the encoding and/or retention of the neutral verbal label. Future work can address this question in a number of ways. First, attention to picture stimuli relative to verbal labels could be measured using methods such as eye-tracking. Second, retrievability of picture-audio clip stimuli could be determined using recognition tests administered after memory retrieval test. Third, future studies could directly compare memory for visual-only, audio-only and visual-audio emotional and neutral stimuli. Finally, the duration of the retention interval (i.e., immediate recall vs. delayed recall with intervening sleep) likely influenced memory results, a point I will expand on in later sections.

3.2 DIRECT EFFECTS OF PSYCHOLOGICAL AND PHYSIOLOGICAL FACTORS AT ENCODING ON MEMORY

Prior work has linked successful memory retrieval to transient emotional reactions to stimuli during their encoding (e.g., greater subjective emotional arousal: Bradley et al., 1992; larger heart rate deceleration responses: Palomba et al., 1997; Buchanan et al., 2006;

Abercrombie et al., 2008; greater functional brain activity in limbic and sensory regions: Murty et al., 2010; Dahlgren et al., 2020). In the present study, emotional stimuli, and negative stimuli in particular, elicited greater autonomic responses and functional brain activity in regions associated with retention of emotional memories. However, with the exception of HRD responses positively predicting negative memory performance, and contrary to prior work, objective markers of emotional reactivity, including HRD responses and functional brain activity in limbic and sensory regions, had little predictive value with regard to which memories would be remembered and which would be forgotten. Instead, subjective rating of emotional intensity, a construct similar to arousal, was the strongest indicator of emotional memory retention. For example, emotional stimuli (both negative and positive), but not neutral stimuli, that were subsequently remembered were rated as more emotionally intense at encoding than stimuli that were subsequently forgotten. Greater emotional intensity also predicted memory vividness for positive stimuli. Though this finding was not completely surprising as stimuli rated as highly arousing have been shown to be retained better than non-emotional stimuli up to one year later (Bradley et al., 1992).

While it is not entirely clear why subjective, rather than objective, emotional reactions at encoding were more diagnostic of memory recall, one factor may be the retention delay used in the present study. Literature supporting memory enhancing effects of HRD responses and limbic and sensory functional brain activity at encoding have tended to test memory either immediately after encoding (Palomba et al.., 1997; Buchanan et al., 2006) or after delays of 24 hours or longer (e.g., Abercrombie et al., 2008; Ritchey et al., 2008; Payne and Kensinger, 2011). It may be that intermediate delays, such as the one used

in the present study, are a grey area between the immediate boost emotion-related cognitive factors exert on memory (Talmi, 2013) and downstream consolidation processes that require days, weeks, or even years (Dudai, 2012), to be fully expressed. Despite intervening sleep in the present study, which will be discussed in the next section, it may be that enhancement of the arousal system during encoding did not have sufficient time to act on the circuits critical for the selective enhancement of emotional memory. While this remains speculative, it will be important for future work to test whether systematically varying retention delays within a 24-hour period alters the relationship between objective markers of arousal at encoding and subsequent patterns of memory performance.

3.3 INTERACTIONS BETWEEN ENCODING FACTORS AND NAP PHYSIOLOGY ON MEMORY

Most studies of sleep and emotional memory have focused on how normative valence and arousal ratings (e.g., Bennion et al., 2016; Cellini et al., 2016; Kaestner et al., 2013; Sawangjit et al., 2013) or elevated baseline stress physiology (e.g., Bennion et al., 2015; Kim et al., 2019; Denis et al., 2021) impact the sleep-dependent strengthening of emotional over neutral memories. Few have explored how transient emotional reactions elicited by study stimuli interact with later sleep to influence memory outcomes, instead focusing on how such transient responses are enhanced or attenuated after sleep (e.g., Ashton et al., 2019; Bolinger et al., 2019; Cox et al., 2018; Jones & Spencer, 2019; Zeng et al., 2021). Only one study to date (Cunningham et al., 2014) has examined the interaction between transient emotional responses to emotional and neutral stimuli at

encoding and post-encoding sleep. In this study, participants encoded negative and neutral objects displayed on neutral backgrounds with event-rated heart rate and skin conductance recordings. The authors found that better recognition memory for negative objects was predicted by greater heart rate deceleration and skin conductance responses only for those who slept after encoding, but not for those who remained awake. However, sleep physiology was not measured, thus which sleep stage or stage-specific oscillations moderated the observed effects remain unknown.

Thus, the present study was the first to examine the interactive effects of individual differences in sleep physiology and transient subjective (i.e., emotional intensity ratings) and objective (HRD response and fMRI activity) markers of emotion-enhanced encoding on subsequent memory performance and memory vividness. My findings suggest that increased REM sleep theta power achieved during the nap shifted memory retrieval toward positive stimuli perceived as more emotionally intense during encoding. Greater NREM spindle density had opposite effects on neutral and negative memory retention, shifting retention toward higher arousing neutral stimuli and toward lower arousing negative stimuli. Increased NREM spindle-slow oscillation coupling number also moderated the association between perceived emotional intensity and memory vividness for negative stimuli. At low levels of coupling, the relationship between emotional intensity and memory vividness was positive, while at high coupling levels this relationship was negative.

Prior work has suggested that REM sleep theta power selectively enhances memory for positive stimuli when participants originally learned these stimuli along with negative and neutral stimuli (Kim et al., 2019). In healthy controls, REM sleep theta also

predicts the retention of adaptive extinction memories over maladaptive fear memories (Bottary et al., 2020; Pace-Schott et al., 2014) and is greater in trauma-exposed individuals resilient to PTSD compared to those with PTSD (Cowdin et al., 2014). REM sleep theta activity may, therefore, facilitate adaptive emotion regulation processes, such as selectively favoring the retention of highly positive memories as was observed in the present study. This interpretation is preliminary as other nap (Cellini et al., 2016) and overnight sleep (Ackermann et al., 2015) studies have not observed a relationship between REM sleep theta activity and retention of positive memories. However, the number of studies investigating this association is very small and none have taken encoding-related reactivity into account. Therefore, the preliminary finding reported here may be a starting point for future investigations aiming to determine whether REM sleep theta may uniquely favor the replay and consolidation of salient positive memories.

NREM spindle activity may selectively strengthen weakly encoded memories (Denis, Mylonas, et al., 2021; Schapiro et al., 2017). For example, Denis, Mylonas, et al. (2021) found that memory for word-pairs presented only a single time, compared to those presented multiple times, was positively associated with sleep spindle density across a post-learning nap. Analogously, I found that NREM sleep spindle density supported a shift in retrieval toward more emotionally intense neutral stimuli (which showed overall signs of weaker encoding compared to emotional stimuli based on subjective and objective encoding-related measures of emotional reactivity) and less emotionally intense negative stimuli. It is not entirely clear why sleep may benefit more weakly encoded memories, but some have used findings from fast-tracking studies (e.g., Brodt et al., 2018; Himmer et al., 2019), in which hippocampal independence and cortical

representations of memory traces are established under conditions of repetitive encoding, as evidence that some memories may surpass an encoding threshold in which additional sleep-dependent processes are not necessary (e.g., Denis, Mylonas et al., 2021).

Sleep has been hypothesized to depotentiate the affective charge of emotional memories (van der Helm & Walker, 2009), though findings remain somewhat mixed with some showing sleep-dependent *depotentiation* (Hutchison et al., 2021; van der Helm et al., 2011; Wassing et al., 2019; Werner et al., 2021; Yoo et al., 2007) and others showing sleep-dependent *potentiation* (Ashton et al., 2019; Baran et al., 2012; Groch et al., 2013; Jones & Spencer, 2019; Lara-Carrasco et al., 2009; Wagner et al., 2002). Though sleep-dependent emotional memory depotentiation was originally believed to rely on REM sleep-related processes, recent work has highlighted the importance of NREM sleep for regulating physiological reactions to aversive memories (e.g., Hauner et al., 2013; He et al., 2015). Further, NREM sleep spindle and slow oscillation dynamics, typically linked to memory enhancement, have recently been shown to promote the *forgetting* of emotional memories encoded under conditions of high baseline stress (Denis et al., 2021). These findings may support an alternative explanation for the moderation of emotional intensity subsequent memory effects for negative stimuli by NREM sleep spindle density observed in the present study; namely that greater NREM sleep spindle density promoted the *forgetting* of highly emotionally intense negative stimuli. Further, the prior work mentioned above somewhat aligns with my finding that participants obtaining a high number of spindle-slow oscillation coupling events exhibited a strong negative association between the perceived emotional intensity of negative stimuli during encoding and the vividness in which they were subsequently remembered. The

diminishment of recall vividness for highly emotionally intense negative stimuli across sleep observed in the present study may be analogous to the weakening or "depotentiation" of highly emotional memories across sleep observed in prior studies. The degree to which memories are vividly recalled has been tied to their emotionality with emotional memories tending to be remembered more vividly than neutral ones (Kensinger & Schacter, 2008; Phelps & Sharot, 2008). Further, autobiographical memory research supports a correspondence between subjective arousal at the time of memory retrieval and subjective memory vividness (Ford et al., 2012) and disturbed sleep may result in less specific details for episodic memories that are recalled (Barry et al., 2019; Thomas et al., 2021; Witkowski et al., 2021). Yet, beyond the findings from the present study and those mentioned above, it remains unknown how sleep impacts memory quality, including memory vividness. Future work including measures of emotional arousal at the time of retrieval and memory vividness could clarify more nuanced effects of sleep on the processing of emotional memories.

Finally, it was interesting that no objective markers of emotional encoding (e.g., HRD or functional brain activity) interacted with nap physiology to predict memory performance. This conflicts with current theories positing that selective emotional memory consolidation occurs as the result of the interaction between objective markers of encoding-related arousal, such as increased autonomic reactivity, elevated levels of arousal neuromodulators, or functional brain activity in emotion networks, and post-encoding sleep oscillation dynamics (e.g., Payne and Kensinger, 2018; Kim and Payne, 2020). However, as mentioned above, the retention delay, as well as the amount of sleep participants obtained in the present study, may have been insufficient to support the

consolidation processes described in current theoretical accounts of sleep-dependent emotional memory consolidation. For example, REM sleep has been implicated in the preferential consolidation of memories tagged by emotion, yet roughly one-quarter of our sample did not obtain REM sleep and the average time spent in REM sleep for those who did achieve it was 13 minutes. While at least one prior nap study linked REM sleep, and REM sleep theta power specifically, to emotional memory retention (Nishida et al., 2009), measures suggestive of memory tagging were not collected and thus it is unclear if the observed effect was mediated by tagging-related mechanisms. Additional limitations and suggestions for future work are detailed below.

3.4 LIMITATIONS

The following limitations are important to consider when interpreting the current set of findings. First, owing to the absence of a wake control group, I was unable to assess the global effect sleep may have had on memory performance or vividness compared to continued wake. Recent meta-analytic evidence has not supported a benefit of sleep compared to continued wake for the selective consolidation of emotional over neutral memories (Lipinska et al., 2019; Schäfer et al., 2020). Future work is necessary do determine whether encoding-related indicators of memory tagging may, in fact, be diagnostic of memory retention benefits across a retention interval with sleep compared to one without sleep. It may be that while specific sleep stages or stage specific oscillations boost memory for tagged memories, other, more nuanced interactions during the global sleep state benefit consolidation compared to wake.

As mentioned above, the choice of a nap compared to overnight sleep may have reduced the magnitude of the observed effects or obscured others. While studies using basic perceptual (Mednick et al., 2003) or procedural (Sugawara et al., 2018) memory tasks have shown similar memory benefits across short daytime naps and overnight sleep, naps tend to be deficient in REM sleep, a stage theorized to be critical for selective strengthening of emotional memories (Hutchison & Rathore, 2015; Kim & Payne, 2020). Indeed, about one-quarter of our sample did not achieve REM sleep, while those who did obtained, on average, 13 mins of REM sleep. While, under the circumstances of a highly powered study, REM disparities might offer a chance to explore the causal nature of REM in emotional memory consolidation, the present study did not include a sample size sufficient enough to do this. While meta-analytic evidence suggests that naps and overnight sleep confer similar benefits to emotional memory retention (Lipinska et al., 2019; Schäfer et al., 2020), these memory benefits have been linked to different sleep stages and stage-specific oscillations across naps and overnight sleep (e.g., Alger et al., 2018; Bottary et al., 2020; Marshall et al., 2014; Payne et al., 2012, 2015). If tagged memories require longer periods of time or sleep to be consolidated, perhaps additional effects are being masked in the present study by using a relatively short interval of sleep.

The present study employed a neutral cue-based memory retrieval test, similar to that used in prior work from our lab (e.g., Ford et al., 2014; Bowen and Kensinger, 2017), including a novel multisensory component during encoding. The choice of a memory retrieval test with neutral cues was made to minimize the influence of online emotion processing which can (1) inflate the rate of vivid false alarm rates (i.e., vividly "remembering" a stimulus that was not previously encoded), specifically for emotional

stimuli (e.g., Phelps and Sharot, 2008) and (2) obscure the effect of emotion on encoding-retrieval overlap of functional brain activity, an ancillary aim of the present study (data not present here). Recent meta-analytic evidence also suggests that recall-based tests tend to show stronger emotional memory effects across sleep (Lipinska et al., 2019). Further, the multisensory component of the task aimed to increase its ecological validity and provide an opportunity to study multisensory integration processes in functional brain activity (see Thakral et al., 2022). This task differs from a majority of sleep and emotional memory studies to date, which have probed retrieval using recognition memory tests (see Schäfer et al., 2020 for comprehensive list of studies) and used visual stimuli only (though see Tempesta et al., 2017). While the design of the present study was by no means a weakness, it makes comparing my results to others in the field difficult. However, I believe that this task design may offer a model of how to improve the ecological validity and translational relevance of sleep and emotional memory tasks in the future.

The present study focused only on encoding-related functional brain activity, thus leaving the possibility open that sleep might influence other interesting brain processes at retrieval as the result of encoding-strength. For example, work from our lab has shown that vivid remembering of negative memories is supported by the reinstatement of encoding-related functional brain activity at retrieval (i.e., "Recapitulation"; Bowen et al., 2018; Bowen & Kensinger, 2017; Kark & Kensinger, 2015, 2019a). This effect has been observed across delays of up to 24 hours (Kark & Kensinger, 2019a), a period which necessarily includes some amount of sleep. Future explorations of sleep's moderating effect on recapitulation may help to support claims that sleep strengthens encoding-

related functional brain activity in, or connections between, nodes in an emotional memory network (Kim and Payne, 2021).

Finally, while the sample size in the present study was similar to, or exceeded, fMRI studies to date exploring the relationship between sleep and emotional memory, it may have lacked sufficient statistical power to identify subtle behavior-autonomic-brain interactions or overestimated some effects. However, statistical power generally remains problematic in psychology and neuroscience, often resulting in poor replicability (Button et al., 2013; Ioannidis, 2005). This problem has been highlighted by recent meta-analyses (e.g., Lipinska et al., 2019; Schäfer et al., 2020; Schenker et al., 2021) and large-scale studies (e.g., Ackermann et al., 2015) that have challenged several axioms of the sleep and emotional memory field. While this problem is multifactorial, and often outside of the researcher's direct control, future efforts to increase statistical power without drastically increasing experimenter burden is a critical step forward. For example, increased use of open science platforms (e.g., McKiernan et al., 2016; Open Science Framework, osf.io) may allow for easier data sharing and increased sample sizes without additional resource burden. Increased use of "crowdworker" sites like Prolific (prolific.co) and Amazon's Mechanical Turk (mturk.com) or other mechanisms of remote data collection such as ambulatory physiology monitoring and smart-phone applications (e.g., Hinrichs et al., 2017) may reduce participant burden and study costs. While, at this time, protocols have not uniformly adapted to this style of "remote research", thus potentially limiting experimental control, advances in remote work technology will likely make this style of research more feasible and thus more rigorous and widely adopted in the near future.

4.0 CONCLUSION

The present study provided preliminary support for a moderating role of REM sleep theta power on the promotion of positive memories perceived as more emotionally intense during encoding. NREM oscillations and oscillatory dynamics had divergent roles for neutral and negative memories. Greater NREM spindle density increased the retention of emotionally intense neutral memories while also promoting the forgetting of emotionally intense negative memories. High numbers of NREM spindle-slow oscillation coupling events resulted in a negative relationship between perceived emotional intensity of negative memories at encoding and the vividness with which they were subsequently recalled, potentially suggesting these coupled events depotentiated the emotional charge of these highly arousing negative memories. Evidence of sleep-dependent strengthening of memories "tagged" by objective measures of emotion at encoding was not observed. The absence of such effects may have been attributable to a retention interval employed in the current study that was insufficient to promote downstream processes implicated in consolidation-based theories of memory tagging. Future work, that will include wake controls, varied retention intervals, and larger sample sizes, is needed to expand on the present set of findings and/or identify additional, and perhaps nuanced, brain-based mechanisms subtending them.

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6.0 APPENDIX

6.1 STIMULUS CHARACTERISTICS

Low-level stimulus characteristics as well as distinctness of emotional compared to neutral stimuli may be confounding factors in the study of emotions effects on memory (Talmi et al., 2013). Because of this, I ran a set of control analyses to rule these factors out as potential confounds.

First, to control for low-level visual confounds, average image saliency was calculated for each picture using the Saliency Toolbox (Itti and Koch, 2001) in MATLAB. A one-way ANOVA revealed no main effect of Emotion on average image salience, $F(2,293) = 1.24$, $p = .290$, $\eta^2 = .008$. Next, for each audio clip, I calculated the root-mean-square (RMS; a measure of loudness) using the *rms* function in MATLAB and extracted the peak frequency (Hz) and frequency range (Hz) using the plot spectrum function in Audacity (audacityteam.org). A one-way ANOVA for RMS revealed a main effect of Emotion, $F(2,297) = 5.20$, $p = .006$, $\eta^2 = .034$, which was driven by greater RMS for negative compared to neutral audio clips, $t(297) = 3.22$, $p_{tukey} = .004$. However, no main effect of Emotion was observed in peak frequency, $F(2,297) = .132$, $p = .877$, $\eta^2 = .001$, or frequency range, $F(2, 297) = .217$, $p = .805$, $\eta^2 = .001$, ANOVAs.

Next, I calculated stimulus "memorability" for each stimulus as the percentage of participants who successfully remembered the stimulus during the memory retrieval test. A one-way ANOVA for memorability revealed a significant main effect of Emotion (i.e.,

negative, neutral or positive), $F(2, 297) = 3.14$, $p = 0.045$, though post-hoc tests revealed this was driven by a trending, but statistically non-significant enhancement of positive over negative stimuli, $t(297) = 2.345$, $p_{Tukey} = .051$, $d = .33$.

Finally, I explored whether low-level stimulus features (i.e., image salience, RMS, peak frequency and frequency range) were associated with stimulus memorability. Memorability was not correlated with image salience (ps > .40), RMS (ps > .09), or peak frequency (ps > .10) for any emotion category. RMS was positively associated with memorability for neutral stimuli, $r_s = .272$, $p = .006$. This association was significantly different from the association with negative stimuli, $r_s = -.114$, $p = .258$, $z = 2.74$, $p = .006$, but not positive stimuli, $r_s = .184$, $p = .067$, $z = .65$, $p = .516$.

Taken together, stimuli were statistically matched for memorability and generally well matched for low-level stimulus features. Importantly, the observed difference between negative and neutral stimuli for RMS and stronger association between memorability and RMS for neutral compared to negative stimuli did not appear to confer a noticeable memory benefit, as evidenced by the lack of a difference in memory performance between negative and neutral stimuli.

6.2 COLINEARITY BETWEEN EMOTIONAL INTENSITY RATINGS AND HEART RATE DECELERATION

Averaging across all stimuli within each emotion category, no significant relationship between emotional intensity and HRD for negative, $r_s = -.091$, $p = .619$,

neutral, r_s = .042, p = .819, or positive stimuli, r_s = -.015, p = .937, was observed. In a further analysis, correlation coefficients were obtained for each participant by correlating trial-level emotion intensity ratings and HRD for each emotion category. Exploring individual participant correlations, only three participants showed a significant correlation in the expected direction (i.e., a positive association between emotional intensity and the magnitude of the HRD response), while two showed significant correlations in the opposite direction (i.e., a negative association between emotional intensity and HRD) for negative stimuli. Two participants showed significant correlations in the expected direction, and 1 in the opposite direction, for neutral stimuli. No participants showed significant correlations in the expected direction, and 1 in the opposite direction, for positive stimuli. Finally, to test whether the degree of correlation between trial-level emotional intensity and HRD differed by emotion category, emotional intensity x HRD correlation coefficients were entered into an Emotion-Category repeated-measures ANOVA. I observed no significant main effect of emotion, F(1.96, 72.38) = .395, p = .67, η^2p = .011.

6.3 IMPACT OF BASELINE SLEEP QUALITY AND SLEEPINESS ON NAPS AND MEMORY

Questionnaires

Pittsburgh Sleep Quality Index (PSQI). The PSQI (Buysse et al., 1989) measures seven areas of sleep quality over the course of the past month: subjective sleep duration, sleep quality, sleep efficiency, sleep latency, use of sleep medications, sleep disturbances,

and daytime dysfunction. The survey is a mix of free response and multiple-choice questions, with all scores transformed into a 0-3 scale. A global score of 5 or less indicates good sleep quality, whereas a score greater than 5 indicates poor sleep quality.

Sleep Diary. The sleep diary is an in-house survey used to assess sleep behavior from the prior night in addition to subjective restedness, stress, and caffeine intake. The present analyses focused only on questions related to sleep duration (i.e., total sleep time) and quality (i.e., sleep latency, wake after sleep onset, and sleep efficiency).

Epworth Sleepiness Scale (ESS). The ESS is a questionnaire used to assess daytime sleepiness (Johns, 1991). Respondents are asked to rate their tendency to become sleepy in eight situations (e.g., when watching TV; when in a car, stopped at a traffic light) using a 4-point scale from 0 ("no chance of dozing") to 3 ("high chance of dozing"). Total scores can range from 0-24, with scores greater than 9 suggest a moderate to high level of daytime sleepiness.

Stanford Sleepiness Scale (SSS). The SSS (Hoddes et al., 1972) is used to measure how alert respondents presently feel using a 7-point scale from 1 ("Feeling active, vital, alert, or wide awake") to 7 ("No longer fighting sleep, sleep onset soon; having dream-like thoughts"). Ratings greater than 4 may suggest that the respondent is experiencing some degree of sleep loss.

Statistical Analysis. Simple correlations between sleep questionnaires and nap physiology variables (i.e., TST, N3 mins and %, REM mins and %, REM theta power, NREM delta power, NREM spindle density and NREM coupling amount) and memory scores (i.e., d' and memory vividness) were conducted using Spearman's Rho.

Results. One significant correlation was observed between ESS score and TST, r_s =.33, p = .036. However, this did not reach the Bonferroni-corrected alpha level (corrected alpha = .001). All other correlations were non-significant (ps > .05).

6.4 APPENDIX REFERENCES

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