# What Drives the Pupil Old/New Effect?
# Recollection, Familiarity, and Memory Strength

By

Wen Jian
B.S., Boston College, 2022

Thesis

Submitted in partial fulfillment of the requirements for the
Degree of Master of Science
in the Department of Cognitive and Psychological Sciences at Brown University

PROVIDENCE, RHODE ISLAND

MAY 2026

This thesis by Wen Jian is accepted in its present form
by the Department of Cognitive and Psychological Sciences as satisfying the
thesis requirements for the degree of Master of Science

Date_____ _____

William Heindel, Advisor

Approved by the Graduate Council

Date_____ _____

David L. Lindstrom, Dean of the Graduate School

**Acknowledgements**

I would like to thank my advisors, Dr. William C. Heindel and Dr. Elena K. Festa, for their immense support and guidance throughout this journey. Without their dedication to research and mentorship, as well as their kindness and positivity, I would not have been able to grow as a researcher and as a person as much as I do today. I am also grateful to Dr. David Badre, the third committee member on this project, for his challenging questions and candid comments that have shaped the way I think and how I approach research. Lastly, I would like to acknowledge my family, my friends in and outside of the Brown community, and everyone in my department, for being a tremendously important part of my time here and beyond. I will continue to cherish the people and the valuable opportunities I am lucky enough to have as I adventure forward.

## Table of Contents

## List of Figures

## Abstract

*Abstract of "What Drives the Pupil Old/New Effect? Recollection, Familiarity, and Memory Strength," by Wen Jian, ScM., Brown University, May 2026.*

During recognition memory, previously studied ("old") items elicit greater pupil dilation than unstudied ("new") items, known as the pupil old/new effect. Traditionally, this effect is often thought to reflect memory trace strength. However, recent findings suggest it reflects the interaction between the retrieval cue and the stored trace, particularly the perceptual match (the "pupil match/no-match effect"). We conducted two experiments to investigate the roles of recollection and familiarity in these effects. In Experiment 1, words were encoded either through distributed (sporadic repetitions) or massed (immediate repetitions) learning. Distributed learning enhances contextual recollection and improves memory performance, while massed learning suppresses recollection and emphasizes familiarity. Pupil dilation varied based on the perceptual cue-trace match rather than the memory strength across conditions. Distributed learning yielded better accuracy and confidence than massed and single-trial learning. The pupil old/new effect was consistent across learning conditions. However, distributed learning showed a pronounced pupil match/no-match effect, while massed learning exhibited a reversed effect. Experiment 2 used a word-stem completion priming task to test if this reversed pattern reflected ease of processing due to familiarity. Successfully primed words, mediated by familiarity, elicited smaller pupil dilation, mirroring the reversed match/no-match effect seen with massed learning in Experiment 1. Overall, our results indicate that during recognition memory, pupil dilation reflects the interaction between the encoded trace and the retrieval cue, rather than memory strength alone. The amplified pupillary match effect for distributed learning suggests enhanced recollection, while the reversed effect for massed learning suggests reduced retrieval effort due to familiarity, akin to implicit priming effects.

## Introduction

Our pupils change sizes not only as a reflexive response to brightness but also as a sensitive indicator of our internal brain states. Pupil dilation has been associated with a variety of cognitive processes, including arousal, attention, cognitive effort, and memory (see Sirois & Brisson 2014, Sara 2015 for review). Strong empirical evidence has demonstrated a link between pupil dilation and the activity of the locus coeruleus norepinephrine (LC-NE) system, which modulates various cognitive functions by increasing the gain of neuronal circuits and reconfiguring functional network connectivity (Aston-Jones & Cohen 2005; Hermans et al. 2011; Joshi et al. 2016; Zerbi et al. 2019).

During tests of recognition memory, previously studied ("old") items have been found to elicit greater pupil dilation than unstudied ("new") items, a phenomenon known as the "pupil old/new effect" (Gardner et al. 1974; Otero et al. 2006; Võ et al. 2008). Despite extensive research over the decades, the underlying mechanism of this effect remains unclear. Võ et al. (2008) initially argued that the old/new effect reflects greater mental effort for recognizing an old item compared to rejecting a new item. However, this mental effort account could not explain several findings of greater pupil dilations for more confident or deeply processed memories, which should be associated with greater ease of retrieval (e.g., Otero et al. 2011; Kafkas & Montaldi 2015). A more strongly supported explanation is that this effect is driven by the strength of the underlying memory trace, with greater pupil dilation elicited by: a) deeply encoded items than shallowly encoded ones (Otero 2011); b) remembered items than known items (Kafkas & Montaldi 2015; Taikh & Bodner 2022); c) hits and false alarms than misses and correct rejections (Montefinese et al., 2013); d) higher than lower confidence ratings (Papesh et al. 2012; Naber et al. 2013); and e) recognition across shorter than longer study-test retention

intervals (Oliveira et al. 2021). Memory strength, defined as the accumulation of evidence of a memory trace (Wickelgren & Norman 1966), is often measured with memory performance (d' or accuracy) or subjective confidence ratings (Murdock & Dufty 1972).

Recently, however, some studies have suggested that the magnitude of old/new effect is not solely driven by memory strength but also by the degree of match between encoded memory trace and cue information presented at retrieval. Papesh and colleagues (2012) found that largest peak pupil diameters were elicited not only by strong memories (i.e., highest-confidence hits) but also by word stimuli with the closest encoding-retrieval voice matches. To further elucidate the effects of memory strength and cue-trace interactions on pupil dilation during recognition memory, Siefert et al. (2024, Experiment 1) asked participants to study words and pictures while engaging in either a shallow ("word or picture?") or deep ("organic or inorganic?") encoding condition, a manipulation of memory strength. During subsequent recognition, participants judged whether each word was "old" (i.e., presented either as a word or picture in study phase) or "new" (i.e., not studied in any format). The deep encoding group yielded higher memory accuracy (and presumably stronger memory traces) than the shallow group, but the magnitude of pupil old/new effect did not differ between the two groups, which was not predicted by the memory-strength account.

In contrast, the shallow encoding group exclusively showed greater pupil dilation for "match" items (i.e., presented as words in both study and test phases) than for "no-match" items (i.e., presented as pictures at study and words at test). This pupil dilation difference observed after shallow encoding is thereafter termed the "match/no-match effect". Siefert and colleagues (2024) argued that the shallow encoding condition enhances the encoding of perceptual details within the memory trace, which maximizes the difference between perceptual "match" versus

"no-match" cue-trace pairs, producing a large pupil match/no-match effect. The authors suggested that the lack of a pupil "match/no-match" effect in the deep encoding condition was due to the focus on the studied items' semantic features, which created similar cue-trace overlaps for the items encoded as words and pictures, thus minimizing the match/no-match difference at retrieval. Experiment 2 further showed that the magnitude of pupil dilation directly and additively reflected the number of studied contextual details subsequently recalled. Based on these findings, the authors proposed that the pupil old/new effect is not driven by memory strength alone, but rather by the synergistic interaction between the retrieval cue and the encoded trace.

Cue-trace interactions reflect a mechanism named "synergistic ecphory" by Tulving (1982), which is the process of extracting appropriate information from the retrieval cue and correlating it with stored trace information. A successful ecphory or cue-trace interaction produces ecphoric information, a conjunction of cue information and trace information, which supports memory retrieval (Tulving 1982). This account emphasizes that successful memory retrieval does not rely solely on the strength of memory trace, but on the joint product of trace and cue information that interacts with each other (Semon 1904; Tulving 1983). The same memory could be successfully retrieved with some cues, but not others, suggesting that the retrieval cue in relation to the memory trace plays an important role in the accessibility of memory trace and the subsequent retrieval success (Tulving & Pearlstone 1966).

Compelling evidence for the role of ecphory in memory shows that higher chance of successful memory retrieval is associated with higher correspondence of contextual information present at encoding and retrieval (Godden & Baddeley 1975; Nairne 2002; Dewhurst & Knott 2010; Goh & Lu 2012), reflecting the "encoding specificity" principle (Tulving & Thomson

1973). Retrieval performance and vividness also involve reinstatement of neural activity patterns observed during encoding (Ritchey et al. 2013; Yaffe et al. 2014; St-Laurent et al. 2015; Staudigl et al. 2015). Similarly, rodent studies have demonstrated that natural contextual cues or neurophysiological stimulation can reactivate the hippocampal neural ensembles active during encoding and trigger memory responses (Liu et al. 2012; Orsini et al. 2013; Frankland et al. 2019). Furthermore, evidence suggests that norepinephrine enhances attention to relevant contextual information during learning and that LC-NE activity plays an important role in memory consolidation and retrieval via its neuromodulatory projections to the neocortex and the hippocampus (Devagues and Sara, 1991; Lemon et al. 2009; Hansen & Manahan-Vaughan 2015; Sara 2015). Therefore, the pupil match/no-match effect may indicate that, during the synergistic interactions between cue and trace at retrieval, a greater degree of cue-trace match elicits greater pupil dilation reflecting increased LC-NE activity, which in turn facilitates contextual memory recall (Siefert et al. 2024).

A more recent study (Albi and Pajkossy, 2025) modified the second experiment of Siefert et al. (2024) and found that pupil dilation reflected contextual recollection in a graded fashion. By showing that pupil dilation during correct recognition linearly tracked the precision of source memory judgement, Albi and Pajkossy argued that the pupil old/new effect might originate from two sources: mere item recognition and strength of recollected contextual information. Within the latter source proposed, the authors integrated the memory strength account (e.g., Otero et al. 2011) and the ecphory account (Siefert et al. 2024) by associating higher memory precision with both greater memory strength and better contextual recollection. While there is certainly overlap between these two components, how they interact and differentially contribute to the pupil old/new effect remains unresolved. Indeed, pupil dilation is an aggregate signal of brain arousal

and may reflect multiple components involved in recognition (Mathot 2018; Kafka 2024), but teasing apart some of these components would be informative to understand the old/new effect.

Therefore, the first aim of this study was to further clarify the mechanism underlying the pupil old/new effect by manipulating memory strength and the ecphoric process against each other. To this end, Experiment 1 of the current study utilized two different patterns of repeated presentations during shallow encoding: distributed learning and massed learning (Greene 1989; Russo et al. 1998). These two kinds of repeated learning have been shown to create memory traces of different strengths and have qualitatively different impacts on the memory traces. Distributed learning refers to learning repeatedly with sporadic, or distributed, repetitions that are spaced by other stimuli. In contrast, massed learning refers to learning repeatedly with immediate, or massed, successions. Distributed learning robustly and consistently leads to better memory performance or stronger memory than massed learning, a phenomenon called the "spacing effect" (Ebbinghaus 1885; Cepeda et al. 2006).

Besides the difference in memory strength of the encoded traces, the two kinds of repetitions also have differential impacts on recollection and familiarity. According to the dual-process model of recognition memory (Atkinson & Juola 1973; Mandler 1980; Jacoby & Dallas 1981; Hintzman & Curran 1994), recollection is a relatively slow, conscious process consisting of retrieving contextual information pertaining to the studied stimulus, while familiarity is a fast, automatic process that allows one to make recognition judgements without retrieving any contextual details. Distributed learning tends to enhance contextual recollection via reactivating stored traces and encoding richer contextual details at each repetition; in contrast, massed learning highlights familiarity by minimizing recollection through repetition

suppression that limits episodic encoding (Bjork 1999; Wagner et al. 2000; Van Strien et al. 2007; Zhao et al. 2015; Feng et al. 2019).

Therefore, the different impacts of distributed learning and massed learning on memory traces may help us separate the effects of memory strength and contextual recollection on pupil activity. If pupil dilation during recognition is mainly driven by memory strength, then we would expect to see greater pupil dilation in the distributed learning condition than that in the massed condition, with the smallest pupil dilation following single-trial learning. If pupil dilation, particularly the match/no-match effect, reflects contextual recollection supported by cue-trace interaction, then we would expect a greater match/no-match effect in the distributed learning condition, in which encoding-related contextual reinstatement is enhanced, than that in the massed learning condition, where contextual recollection is diminished.

Despite ongoing debates about whether recollection and familiarity are distinct processes or not, as suggested by the single-process signal-detection model of recognition memory (Ratcliff et al. 1992; Wais et al. 2006; Wixted 2007; Squire et al. 2007), studies measuring event-related potentials (ERP) have shown independent neural patterns for recollection and familiarity (Düzel et al. 1997; Rugg & Curran 2007; Shimamura 2011; Kwon et al. 2023). Recollection is often associated with a late temporal-parietal positivity during recognition tests, while familiarity is linked to an early positive deflection in the frontal N400 range (Duzel et al. 1997; Rugg & Curran 2007; Shimamura 2011). Functional MRI (fMRI) studies have also identified distinct neural indices for these two memory components: recollection is typically associated with bilateral hippocampal and parahippocampal activation, whereas familiarity shows inconsistent activation in the perirhinal cortex, the left inferior temporal-occipital regions, or right lateral and medial frontal cortex (Henson et al. 1999; Yonelinas et al. 2001; Aggleton &

Brown 2006; Kafkas & Montaldi 2012). However, it remains unclear whether human pupillary responses can reflect these two memory components, despite a few investigations (Kafkas & Montaldi 2011, 2012; Brocher & Graf 2016; Taikh & Bodner 2022). For example, Kafkas and Montaldi (2011, 2012) showed larger pupil dilations and more dispersed fixation patterns for recollection than strength-matched familiarity using a modified remember/know paradigm. Other studies that used the remember/know paradigm to separate the two components found either no pupillary distinction (Brocher & Graf 2016) or attributed the pupillary effect to memory strength (Otero et al. 2011; Taikh & Bodner 2022). Manipulating distributed and massed learning may help dissociate the effects of recollection and familiarity on pupillary activity from a different route, which was the second aim of this study.

Interestingly, familiarity is closely related to priming given their overlapping behavioral and neural signatures. Priming is a form of implicit memory in which the processing of previously encountered stimuli is unconsciously altered or facilitated due to their prior occurrence (Schacter & Buckner 1998; Henson 2003). Although familiarity-based recognition has been well established as a conscious, explicit form of memory, other theories claim that familiarity can be supported by or co-occur with some implicit, automatic processes, including priming (Mandler 1980; Jacoby & Dallas 1981; Yonelinas 2002). Further, some research suggests that the ERP frontal N400 “familiarity effect” obtained in recognition tests could be “conflated” by priming due to their co-occurrence in those experimental designs (Paller et al. 2007; Stenberg et al. 2009; Voss et al. 2010; Lucas et al. 2012). Some fMRI studies also demonstrated that familiarity and priming have overlapping neural correlates in perirhinal cortex and parietal cortex (Wang et al. 2015; Thakral et al. 2016), although they may engage distinct cortical networks (Voss et al. 2008). However, neither priming itself nor its relation with

familiarity has been extensively studied with pupillometry, except for a few explorations. For example, amnesic patients showed decreased pupil dilation for seen but unrecognized items than new items (Laeng et al. 2007); repetition priming elicited smaller pupil dilation than an explicit change of color (Pomè et al. 2020); a "pupil priming" effect was defined as an increase in mean/peak pupil dilation for missed than correct rejections following perceptual encoding while the reversed pattern was found following conceptual encoding (Gomes et al. 2015). Therefore, the third aim of this study was to investigate the relationship between familiarity and priming through pupillary activity.

In Experiment 1 of this study, we employed distributed and massed learning to manipulate memory strength and degree of recollection. This approach was used to resolve the mechanism underlying the pupil old/new effect (aim 1) and dissociate the pupillary effects of recollection and familiarity (aim 2). We expected distributed learning to create stronger memory traces and facilitate contextual recollection by enhancing cue-trace interaction. Conversely, massed learning was anticipated to create weaker memory traces and exhibit a prominent familiarity effect. Additionally, a baseline single-trial learning condition was included to produce the weakest memory traces and replicate the shallow encoding results in Siefert et al. 2024. We hypothesized that the magnitude of pupil old/new effect will remain consistent across the three learning conditions, despite differences in memory strength. If the pupil old/new effect merely reflects memory strength, we would expect its magnitude to track memory strength, forming a linear relationship among distributed, massed, and single-trial learning. If the effect reflects cue-trace interaction, we would expect a greater pupil match/no-match effect in distributed learning due to the enhanced contextual reinstatement and recollection, and a reduced effect in massed learning due to diminished recollection and dominant familiarity effect. In Experiment 2,

we aimed to test whether the pupillary responses of the massed learning condition reflect a common processing-facilitating effect shared by familiarity and priming (aim 3), using an implicit repetition priming paradigm. Given the similarity of familiarity and priming, we expect to see similar pupillary response patterns for massed learning and repetition priming.

In summary, this study aims to investigate the following questions: 1) Does the pupil old/new effect, particularly the pupil match/no-match effect, reflect memory strength or cue-trace interaction during recognition memory? 2) Can pupillary response during recognition differentiate between recollection and familiarity? 3) Is there a pupillary effect for priming, and how does it relate to the pupillary effect for familiarity? We address these questions through two pupillometry experiments. Experiment 1 follows the shallow encoding recognition paradigm of Siefert et al. (2024), adding distributed and massed learning conditions. Experiment 2 adapts the word-stem completion priming task from Kane et al. (2015) to investigate the pupillary effect of repetition priming.

## Experiment 1: Pupil cue-trace match effect across differential shallow encoding conditions

Experiment 1 investigated how different patterns of repeated stimuli presentations at shallow encoding may impact the pupillary effect of cue-trace match during recognition. We predicted that single-trial presentations will replicate the shallow encoding results from Siefert et al. (2024). Additionally, we predicted that massed learning will increase memory strength but decrease the pupil match/no-match effect compared to single-trial learning, due to repetition suppression and diminished contextual encoding. In contrast, we expected that distributed learning will produce stronger memory traces than massed learning and show the largest match/no-match effect among the three conditions, due to richer contextual details encoded in the traces and enhanced recollection. If these predictions hold, this will support the argument that

the pupil match/no-match effect is driven by the cue-trace interaction. Alternatively, if the pupillary response is driven by memory strength alone, we would expect the magnitude of pupil old/new effect to track memory strengths across the three repetition conditions.

## ***Methods***

### *Participants*

We conducted power analysis using G*Power 3.1 (Faul et al. 2019) to estimate the appropriate sample size. Several previous pupillometry studies reported large (d=0.80, Võ et al. 2008), medium (d=0.47, Otero et al. 2011), and small (d=0.28, Kafkas & Montaldi 2015) pupil old/new effects. One study reported a medium pupil match/no-match effect size (dz=0.46, Siefert et al. 2024). Thus, to detect match/no-match effects across our three encoding conditions, we estimated 27 participants were needed for a medium effect size (d=0.5) under a type I error threshold of 0.05 and power of 0.8.

Fifty-three young adults were recruited from Brown University and received monetary payment or course credit. The study protocol was approved by Brown University Institutional Review Board under the Helsinki Declaration, and informed consent was obtained from all participants prior to testing. Following the informed consent procedure, participants completed a demographic and medical history questionnaire, the Pittsburgh Sleep Quality Index (PSQI, Buysse et al., 1989), and were administered the Tumbling-E visual acuity test. All participants reported normal or corrected-to-normal vision, English language fluency, and no psychological or neurological disorders. Participants with poor pupil tracking quality (n=4) or task performance (n=17) were excluded from analyses to ensure >50% usable trials of pupil data in each of the 3 encoding conditions and the new condition. Data from the remaining thirty-two young adults (mean age: 22.4 years, std dev: 3.72, range: 18-31 years; 21 females) were included in the

analyses. Visual acuity at 100% contrast ranged from 20/16 to 20/32 across participants with an average of 20/16.9 (1 participant scored 20/32). Average PSQI global score across participants was 5.34 (std dev: 2.27; range: 1-9; 13 people scored >5, 19 scored ≤5), indicating good to mediocre sleep quality over the past month before testing.

*Stimuli*

For this experiment, we utilized the stimuli from Siefert et al. (2024). The original stimuli comprised 120 images paired with their corresponding words, initially selected from the Snodgrass and Vanderwart (1980) picture naming set. We chose 72 images and added another 24 words to be used in the retrieval phase, resulting in a total of 144 words in this stimuli set. The selection criteria were strong picture-name associations, high frequency, high familiarity, low complexity, low emotional salience, and word lengths of 3-6 letters. Word stimuli were presented in black Arial font (visual angle: 1.59°- 3.61° × 0.5°; average pixel intensity: 233.3; average contrast: 67.7) on a white background (luminance: 121.54 cd/$m^2$; visual angle: 35.34° × 20.37°). Image stimuli were presented as black outlines (average visual angle: 2.47° × 2.22°; average pixel intensity: 248.99; average contrast: 31.72). The fixation cross was a black + in Arial font (visual angle: 0.53° × 0.53°; pixel intensity: 251.1; contrast: 30.5).

*Procedure*

The experiment consisted of an encoding phase immediately followed by a recognition phase. During the encoding phase, participants studied 72 stimuli (24 per encoding condition, 36 images and 36 words) that were shown once (Single condition), three times consecutively (Massed Repetition condition), or three times distributed across the trials (Distributed Repetition condition; mean interval 28 stimuli, range 24-34). This resulted in a total of 168 encoding trials of which 72 contained novel stimuli and 96 contained repeated stimuli. Two pseudo-randomized

stimulus lists were created, with half the items assigned to be images and half as words. The identity of the stimuli assigned as images or words in these lists was counterbalanced across participants, yielding four pseudo-randomized encoding lists.

During the recognition phase, participants were shown 144 word stimuli (72 old, 72 new) in randomized orders across participants. “New” words were stimuli that were not presented during the encoding phase, while “Old” words were those presented during the encoding phase in either image or word form.

**Figure 1a** illustrates the sequence of events that occurred within a trial in each phase, and **Figure 1b** illustrates the three encoding conditions across an example sequence of stimuli. In the encoding phase, a fixation cross was shown at the center of the screen for 2 seconds, then replaced by the stimulus for 2 seconds. The prompt “word or picture” then appeared and remained on the screen for a maximum of 2 seconds unless the participant responded sooner. In the recognition phase, each trial began with a fixation cross for 2 seconds, followed by a word stimulus for 2 seconds. The prompt “old or new” then appeared and remained on the screen until the participant responded. A confidence rating prompt was then displayed, and participants indicated their confidence level regarding their old/new response on a scale of 1 to 5 (low/guess to high/certain) by pressing one of five response keys.

Before the encoding phase, participants were instructed that their task was to determine whether each stimulus presented was an image or a word by pressing one of two response keys. They were told to withhold their response until the prompt “word or picture” appeared and to refrain from blinking while the stimulus was on the screen. Participants were not informed of the subsequent memory recognition task. Before the recognition phase, participants were instructed that their task was to decide whether each word had been shown as either an image or word in

the encoding phase. They were told to respond "old" regardless of the presentation format, and to respond "new" only if the stimulus had not been presented as either an image or a word in the encoding phase. Participants were instructed to withhold their responses until the prompt "old or new" appeared and to refrain from blinking while the stimulus was on the screen. An eye-tracking calibration procedure was performed at the start of each phase, and participants were given the opportunity to take a brief break between the two phases.

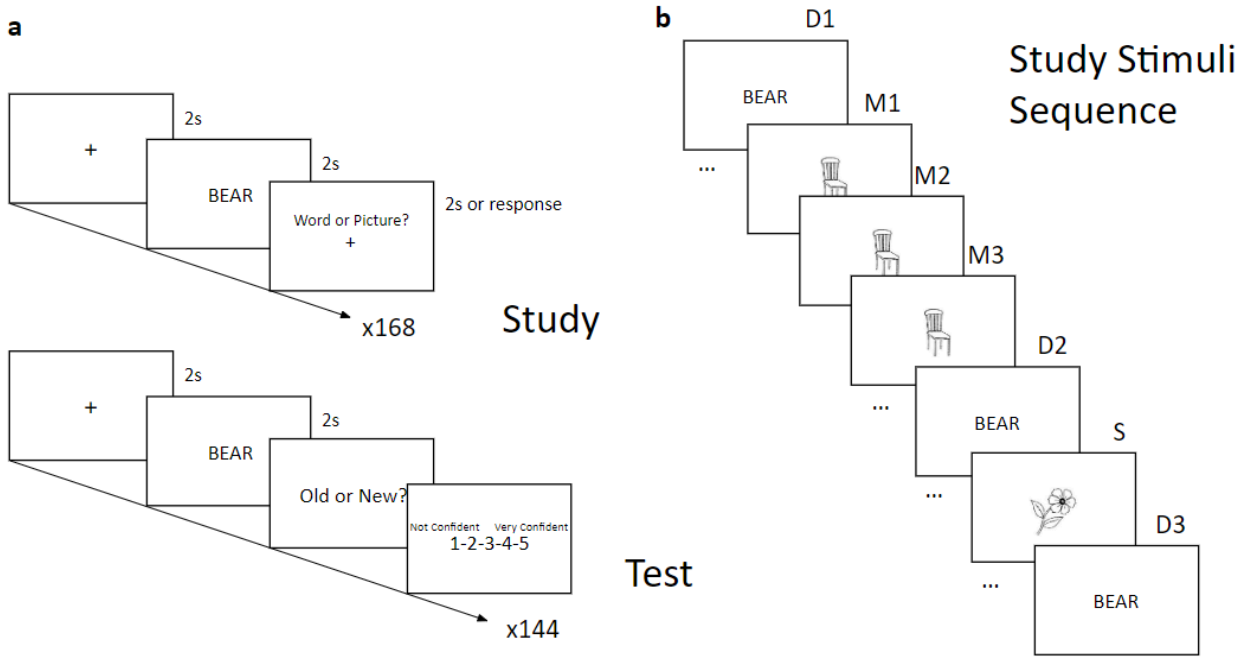



**Figure 1**. Schematic of trial events and stimulus conditions of Experiment 1. (A) The left panel illustrates trial events for the encoding phase (top) and for the recognition phase (bottom). During the encoding phase, participants viewed a series of images and words and indicated the stimulus format (word or picture) with a button press. During the test phase, participants viewed a series of words and responded to whether the stimulus was old or new, and then provided a confidence rating of their response. (B) The right panel illustrates the three encoding conditions across an example sequence of stimuli in the encoding phase. D = Distributed Repetition, M = Massed Repetition, S = Single-trial.

*Data Acquisition*

The tasks were delivered using E-Prime 3.0 on a Dell Precision M4800 laptop (344x194 mm; 1920x1080 pixel resolution; 60Hz refresh rate). Behavioral responses were collected with the Chronos Response and Stimulus Device (Psychology Software Tools, Pittsburg, PA). Pupillary data were collected using SMI iView RED250 mobile desktop-mounted eye tracking device with a sampling rate of 250 Hz (SensoMotoric Instruments, version 4.4, 2017) at a viewing distance of 54cm under ambient lighting conditions of 72.35 lux. Pupil diameter data was collected during both the encoding phase and recognition phase, with only the recognition phase data reported here. Before each phase, 9-point SMI calibration and validation procedures were completed. Participants positioned their head on a chin and forehead rest to minimize movement artifacts in the pupil data. They were instructed to keep their gaze at the center of the screen and avoid blinking during the stimulus presentation, but were encouraged to blink during the response periods. Pupil diameter data in millimeters (mm) from the right eye were exported with Begaze 3.7 before preprocessing and analyses were done using MATLAB R2022a custom scripts (MathWorks, Natick, MA).

*Data Analyses*

Behavioral accuracy and confidence ratings from the recognition phase were analyzed using JASP 0.17.1 statistics software. A repeated-measures ANOVA was performed to compare the memory accuracy across the three encoding conditions (Distributed, Massed, and Single-trial), followed by two planned repeated contrasts comparing distributed vs. massed and massed vs. single-trial. The same analysis was done for confidence ratings as the dependent variable.

Pupillary data were preprocessed and then analyzed using a trial-level regression model approach that has been adopted in several recent studies (Krishnamurthy et al. 2017; Hämmerer et al. 2019; He et al. 2020; Siefert et al. 2024). Baseline and trial data from the recognition phase were time-locked to the stimulus onset: baseline was defined as the 200 ms prior to the onset and the trial period was defined as full 2 second stimulus duration. Artifacts (i.e., abrupt changes in diameter and blinking) in these epoched data were removed and trials with more than 50% data loss were discarded. Data from participants with more than 50% discarded trials were excluded from analyses (n=3). Linear interpolation was performed on the missing data in each trial and then baseline-corrected by subtracting the mean pupil diameter of the baseline period from the pupil diameter at each time point for each trial.

Separate regression models for the old/new effect (I) and the match/no-match effect (II) were performed for each encoding condition (Distributed, Massed, and Single-trial):

(I) *Trial Pupil Diameter = Intercept + b1(OldorNew) + b2(Baseline) + b3(ToT);*

(II) *Trial Pupil Diameter = Intercept + b1(MatchNoMatch) + b2(Baseline) + b3(ToT)*

where *OldorNew* is a variable coded for Old (1) or New (0) conditions, *MatchNoMatch* is a variable coded for Match (1) or NoMatch (0) conditions, *Baseline* is the average baseline pupil diameter, and *ToT* is time-on-task defined as the log of trial number. Independent variables included in the models were mean-centered, and only accurate trials were included in the analyses, as both effects have been observed for accurate but not inaccurate trials (Kafkas & Montaldi 2015; Siefert et al. 2024). Confidence variable was not included in the regression models because that measure shares variance with the old/new response measure (i.e. confidence ratings were higher for the old trials relative to new) and with the match/no-match conditions (i.e. confidence ratings were higher in the match trials relative to no-match).

Trial-level regression analyses of the pupillary data using the above models were performed at every sampled time point across the 2 second trial window (He et al. 2020). One-sample t-tests were then applied to test the statistical significance of the resulting regression coefficients at each time point. To correct for multiple comparisons, cluster-size-based permutation testing was employed. A cluster size was calculated by summing the number of time points with $p<0.05$ across the one-sample t-tests for regression coefficients. A permutation-corrected p-value was determined by calculating the average frequency of this cluster size exceeding the cluster sizes in a permutation distribution obtained by running one-sample t-tests after randomizing the sign of coefficients among participants (Krishnamurthy et al. 2017; He et al. 2020; Siefert et al. 2024).

## ***Results***

### *Behavioral Results*

Behavioral results showed converging patterns for accuracy (**Figure 2**a) and confidence ratings (**Figure 2**b) across the three encoding conditions. Both measures showed an increase across the Single, Massed, and Distributed conditions, consistent with an expected increased memory encoding strength across these conditions. A one-way repeated measures ANOVA with Accuracy as the dependent variable and Repetition Condition (Distributed, Massed, and Single) as the fixed factor indicated significant differences between the conditions [$F_{2,62} = 41.45$, $p < 0.001$, $\eta^2 = 0.57$]. Planned repeated contrasts revealed greater accuracy in the Distributed compared to the Massed condition [mean(SD): 0.80(0.11) vs. 0.72(0.15); $t(62) = 3.39$, $p = 0.001$) and in the Massed compared to the Single condition [mean(SD): 0.72(0.15) vs. 0.59(0.12); $t(62) = 5.62$, $p < 0.001$]. A similar repeated measures ANOVA with Confidence Rating as the dependent variable and Repetition Condition (Distributed, Massed, and Single) as

the fixed factor indicated significant differences between the conditions [$F_{2,62} = 27.08$, $p < 0.001$, $\eta^2 = 0.47$]. Planned repeated contrasts revealed greater confidence ratings in the Distributed compared to the Massed condition [mean(SD): 4.07(0.44) vs. 3.76(0.48); $t(62) = 4.72$, $p < 0.001$], and a trending difference in the Massed compared to the Single condition [mean(SD): 3.76(0.48)vs. 3.59(0.58); $t(62) = 2.53$, $p = 0.014$].

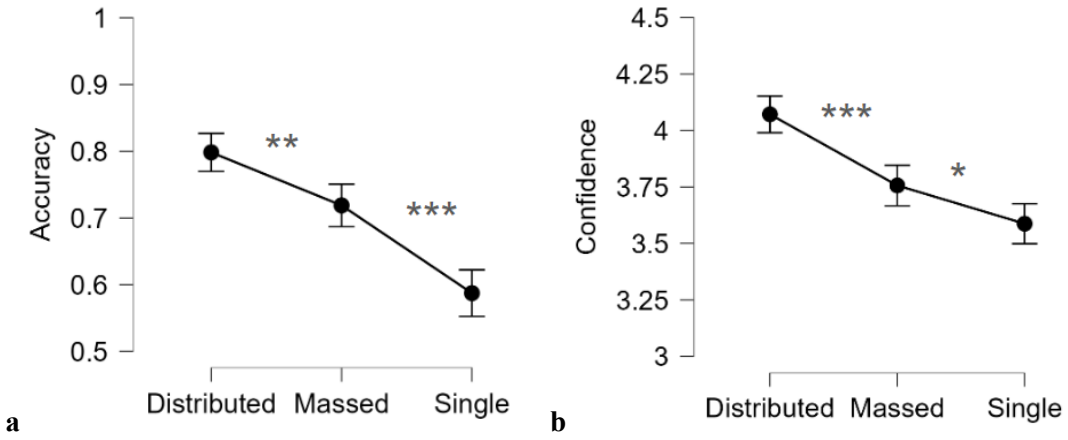


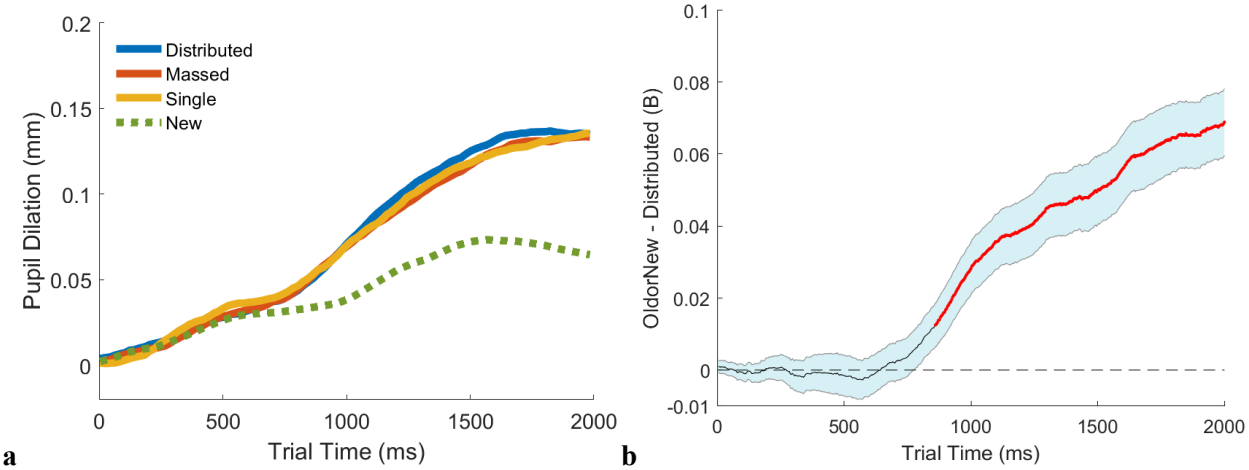

**Figure 2**. (a) Mean recognition accuracy and (b) mean confidence ratings across three repetition encoding conditions. Error bars indicate 95% confidence intervals. *p<0.05, **p<0.01, ***p<0.001.

*Pupillary Results*

We applied the following regression models to the accurate trials separately for each repetition condition: (I) *Trial Pupil Diameter = Intercept + b1(OldorNew) + b2(Baseline) + b3(ToT)*; (II) *Trial Pupil Diameter = Intercept + b1(MatchNoMatch) + b2(Baseline) + b3(ToT)*. We found the expected effects of baseline pupil diameter and time-on-task in line with previous findings (Krishnamurthy et al. 2017; Hämmerer et al. 2019; He et al. 2020; Siefert et al. 2024). First, larger trial pupil diameter was associated with larger baseline pupil diameter [permutation test of duration: (I) Old/New effect: Distributed: 2000ms, p=0.027; Massed: 2000ms, p=0.022; Single: 2000ms, p=0.021; (II) Match/NoMatch effect: Distributed: 2000ms, p=0.016; Massed:

2000ms, p=0.016; Single: 2000ms, p=0.018]. Second, time-on-task was negatively associated with trial pupil diameter in both models [permutation test of duration: (I) Old/New effect: Distributed: 1484ms, p=0.012; Massed: 1428ms, p=0.028; Single: 1500ms, p=0.019; (II) Match/NoMatch effect: Distributed: 1540ms, p=0.010; Massed: 1100ms, p=0.023; Single: 780ms, p=0.040].

**We observed comparable pupil old/new effects across the three encoding conditions.** The trial-averaged pupil response curves for the Distributed, Massed, and Single conditions (all of which constitute the Old condition) compared to the pupil response curve for the new stimuli are shown in **Figure 3a**. Qualitatively, the "old" pupil response curves for all three conditions are similar in shape and magnitude and larger than that of the "new" condition. The old/new regression models (I), revealed significant positive effects of the Old condition on the trial pupil diameter across all three encoding conditions (**Figure 3 b-d**). Permutation tests confirmed that the pupil old/new effect was significant after correcting for multiple comparisons across all three conditions [permutation test of duration: Distributed: 1144ms, p=0.006; Massed: 1132ms, p=0.012; Single: 1216ms, p=0.006].




**a** **b**

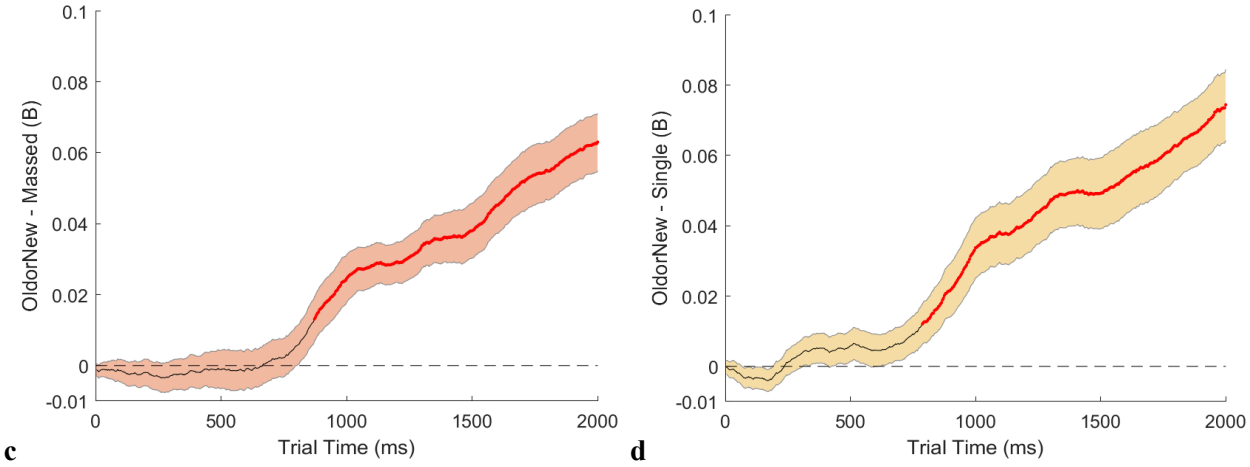
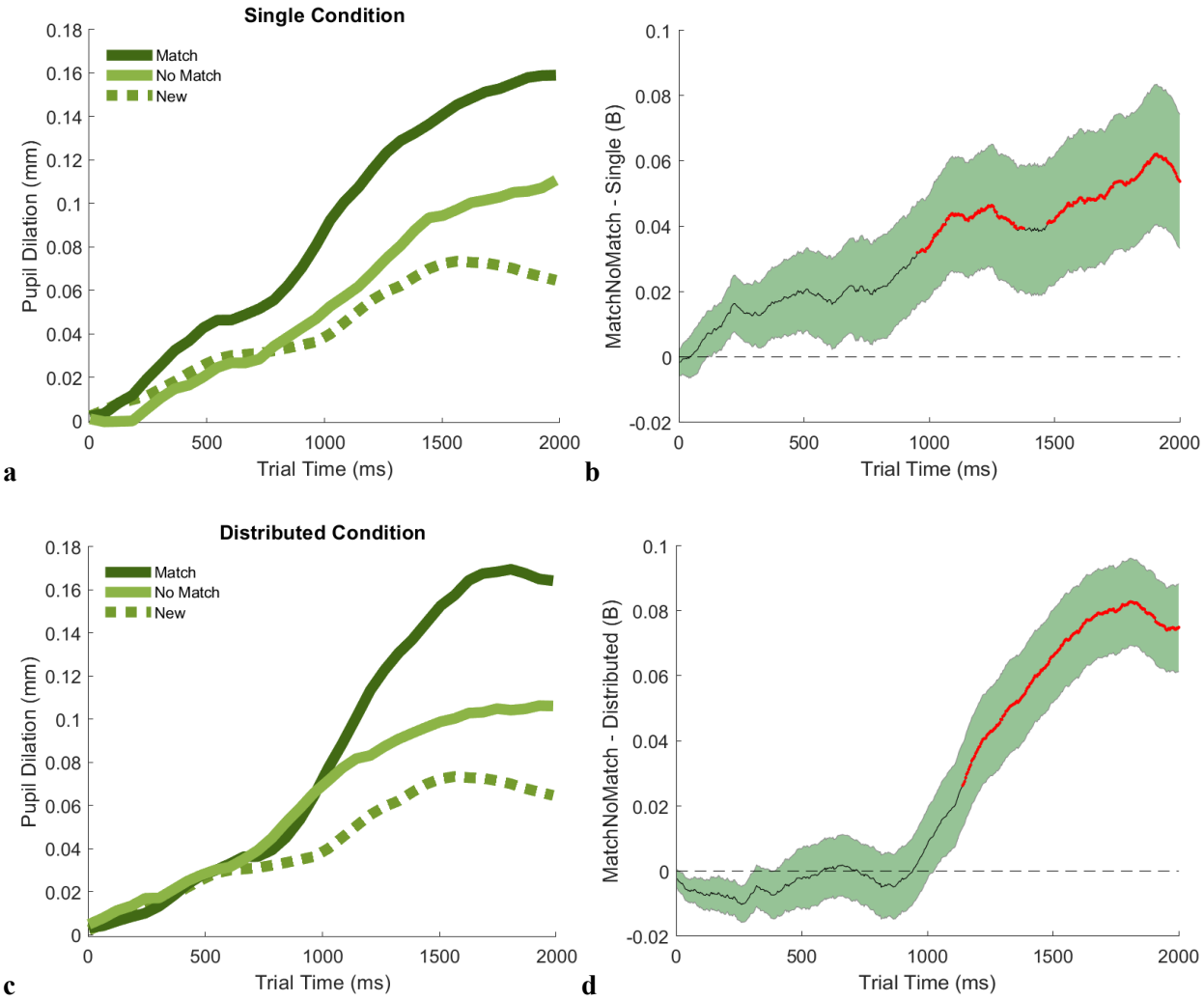



**Figure 3**. Pupil old/new effect across repetition conditions. (a) Trial-level raw time-series plot of pupil dilation averaged across participants. Trial time is relative to the onset of the target stimulus. Regression coefficients of *OldorNew* factor plotted across trial time for (b) Distributed learning, (c) Massed learning, and (d) Single-trial learning. In the coefficient plots, significant time points are marked in red ($p<0.01$ for Distributed and Single-trial, $p<0.05$ for Massed); the shaded area represents standard error.

**We found that the magnitude of pupil old/new effect was positively correlated with the encoding-retrieval perceptual match in Distributed and Single-trial conditions, but negatively correlated in the Massed condition (Figure 4).** The raw pupillary response curves and the match/no-match regression models (II) both revealed differential match/no-match effects across the three repetition conditions. In the Single-trial condition (**Figure 4**, a and b), significantly greater pupil dilation was found for Match compared to NoMatch trials, replicating the shallow encoding results observed in Siefert et al (2024). The Distributed condition (**Figure 4**, c and d) also showed a significant match/no-match effect with a greater peak of coefficient values than in the Single-trial condition, in line with our hypothesis that distributed learning enhances cue-trace interaction due to strengthened contextual recollection. In contrast, the Massed condition (**Figure 4**, e and f) does not show a significant match/no-match effect during

the same trial time period as the other two conditions. Rather, there was a reversed match/no-match effect (i.e., smaller pupil dilation for match than no match) earlier in the trial time, as indicated by the negative coefficients between 300-1000 ms of the trial time. These results are also consistent with our hypothesis that massed learning reduces recollection through contextual encoding. Permutation tests confirmed that these pupil match/no-match effects are significant in all three conditions after correcting for multiple comparisons [permutation test of duration: Distributed: 864ms, p=0.017; Massed: 704ms, p=0.040; Single: 944ms, p=0.027].



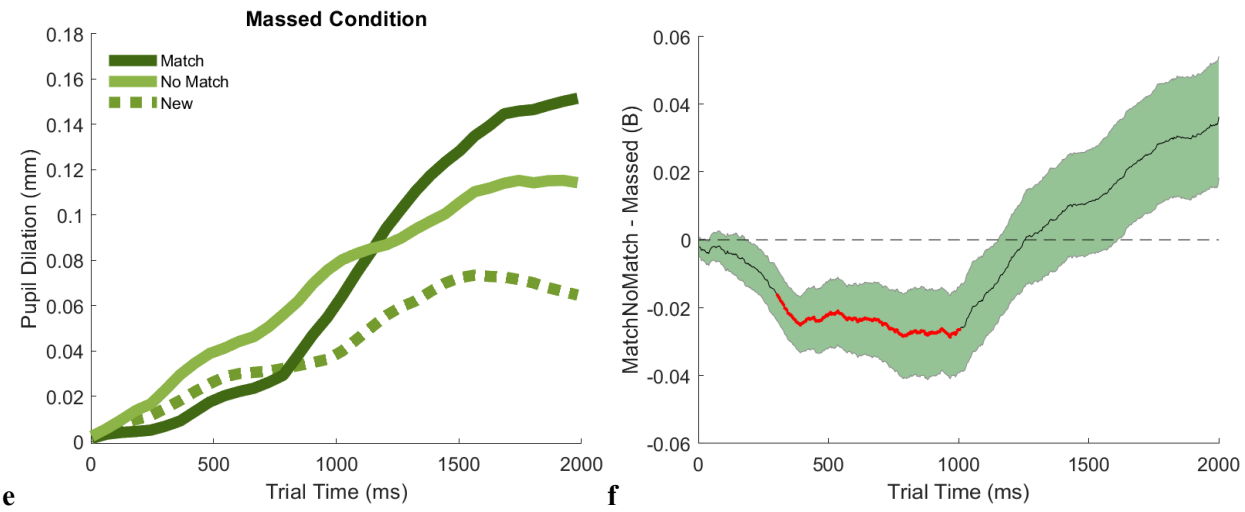



**Figure 4**. Pupil match/no-match effect across repetition conditions. Trial-level pupil response time-series curves for (a) Single-trial, (c) Distributed, and (e) Massed learning conditions. Regression coefficients of *MatchNoMatch* plotted across trial time for (b) Single-trial, (d) Distributed, and (f) Massed learning conditions. For coefficient plots, significant time points are marked in red ($p<0.05$); green shaded area represents standard error.

*Experiment 1 Discussion*

The behavioral results indicate increasingly stronger memory traces across the single-trial, massed, and distributed learning conditions. Despite this, we found similar magnitudes of pupil dilation and comparable pupil old/new effects across the conditions. Notably, pupil dilation was greater for Match than NoMatch trials in both the Single-trial and Distributed learning conditions, but not in the massed learning condition. This observed pupil match/no-match effect may reflect the amount of contextual details encoded in the memory trace that subsequently supported recollection. Compared to massed learning, distributed and single-trial shallow encoding may enhance the encoding of contextual and perceptual details, and the subsequent retrieval of those details may be significantly strengthened by cue-trace match and accompanied by greater pupil dilation. These results indicate that pupil dilation in

recognition memory is influenced by the nature of encoding that affects the subsequent cue-trace interaction during memory retrieval. Taken together, the results from Experiment 1 provided support for the role of cue-trace interaction, rather than memory strength alone, in the pupil old/new effect.

Interestingly, a reversed pupil match/no-match effect was observed early in the time course for the Massed learning condition. This effect may be driven by pronounced familiarity signals following massed learning, where Match trials may be processed with greater fluency than NoMatch trials. As a result, the smaller pupil dilation may be due to reduced cognitive effort for recognizing items in Match trials than in NoMatch trials. To test this processing fluency hypothesis, we conducted Experiment 2 in a priming paradigm to examine whether the pupillary response for the priming effect reflects ease of processing, as suspected for massed learning. Given the functional overlap between familiarity and priming, we expected their pupillary effects to be similar, which may corroborate the hypothesized role of facilitated processing in the reversed pupil match/no-match effect for massed learning.

**Experiment 2: Pupil old/new effect in a word-stem completion priming task**

To investigate the hypothesis that the familiarity effect drives the reversed pupillary match/no-match effect observed in massed learning, we assessed the pupillary response in the context of a stem-completion priming paradigm adopted from Kane et al. (2015), originally adapted from Shimamura et al. (1987). Given that priming implies unconsciously facilitated processing due to prior exposure, successful priming may result in stronger memory traces than unsuccessful priming. If the pupillary response in priming is directly related to memory strength, we would expect to see greater pupil dilation for successfully primed items (associated with stronger memory trace) than unsuccessfully primed items (associated with weaker memory

trace). Conversely, if the pupillary priming effect is related to the ease of processing the primed items, we may observe smaller pupil dilation for successfully primed items than for unsuccessfully primed items. Because pupil size robustly tracks cognitive effort (Hess & Polt 1964; Kahneman & Beatty 1966; Piquado et al. 2010; Alnæs et al. 2014; van der Wel & van Steenbergen 2018), successful priming may reduce cognitive effort in the stem-completion task, resulting in smaller pupil dilation compared to unsuccessful priming.

## *Methods*

### *Participants*

As in Experiment 1, we conducted power analysis using G*Power 3.1 (Faul et al. 2009) to estimate the appropriate sample size. Here we are again interested in the pupil old/new effect but within a stem-completion priming paradigm. Thus, we estimated 27 participants were needed for a medium effect size ($d = 0.5$) under a type I error threshold of 0.05 and power of 0.8.

Thirty-one young adults were recruited from Brown University and received monetary payment or course credit. The study protocol was approved by Brown University Institutional Review Board under the Helsinki Declaration, and informed consent was obtained from all participants prior to testing. Following the informed consent procedure, participants completed a demographic and medical history questionnaire, the Pittsburgh Sleep Quality Index (PSQI, Buysse et al., 1989), and were administered the Tumbling-E visual acuity test. All participants reported normal or corrected-to-normal vision, English language fluency, and no psychological or neurological disorders. Participants were excluded from analyses if they had stem completion hit rate higher or lower than 2 standard deviations from the mean (n=4), diagnosis of psychological/neurological disorder (n=1, oppressive compulsive disorder, head injury, severe headaches), poor pupil data quality (>50% trial loss, n=1), or incomplete data (n=1). Data from

the remaining 24 young adults (mean age: 19.7 years, range: 18-22 years; 15 females) were included in the analyses. Visual acuity at 100% contrast ranged from 20/16 to 20/32 across participants (1 person scored 20/32, 23 scored 20/16). Average PSQI global score across participants was 5.08 (std: 2.78; range: 2-13; 6 people scored >5, 18 scored ≤5), indicating good to mediocre sleep quality over the past month.

*Stimuli*

The stimuli used in this experiment were adopted from the Kane et al. (2015) study and consisted of 80 nouns and verbs, each 5-8 letters long. Each word's first three letters could generate at least 10 different common words according to dictionary entries. The stimuli were divided into four lists: Two lists (40 words) served as targets during the likeability rating task, and two lists (40 words) served as distractors and were not presented during the likeability rating task. Both the word stems of the target and distractors were presented during the stem completion task. The assignment of word lists as targets or distractors was counterbalanced across participants, ensuring that words serving as targets for half of the participants acted as distractors for the other half. This design allowed food the determination of baseline guessing rates for each word. Each combination of target and distractor lists was randomly assigned to the two blocks of the experiment, with words or word stems presented in a randomized order within each task.

All the stimuli were displayed in an isoluminant color-scheme created by using modified colors from the Teufel colors set (Teufel & Wehrhahn, 2000). A slate blue (RGB = [55, 123, 170], CIE-xyY = [0.196, 0.199, 25.5]) background and dark orange (RGB = [186, 94, 47], CIE-xyY = [0.234, 0.226, 25.8]) task stimuli were used to maintain a constant light intensity at 25 cd/m2 throughout all tasks, verified with ColorCAL MKII Colorimeter (Cambridge Research

Systems, Rochester, UK). Word stimuli (visual angle: 3.06° - 4.89° × 0.65°; average pixel intensity: 112.1; average contrast: 6.1) and word stem stimuli (visual angle: 1.45° - 1.99° × 0.65°; average pixel intensity: 109.7; average contrast: 4.2) were presented in dark orange Arial font on a slate blue background (27.35° × 20.78° visual angle). The fixation cross was a dark orange + in Arial font (visual angle: 0.53° × 0.53°; pixel intensity: 111.7, contrast: 5.0).

*Experimental Procedure*

A schematic of the experimental procedure is summarized in **Figure 5**. Experiment 2 included two blocks, each consisting of a likeability rating task immediately followed by a stem completion task. Participants completed a ten-minute spatial orienting of attention task (not reported in this paper) between the two blocks of trials.

Likeability Rating Task:

Each trial in the rating task consisted of a 2-second fixation cross followed by a target word that remained on the screen for 4 seconds. To ensure deep encoding during the target presentation, participants rated how much they liked each word on a scale from 1 to 5 (1="strongly dislike" 5="strongly like") by pressing buttons on a Serial-Response button box (Psychology Software Tools, 2012). Twenty unique target words (e.g. MOTEL) were presented individually on the screen in each block of the likeability rating task (40 total target words). Participants were neither told to remember the words, nor informed of the subsequent stem completion task.

Stem Completion Task:

Immediately after the likeability rating task, participants completed the stem completion task with no reference to the prior rating task. A total of 80 word stems (i.e., 40 in each block) with the first three letters of each word (e.g. MOT_) were presented. Each trial included a

2-second central fixation cross followed by a word stem presented on the screen for 4 seconds. During the word stem presentation, participants were asked to complete the word stems verbally with the first complete word that came to mind. Half of the word stems could be completed with studied words from the preceding rating task ("target stems"), and the other half could not ("novel distractor stems"). Verbal responses were immediately transcribed by an experimenter and recorded via a microphone to ensure accurate response coding.

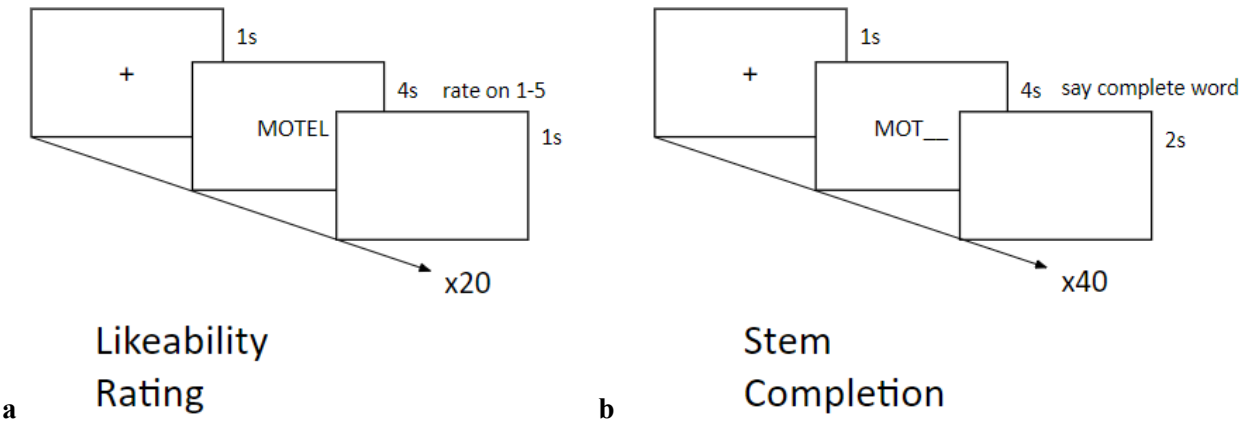



**Figure 5**. Experiment 2 task procedure. (a) Study phase: Participants rated the likeability of a series of words during the presentation of each word. (b) Test phase: Participants completed word stems with the first word that comes to mind. Half of the word stems could be completed by words from the preceding likeability rating task, and the other half could not.

*Apparatus and Pupil Diameter Acquisition*

The apparatus and lighting conditions were identical to those used in He et al. (2020). Stimuli were displayed on a 19-inch CRT monitor (1152x864 pixel resolution, 72 Hz, Viewsonic G90fb) situated 75 cm from the participants' eyes. The task was delivered and controlled on an Intel Core 2 Quad 2.836 GHz PC (OS Windows XP SP3 32 bit, 2002) with Nvidia GeForce GT440 graphics card using E-Prime v2.0 (Psychology Software Tools, Pittsburgh, PA, USA).

Pupil diameter data were recorded using an Eye-Link1000 video-based desktop-mounted eye tracker (EyeLink1000, SR Research, Ontario, Canada) with a sampling rate of 250 Hz. Participants' heads were stabilized on a chin rest, and pupil diameter from the left eye was captured using the Centroid Pupil Tracking Algorithm (EyeLink1000) by an infrared-sensitive camera. Pupil data was collected throughout the experiment, with only the test phase data reported here. A 9-point grid calibration was done before each eye-tracking session to calibrate and validate the system to <1° average visual angle Cartesian prediction error. Behavioral and pupillary data were processed and analyzed in the same way as in Experiment 1 using MATLAB R2022a custom scripts (MathWorks, Natick, MA).

*Data Analysis*

Successful priming, or hits, was defined as completing the target stems with the corresponding studied words shown in the rating task, while unsuccessful priming, or misses, was defined as not using the studied words to complete the target stems. The completion of novel distractor stems was used to calculate the baseline guessing rate for each word, which equals the proportion of completing novel distractor stems with the words in the stimulus list. The successful priming rate was then compared with the baseline guessing rate using a paired samples t-test to measure the behavioral priming effect.

Pupillary data were analyzed using a trial-level linear regression model and cluster-size-based permutation testing approach, similar to Experiment 1. The regression model, with mean-centered predictors, was applied to target trials to examine the effect of successful priming relative to unsuccessful priming:

(III) $Trial\ Pupil\ Diameter = Intercept + b1(PrimedUnprimed) + b2(Baseline) + b3(ToT)$.

In this model (III), *PrimedUprimed* is a variable coded as 1 for successfully primed trials and 0 for unsuccessfully primed trials. *Baseline* is the variable for baseline pupil diameter averaged at each time point, and *ToT* (time-on-task) was defined as the log of trial number. Novel distractor stems were not analyzed with regression because the main interest of this study was to test the priming effect of target stems on pupillary responses.

## ***Results***

### *Behavioral Results*

The mean behavioral priming rate (i.e. the proportion of target stems being completed with studied words from the rating task relative to all target stems) was 47.9%, with a baseline guessing rate of 7.2%. A planned paired samples t-test confirmed significant behavioral priming effects above baseline guessing rates: $t(23) = 13.964$, $p < 0.001$.

### *Pupillary Results*

To analyze the priming effect on pupillary response, we applied the following regression model: (III) *Trial Pupil Diameter = Intercept + b1(PrimedUnprimed) + b2(Baseline) + b3(ToT).* The effects of baseline pupil diameter and time-on-task (ToT) were consistent with previous findings (Krishnamurthy et al. 2017; Hämmerer et al. 2019; He et al. 2020; Siefert et al. 2024).

Regression analysis indicated significantly smaller pupil dilation for successfully-primed compared to unsuccessfully-primed words, as evidenced by the negative coefficients at the time points marked red in the coefficients plot over trial time (**Figure 6**). This finding supports the hypothesis that the pupillary priming effect reflects the cognitive effort required to generate appropriate words to complete the stems. Successfully-primed words were easier to generate, required less cognitive effort, and thus elicited smaller pupil dilation than unsuccessfully-primed

words. 10,000 permutations were run to confirm the significance of this pupillary priming effect after correcting for multiple comparisons [permutation test of duration: 2792ms, p<0.001].

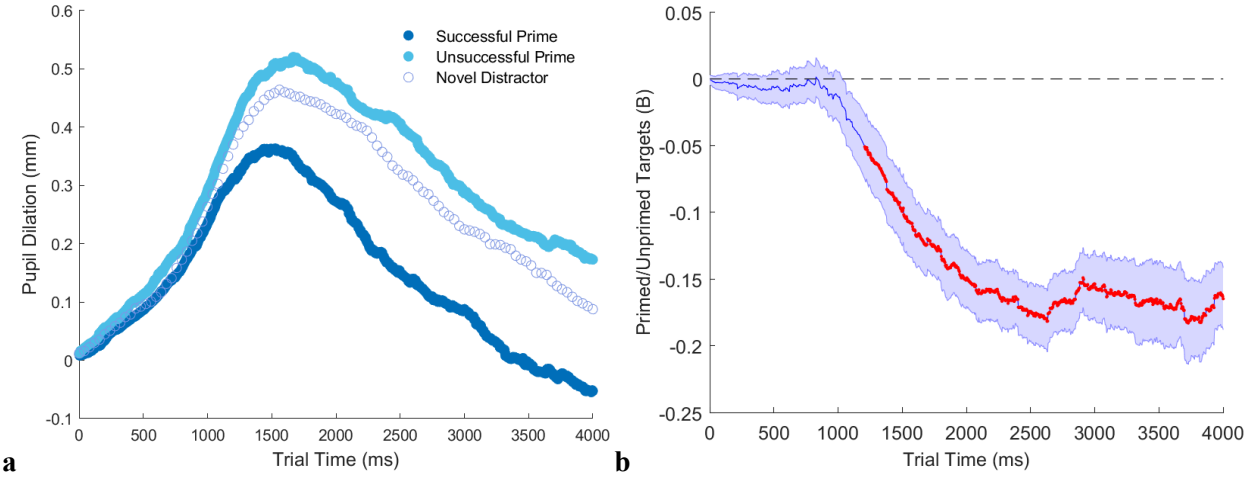



**Figure 6**. Pupil stem-completion priming effect. (a) Trial-level raw time-series plot of pupil dilation. (b) Regression coefficients of *PrimedUnprimed* plotted across trial time. For the coefficient plot, significant time points are marked in red (p<0.001); the shaded area represents standard error.

*Experiment 2 Discussion*

Results from Experiment 2 demonstrated smaller pupil dilation for successfully primed words than unsuccessfully primed ones, likely indicating reduced cognitive effort due to priming. This pupillary priming effect contrasts with the pupil old/new effect observed in recognition memory across all three conditions in Experiment 1. Specifically, in priming, stronger memory traces (successfully primed) lead to smaller pupil dilation, whereas in recognition, stronger memory traces (old) result in larger pupil dilation. These opposing patterns suggest that pupil size does not directly track memory strength but reflects the nature of task demands and the cue-trace interactions. The LC-NE system, which influences pupillary response, may facilitate different cognitive processes depending on the task context. During recognition, the salience of the cue-trace match may engage the LC-NE system to enhance cue-trace interaction, while the

difficulty of generating appropriate words in the stem-completion task may activate the LC-NE system more for unsuccessfully-primed word stems.

Additionally, this reversed pupillary effect mirrors the flipped match/no-match effect observed in massed learning during Experiment 1. Easier-to-process items (successfully-primed and Match) show smaller pupil dilation compared to more cognitively-demanding ones (unsuccessfully-primed and NoMatch). This alignment supports the hypothesis that the reversed pupil match/no-match effect in massed learning is driven by processing fluency, potentially combining or overlapping familiarity and priming effects. This processing fluency pupillary effect becomes evident when task demands are high, as seen in the stem-completion task, where the retrieval cue provides limited information, and in the recognition task following massed learning, where stored trace contextual information is insufficient.

**General Discussion**

We conducted two pupillometry experiments to investigate the mechanisms behind pupillary responses during tests of recognition memory and priming. In Experiment 1, we explored the impact of different repetition modes (Distributed vs. Massed repetition, with a Single-trial condition as the baseline) on shallow encoding of words and pictures. Our findings replicate the pupil match/no-match effect observed by Siefert et al. (2024) in the Single-trial condition, where items with greater perceptual cue-trace match elicited larger pupil dilation. This effect was even stronger following Distributed learning, known to enhance contextual recollection (Zhao et al. 2015; Feng et al. 2019). Conversely, Massed learning showed a reduced standard pupil match/no-match effect and a reversed effect at an earlier time course, likely due to diminished contextual recollection and a strong familiarity effect enhancing processing fluency. Experiment 2 tested our hypothesis regarding the Massed learning results using a word-stem

priming task. The results revealed smaller pupil dilation for successfully-primed words compared to unsuccessfully-primed words, mirroring the reversed pattern observed in Massed learning. This suggests that stronger memory traces from successfully-primed and Match items demand less cognitive effort, resulting in smaller pupil dilation. These findings indicate that the pupil old/new effect is driven by cue-trace interactions influenced by encoding and retrieval nature, rather than memory strength alone.

**Memory Strength and Pupillary Effects**

In Experiment 1, we observed that memory strength did not directly affect the magnitude of pupillary effects.. Repetitions in learning have long been associated with better memory outcomes (see Rugg 1996; Mecklinger 2000 for reviews), and the memory advantage of distributed learning over massed learning has been characterized as the "spacing effect" (Ebbinghaus 1885; Cepeda et al. 2006). Prior studies supporting the memory strength account in the pupil old/new effect have found greater pupil dilation for items with greater memory strengths (Otero et al. 2011; Montefinese et al., 2013; Kafkas & Montaldi 2015; Taikh & Bodner 2022). Despite varying levels of memory strength across different learning conditions, the pupil old/new effect remained comparable. Memory traces encoded through Massed learning were stronger than those through Single-trial learning and weaker than those through Distributed learning, and yet the pupil old/new effect was comparable across the three conditions. This finding of non-correlation between memory strength and the magnitude of the pupil old/new effect suggests that memory strength is not the only mechanism underlying the pupil old/new effect.

In addition, we showed that the pupil match/no-match effect was not modulated by memory strength, either. Siefert et al. (2024) found greater pupil dilation for Match than

No-match trials in the weaker memory traces of the shallow encoding condition, but not in the stronger memory traces of the deep encoding condition. Here, we found the opposite or a nonlinear relationship between memory strength and the pupil match/no-match effect. The standard match/no-match effect was found in the weakest memory traces of the Single-trial learning condition and the strongest memory traces of the Distributed learning condition, but not in the memory traces of intermediate strength of the Massed learning condition, where a reversed match/no-match effect was found instead. Increasing memory strength with repetitions at encoding did not necessarily lose the match/no-match effect in the same way as increasing memory strength with deep encoding in Siefert et al. (2024). This finding supported our hypothesis that memory strength does not account for the pupil match/no-match effect patterns.

These results indicate that the underlying mechanism contributing to the pupillary response during recognition is the interaction between retrieval cue and memory trace, rather than the strength of memory trace alone. The process of memory recognition is reactivating and reinstating the stored information with the available retrieval cue (Tulving 1983; Savarimuthu et al. 2023), hence the pupillary response during retrieval potentially tracks the joint synergistic effects of stored memory trace and retrieval cue. The role of cue-trace interaction is made more conspicuous by manipulating the nature of encoding and retrieval, as discussed in the next section.

**Encoding and Retrieval Demands Impact Pupil Response.**

Employed in Experiment 1, distributed learning and massed learning differ in not only memory strength but also their impact on encoding. Two influential models have been proposed and tested to explain the spacing effect: the encoding variability hypothesis posits that greater contextual variability across learning repetitions, as a result of longer inter-repetition intervals

(IRIs), creates more routes to effective retrieval (Glenberg 1979; Appleton-Knapp et al. 2005); the study-phase retrieval hypothesis states that each learning repetition serves as a retrieval cue that reactivates and strengthens the stored memory trace (Thios & D'Agostino, 1976), and longer ISIs make the momentary retrieval more cognitively demanding, thus leading to better subsequent memory retrieval (Bjork 1988). The commonality between the two models is that massed learning induces stronger repetition suppression (Wagner et al. 2000; Callan & Schweighofer, 2010; Xue et al., 2011) and that distributed learning enhances contextual encoding during repetitions and thus richer memory traces for contextual reinstatement and later retrieval (Van Strien et al. 2007; Zhao et al. 2015; Feng et al. 2019).

Pupillary results from Experiment 1 fit our prediction and current understanding of distributed and massed learning. Distributed learning repetitions reactivate the stored memory trace and encode greater and richer contextual details pertaining to the trace, which in turn helps enhance the contextual reinstatement and recollection as the cue and trace interact during retrieval. A higher degree of perceptual match between the cue and trace creates greater resonance in their interaction, which serves as a salient signal to the LC-NA system. Activation of the LC-NA system then dilates the pupils and boosts memory retrieval via neuromodulation (Sara 1985; Murchison et al. 2014; Poe et al. 2020). Distributed learning increases the sensitivity of the context-rich traces to the perceptual match with the cues, thus maximizing the match/no-match difference. On the other hand, massed learning repetitions exhibit a strong momentary retrieval signal, which produces strong neural repetition suppression and inhibits additional contextual encoding (Wagner et al. 2000; Zhao et al. 2015). The lack of contextual information in the trace diminishes the role of recollection and potentially makes the familiarity signal more prominent, which may amplify the match/no-match difference in a faster, more

automatic manner. According to our data, this process is manifested by the early reversed pupil match/no-match effect in the Massed learning condition. Such a drastic difference in the pupillary response patterns between Distributed and Massed learning implies that pupillary responses during recognition index the nature of encoding.

Comparing our data from Experiment 1 to that in Siefert et al. (2024) further reveals the role of encoding nature, rather than memory strength, in pupillary responses at recognition. Deep encoding in Siefert et al. increased memory strength but lost the match/no-match effect compared to Shallow encoding. In the current study, both Distributed and Massed repetitions at encoding increased memory strength relative to Single-trial learning but demonstrated different pupillary effects: Distributed learning showed a similar (if not larger) match/no-match effect to Single-trial learning, whereas Massed learning diminished this effect and showed an earlier reversed match/no-match effect. Together, these results suggest that the pupil match/no-match effect is modulated by the encoding nature and is independent of memory strength.

Similarly, data from Experiment 2 suggest that in a repetition priming paradigm, the pupil size response follows a negative relationship with memory strength: successfully-primed words with greater memory strength elicited smaller pupil dilation than unsuccessfully-primed words, an opposite pattern to what the memory strength theory for the pupil old/new effect would predict. Such a pupillary pattern may be driven by cognitive effort in generating words to complete the stems: successfully-primed words are implicitly easier to come up with for the word stems, and the associated decrease in the cognitive effort required in turn triggered a smaller pupil dilation.

The cognitively-demanding nature of the stem completion task may highlight the prominent effect of mental effort in the pupillary response. Interestingly, a similar pupillary

response pattern has been reported in cued recall experiments. When strong retrieval cues are not provided but required to be generated internally, weaker memory traces elicited greater pupillary responses than strong memory traces (Rijn et al. 2012; Pajkossy & Racsmany 2019). In the current priming task, the presentation of only weak retrieval cues (i.e. word stems) demands greater mental effort for word retrieval compared to a recognition task. The "flipped" pupil old/new effect observed in the current priming experiment and the previous cued recall studies is consistent with the recruitment of the LC-NA system in situations where increased top-down, effortful processing is required (Varazzani et al. 2015; Borderies et al. 2020).

**Distinct recollection, familiarity and priming influences on pupil response**

As suggested by previous studies, distributed learning may enhance recollection compared to massed learning via richer contextual encoding (Van Strien et al. 2007; Zhao et al. 2015; Feng et al. 2019). In contrast, massed learning shows a strong repetition suppression effect that hinders contextual encoding and subsequent recollection (Wagner et al. 2000; Callan & Schweighofer, 2010; Xue et al., 2011). Our data from Experiment 1 showed distinct pupil match/no-match effects following Distributed learning versus Massed learning, and this distinction seems to fit well with the differential encoding nature of the two types of repeated learning. The amplified match/no-match effect in Distributed learning may be driven by enhanced cue-trace interaction that is supported by contextual recollection; the rich contextual details encoded in the memory trace increase the sensitivity to perceptual match between the trace and the retrieval cue, such that greater cue-trace match significantly activates the LC-NE system (and increases pupil dilation) to boost contextual recollection. However, the lack of contextual encoding due to Massed learning diminishes the effect of contextual reinstatement

and recollection, and thus greater perceptual cue-trace match does not elicit bigger pupil dilation than the less matched cue-trace pairs.

While extensive research supporting the dual-process model of recognition memory has claimed to show dissociable neural signatures of recollection and familiarity (see Mecklinger 2006; Rugg & Curran 2007 for review), contentious debates remain in the potential conflation or co-occurrence of priming in these nominal familiarity signatures (Paller, Voss & Boehm 2007). A controversial speculation is that priming reflects an early stage of processing that ultimately produces familiarity (Yonelinas 2002; Rajaram & Geraci, 2000; Whittlesea & Williams, 1998; Wagner, Gabrieli, & Verfaellie, 1997; Jacoby & Dallas, 1981). Therefore, with the currently limited understanding of the relationship and distinction between familiarity and priming, we may conjecture that massed learning reflects a combined effect of the two processes.

Our data from Massed learning in Experiment 1 and stem-completion priming in Experiment 2 showed parallel pupillary response patterns, suggesting that the two tasks may have employed similar or overlapping processes of familiarity and priming. Both familiarity and priming may automatically facilitate cognitive processing, and such processing fluency is reflected in smaller pupil dilation, as pupil size has been shown to robustly track cognitive effort (Hess & Polt 1964; Kahneman & Beatty 1966; Piquado et al. 2010; van der Wel & van Steenbergen 2018). The effect of cognitive effort on pupillary responses may become more prominent under difficult task circumstances, where limited contextual details are encoded following massed learning, and only retrieval cue that contains partial information is present in the stem-completion task.

Our findings suggest that the pupil old/new effect is driven by cue-trace interactions influenced by encoding and retrieval nature, rather than memory strength alone. Pupillary

responses may reflect distinct influences of recollection and familiarity, with familiarity and repetition priming showing converging patterns driven by cognitive effort. These insights support a theoretical framework based on synergistic ecphory, integrating pupillary and neurobiological mechanisms of LC-NE function. Understanding these mechanisms can provide insights into age-related cognitive impairments and neurodegenerative diseases, highlighting the potential for early diagnosis and intervention (Braak & Del Tredici 2012; Mather & Harley 2016; Hämmerer et al. 2019).

Future studies should apply a process-dissociation paradigm (Jacoby 1991) to further investigate distinct pupillary patterns of recollection and familiarity. Analyzing receiver operating characteristics (ROC) using confidence ratings to tease apart the influences of recollection and familiarity (Yonelinas 2001) and incorporating EEG experiments can elucidate the temporal dynamics of different memory components.

References

Aggleton, J. P., & Brown, M. W. (2006). Interleaving Brain Systems for episodic and recognition memory. *Trends in Cognitive Sciences*, *10*(10), 455–463. https://doi.org/10.1016/j.tics.2006.08.003

Albi, Á., & Pajkossy, P. (2025). Pupil dilation accompanying successful recognition is linearly related to memory precision. *Journal of Experimental Psychology: Learning, Memory, and Cognition*.

Alnæs, D., Sneve, M. H., Espeseth, T., Endestad, T., van de Pavert, S. H. P., & Laeng, B. (2014). Pupil size signals mental effort deployed during multiple object tracking and predicts brain activity in the dorsal attention network and the locus coeruleus. *Journal of Vision*, *14*(4). https://doi.org/10.1167/14.4.1

Appleton-Knapp, S. L., Bjork, R. A., & Wickens, T. D. (2005). Examining the spacing effect in advertising: Encoding variability, retrieval processes, and their interaction. *Journal of Consumer Research*, *32*(2), 266–276. https://doi.org/10.1086/432236

Aston-Jones, G., & Cohen, J. D. (2005). An integrative theory of locus coeruleus-norepinephrine function: Adaptive gain and optimal performance. *Annual Review of Neuroscience*, *28*, 403–450. https://doi.org/10.1146/annurev.neuro.28.061604.135709

Atkinson, R. C., & Juola, J. F. (1974). Search and decision processes in recognition memory. In D. H. Krantz, R. C. Atkinson, R. D. Luce, & P. Suppes (Eds.), *Contemporary developments in mathematical psychology: I. Learning, memory and thinking.* W. H. Freeman.

Borderies, N., Bornert, P., Gilardeau, S., & Bouret, S. (2020). Pharmacological evidence for the implication of noradrenaline in effort. *PLOS Biology*, *18*(10), e3000793. https://doi.org/10.1371/journal.pbio.3000793

Bjork, R. A. (1988). Retrieval practice and the maintenance of knowledge. In M. M. Gruneberg, P. E. Morris, & R. N. Sykes (Eds.), *Practical aspects of memory II* (pp. 396-401). London: Wiley.

Bjork, R. A. (1999). Assessing our own competence: Heuristics and illusions. *Attention and Performance XVII*, 435–460. https://doi.org/10.7551/mitpress/1480.003.0023

Braak, H., & Del Tredici, K. (2012). Where, when, and in what form does sporadic Alzheimer's disease begin? *Current Opinion in Neurology*, *25*(6), 708–714. https://doi.org/10.1097/WCO.0b013e32835a3432

Brocher, A., & Graf, T. (2016). Pupil old/new effects reflect stimulus encoding and decoding in short‐term memory. *Psychophysiology*, *53*(12), 1823–1835. https://doi.org/10.1111/psyp.12770

Buysse, D.J., Reynolds, C.F., Monk, T.H., Berman, S.R., & Kupfer, D.J. (1989). The Pittsburgh sleep quality index: A new instrument for psychiatric practice and research. *Psychiatry Research, 28*, 193-213.

Callan, D. E., & Schweighofer, N. (2010). Neural correlates of the spacing effect in explicit verbal semantic encoding support the deficient‐processing theory. *Human Brain Mapping*, *31*(4), 645–659. https://doi.org/10.1002/hbm.20894

Cepeda, N. J., Pashler, H., Vul, E., Wixted, J. T., & Rohrer, D. (2006). Distributed practice in verbal recall tasks: A review and Quantitative Synthesis. *Psychological Bulletin*, *132*(3), 354–380. https://doi.org/10.1037/0033-2909.132.3.354

Devagues, V. & Sara, S. J. (1991). Memory retrieval enhancement by locus coeruleus stimulation: evidence for mediation by beta-receptors. *Behavioral Brain Research*, *43*, 93–97. https://doi.org/10.1016/S0166-4328(05)80056-7

Dewhurst, S. A., & Knott, L. M. (2010). Investigating the encoding—retrieval match in recognition memory: Effects of experimental design, specificity, and retention interval. *Memory & Cognition*, *38*(8), 1101–1109. https://doi.org/10.3758/MC.38.8.1101

Düzel, E., Yonelinas, A.P., Mangun, G.R., Heinze, H., Tulving, E., & Tulving, E. (1997). Event-related brain potential correlates of two states of conscious awareness in memory. *Proceedings of the National Academy of Sciences of the United States of America, 94 11*, 5973-8. https://doi.org/10.1073/PNAS.94.11.5973

Ebbinghaus, H. (1885). Memory: A contribution to experimental psychology (H. A. Ruger & C. E. Bussenius, Trans.). Leipzig: Von Duckner and Humblot (Reprinted from: Dover Publications).

Faul, F., Erdfelder, E., Buchner, A., & Lang, A.-G. (2009). Statistical power analyses using G*Power 3.1: Tests for correlation and regression analyses. *Behavior Research Methods*, *41*(4), 1149–1160. https://doi.org/10.3758/BRM.41.4.1149

Feng, K., Zhao, X., Liu, J., Cai, Y., Ye, Z., Chen, C., & Xue, G. (2019). Spaced learning enhances episodic memory by increasing neural pattern similarity across repetitions. *The Journal of Neuroscience*, *39*(27), 5351–5360. https://doi.org/10.1523/jneurosci.2741-18.2019

Frankland, P. W., Josselyn, S. A., & Köhler, S. (2019). The neurobiological foundation of memory retrieval. *Nature neuroscience*, *22*(10), 1576–1585. https://doi.org/10.1038/s41593-019-0493-1

Gardner, R. M., Mo, S. S., & Borrego, R. (1974). Inhibition of pupillary orienting reflex by novelty in conjunction with recognition memory. *Bulletin of the Psychonomic Society, 3*(3-B), 237–238. https://doi.org/10.3758/BF03333458

Glenberg, A. M. (1979). Component-levels theory of the effects of spacing of repetitions on recall and recognition. *Memory & Cognition*, *7*(2), 95–112. https://doi.org/10.3758/bf03197590

Godden, D. R., & Baddeley, A. D. (1975). Context-dependent memory in two natural environments: On land and underwater. *British Journal of Psychology*, *66*(3), 325–331. https://doi.org/10.1111/j.2044-8295.1975.tb01468.x

Goh, W. D., & Lu, S. H. X. (2012). Testing the myth of the encoding–retrieval match. *Memory & Cognition*, *40*(1), 28–39. https://doi.org/10.3758/s13421-011-0133-9

Gomes, C.A., Montaldi, D. and Mayes, A. (2015), The pupil as an indicator of unconscious memory: Introducing the pupil priming effect. *Psychophysiology*, *52*: 754-769. https://doi.org/10.1111/psyp.12412

Greene, R. L. (1989). Spacing effects in memory: evidence for a two-process account. Journal of Experimental Psychology: *Learning, Memory, and Cognition*, *15*(3), 371.

Hämmerer, D., Liu, K., Loane, C., Callaghan, M., Howard, R., & Duzel, E. (2019). Targeting the noradrenergic system in aging and early Alzheimer's disease. *Alzheimer's & Dementia*, *15*, P100–P101. https://doi.org/10.1016/j.jalz.2019.06.4233

Hansen, N., & Manahan-Vaughan, D. (2014). Locus coeruleus stimulation facilitates long-term depression in the dentate gyrus that requires activation of β-adrenergic receptors. *Cerebral Cortex*, *25*(7), 1889–1896. https://doi.org/10.1093/cercor/bht429

He, M., Heindel, W. C., Nassar, M. R., Siefert, E. M., & Festa, E. K. (2020). Age-related changes in the functional integrity of the phasic alerting system: A pupillometric investigation. *Neurobiology of Aging*, *91*, 136–147. https://doi.org/10.1016/j.neurobiolaging.2020.02.025

Henson, R. N. A. (2003). Neuroimaging studies of priming. *Progress in Neurobiology*, *70*(1), 53–81. https://doi.org/10.1016/s0301-0082(03)00086-8

Hermans, E. J., van Marle, H. J., Ossewaarde, L., Henckens, M. J., Qin, S., van Kesteren, M. T., Schoots, V. C., Cousijn, H., Rijpkema, M., Oostenveld, R., & Fernández, G. (2011). Stress-related noradrenergic activity prompts large-scale neural network reconfiguration. *Science*, *334*(6059), 1151–1153. https://doi.org/10.1126/science.1209603

Hess, E. H., & Polt, J. M. (1964). Pupil size in relation to mental activity during simple problem-solving. *Science*, *143*(3611), 1190–1192. https://doi.org/10.1126/science.143.3611.1190

Hintzman, D. L., & Curran, T. (1994). Retrieval dynamics of recognition and frequency judgments: Evidence for separate processes of familiarity and recall. *Journal of Memory and Language*, *33*(1), 1–18. https://doi.org/10.1006/jmla.1994.1001

Jacoby, L. L., & Dallas, M. (1981). On the relationship between autobiographical memory and Perceptual Learning. *Journal of Experimental Psychology: General*, *110*(3), 306–340. https://doi.org/10.1037/0096-3445.110.3.306

Joshi, S., Li, Y., Kalwani, R. M., & Gold, J. I. (2016). Relationships between pupil diameter and neuronal activity in the locus coeruleus, colliculi, and cingulate cortex. *Neuron*, 89(1), 221–234. https://doi.org/10.1016/j.neuron.2015.11.028

Kafkas, A., & Montaldi, D. (2011). Recognition memory strength is predicted by pupillary responses at encoding while fixation patterns distinguish recollection from familiarity. *Quarterly Journal of Experimental Psychology*, 64, 1971–1989. doi:10.1080/17470218.2011.588335

Kafkas, A., & Montaldi, D. (2012). Familiarity and recollection produce distinct eye movement, pupil and medial temporal lobe responses when memory strength is matched. *Neuropsychologia*, 50, 3080–3093. doi:10.1016/j.neuropsychologia.2012.08.001

Kafkas, A., & Montaldi, D. (2015). The pupillary response discriminates between subjective and objective familiarity and novelty. *Psychophysiology*, *52*(10), 1305–1316. https://doi.org/10.1111/psyp.12471

Kahneman, D., & Beatty, J. (1966). Pupil diameter and load on memory. *Science*, *154*(3756), 1583–1585. https://doi.org/10.1126/science.154.3756.1583

Kane, A. E., Festa, E. K., Salmon, D. P., & Heindel, W. C. (2015). Repetition priming and cortical arousal in healthy aging and Alzheimer's disease. *Neuropsychologia*, *70*, 145–155. https://doi.org/10.1016/j.neuropsychologia.2015.02.024

Krishnamurthy, K., Nassar, M. R., Sarode, S., & Gold, J. I. (2017). Arousal-related adjustments of perceptual biases optimize perception in dynamic environments. *Nature Human Behaviour*, 1. https://doi.org/10.1038/s41562-017-0107

Kwon, S., Rugg, M. D., Wiegand, R., Curran, T., & Morcom, A. M. (2023). A meta-analysis of event-related potential correlates of recognition memory. *Psychonomic Bulletin & Review*. https://doi.org/10.3758/s13423-023-02309-y

Laeng, B., Waterloo, K., Johnsen, S. H., Bakke, S. J., Låg, T., Simonsen, S. S., & Høgsaet, J. (2007). The eyes remember it: Oculography and pupillometry during recollection in three amnesic patients. *Journal of Cognitive Neuroscience*, 19, 1888–1904. doi:10.1162/jocn.2007.19.11.1888

Lemon, N., Aydin-Abidin, S., Funke, K., & Manahan-Vaughan, D. (2009). Locus Coeruleus activation facilitates memory encoding and induces hippocampal LTD that depends on β-adrenergic receptor activation. *Cerebral Cortex*, *19*(12), 2827–2837. https://doi.org/10.1093/cercor/bhp065

Liu, X., Ramirez, S., Pang, P. T., Puryear, C. B., Govindarajan, A., Deisseroth, K., & Tonegawa, S. (2012). Optogenetic stimulation of a hippocampal Engram activates fear memory recall. *Nature*, *484*(7394), 381–385. https://doi.org/10.1038/nature11028

Lucas, H. D., Taylor, J. R., Henson, R. N., & Paller, K. A. (2012). Many roads lead to recognition: Electrophysiological correlates of familiarity derived from short-term masked repetition priming. *Neuropsychologia*, *50*(13), 3041–3052. https://doi.org/10.1016/j.neuropsychologia.2012.07.036

Mandler, G. (1980). Recognizing: The judgment of previous occurrence. *Psychological Review*, *87*(3), 252–271. https://doi.org/10.1037/0033-295x.87.3.252

Mather, M., & Harley, C. W. (2016). The locus coeruleus: Essential for maintaining cognitive function and the aging brain. *Trends in Cognitive Sciences*, *20*(3), 214–226. https://doi.org/10.1016/j.tics.2016.01.001

Mecklinger, A. (2000). Interfacing mind and brain: A neurocognitive model of recognition memory. *Psychophysiology*, *37*(5), 565–582. https://doi.org/10.1111/1469-8986.3750565

Mecklinger, A. (2006). Electrophysiological measures of familiarity memory. *Clinical EEG and Neuroscience*, *37*(4), 292–299. https://doi.org/10.1177/155005940603700406

Montefinese, M., Ambrosini, E., Fairfield, B., & Mammarella, N. (2013). The "subjective" pupil old/new effect: Is the truth plain to see? *International Journal of Psychophysiology*, *89*(1), 48–56. https://doi.org/10.1016/j.ijpsycho.2013.05.001

Murdock, B. B., & Dufty, P. O. (1972). Strength theory and recognition memory. *Journal of Experimental Psychology*, *94*(3), 284–290. https://doi.org/10.1037/h0032795

Naber, M., Frässle, S., Rutishauser, U., & Einhäuser, W. (2013). Pupil size signals novelty and predicts later retrieval success for declarative memories of natural scenes. *Journal of vision*, *13*(2), 11. https://doi.org/10.1167/13.2.11

Nairne, J. S. (2002). The myth of the encoding-retrieval match. *Memory*, *10*(5–6), 389–395. https://doi.org/10.1080/09658210244000216

Oliveira, J., Fernandes, M., Rosa, P. J., & Gamito, P. (2021). Is Pupil Activity Associated With the Strength of Memory Signal for Words in a Continuous Recognition Memory Paradigm?. *Frontiers in psychology*, *12*, 686183. https://doi.org/10.3389/fpsyg.2021.686183

Orsini, C. A., Yan, C., & Maren, S. (2013). Ensemble coding of context-dependent fear memory in the amygdala. *Frontiers in Behavioral Neuroscience*, *7*. https://doi.org/10.3389/fnbeh.2013.00199

Otero, S.C., Weekes, B.S. and Hutton, S.B. (2011), Pupil size changes during recognition memory. *Psychophysiology*, *48*: 1346-1353. https://doi.org/10.1111/j.1469-8986.2011.01217.x

Paller, K. A., Voss, J. L., & Boehm, S. G. (2007). Validating neural correlates of familiarity. *Trends in Cognitive Sciences*, *11*(6), 243–250. https://doi.org/10.1016/j.tics.2007.04.002

Pajkossy, P., & Racsmány, M. (2019). How the size of the to-be-learned material influences the encoding and later retrieval of associative memories: A pupillometric assessment. *PloS one*, *14*(12), e0226684. https://doi.org/10.1371/journal.pone.0226684

Papesh, M. H., Goldinger, S. D., & Hout, M. C. (2012). Memory strength and specificity revealed by pupillometry. *International journal of psychophysiology : official journal of the International Organization of Psychophysiology*, *83*(1), 56–64. https://doi.org/10.1016/j.ijpsycho.2011.10.002

Piquado, T., Isaacowitz, D. and Wingfield, A. (2010), Pupillometry as a measure of cognitive effort in younger and older adults. *Psychophysiology*, *47*: 560-569. https://doi.org/10.1111/j.1469-8986.2009.00947.x

Poe, G. R., Foote, S., Eschenko, O., Johansen, J. P., Bouret, S., Aston-Jones, G., Harley, C. W., Manahan-Vaughan, D., Weinshenker, D., Valentino, R., Berridge, C., Chandler, D. J., Waterhouse, B., & Sara, S. J. (2020). Locus Coeruleus: A new look at the Blue Spot. *Nature Reviews Neuroscience*, *21*(11), 644–659. https://doi.org/10.1038/s41583-020-0360-9

Pomè, A., Binda, P., Cicchini, G. M., & Burr, D. C. (2020). Pupillometry correlates of visual priming, and their dependency on autistic traits. *Journal of Vision*, *20*(3), 3. https://doi.org/10.1167/jovi.20.3.3

Rajaram, S., & Geraci, L. (2000). Conceptual fluency selectively influences knowing. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *26*(4), 1070–1074. https://doi.org/10.1037/0278-7393.26.4.1070

Ratcliff, R., Sheu, C.-f., & Gronlund, S. D. (1992). Testing global memory models using ROC curves. *Psychological Review, 99*(3), 518–535. https://doi.org/10.1037/0033-295X.99.3.518

Rijn, H. van, Dalenberg, J. R., Borst, J. P., & Sprenger, S. A. (2012). Pupil dilation co-varies with memory strength of individual traces in a delayed response paired-associate task. *PloS one*, 7(12), e51134. https://doi.org/10.1371/journal.pone.0051134

Ritchey, M., Wing, E. A., LaBar, K. S., & Cabeza, R. (2013). Neural similarity between encoding and retrieval is related to memory via hippocampal interactions. *Cerebral Cortex*, *23*(12), 2818–2828. https://doi.org/10.1093/cercor/bhs258

Rugg, M. D. (1996). ERP studies of memory. *Electrophysiology of Mind*, 132–170. https://doi.org/10.1093/acprof:oso/9780198524168.003.0005

Rugg, M. D., & Curran, T. (2007). Event-related potentials and recognition memory. *Trends in Cognitive Sciences*, *11*(6), 251–257. https://doi.org/10.1016/j.tics.2007.04.004

Russo, R., Parkin, A. J., Taylor, S. R., & Wilks, J. (1998). Revising current two-process accounts of spacing effects in memory. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *24*(1), 161–172. https://doi.org/10.1037/0278-7393.24.1.161.

Sara, S. J. (1985). The locus coeruleus and cognitive function: Attempts to relate noradrenergic enhancement of signal/noise in the brain to behavior. *Physiological Psychology*, *13*(3), 151–162. https://doi.org/10.3758/BF03326515

Sara, S. J. (2015). Locus Coeruleus in time with the making of memories. *Current Opinion in Neurobiology*, *35*, 87–94. https://doi.org/10.1016/j.conb.2015.07.004

Savarimuthu, A., & Ponniah, R. J. (2023). Receive, retain and retrieve: Psychological and neurobiological perspectives on memory retrieval. *Integrative Psychological and Behavioral Science*. https://doi.org/10.1007/s12124-023-09752-5

Schacter, D. L., & Buckner, R. L. (1998). Priming and the brain. *Neuron*, *20*(2), 185–195. https://doi.org/10.1016/s0896-6273(00)80448-1

Semon, R. (1904). *Die Mneme als erhaltendes Prinzip im Wechsel des organischen Geschehens*. Wilhelm Engelmann.

Siefert, E. M., He, M., Festa, E. K., & Heindel, W. C. (2024). Pupil size tracks cue–trace interactions during episodic memory retrieval. *Psychophysiology*, *61*, e14409. https://doi.org/10.1111/psyp.14409

Sirois, S., & Brisson, J. (2014). Pupillometry. *WIREs Cognitive Science*, 5(6), 679–692. https://doi.org/10.1002/wcs.1323

Shimamura, A. P. (2011). Episodic retrieval and the cortical binding of relational activity. *Cognitive, Affective, & Behavioral Neuroscience*, *11*(3), 277–291. https://doi.org/10.3758/s13415-011-0031-4

Shimamura, A. P., Salmon, D. P., Squire, L. R., & Butters, N. (1987). Memory dysfunction and word priming in dementia and amnesia. *Behavioral Neuroscience, 101*(3), 347–351. https://doi.org/10.1037/0735-7044.101.3.347

Snodgrass, J. G., & Vanderwart, M. (1980). A standardized set of 260 pictures: Norms for name agreement, image agreement, familiarity, and visual complexity. *Journal of Experimental Psychology: Human Learning and Memory*, *6*(2), 174–215. https://doi.org/10.1037/0278-7393.6.2.174

Squire, L. R., Wixted, J. T., & Clark, R. E. (2007). Recognition memory and the medial temporal lobe: A new perspective. *Nature Reviews Neuroscience*, *8*(11), 872–883. https://doi.org/10.1038/nrn2154

Staudigl, T., Vollmar, C., Noachtar, S., & Hanslmayr, S. (2015). Temporal-pattern similarity analysis reveals the beneficial and detrimental effects of context reinstatement on human

memory. *The Journal of neuroscience : the official journal of the Society for Neuroscience*, *35*(13), 5373–5384. https://doi.org/10.1523/jneurosci.4198-14.2015

Stenberg, G., Hellman, J., Johansson, M., & Rosén, I. (2009). Familiarity or conceptual priming: Event-related potentials in name recognition. *Journal of Cognitive Neuroscience*, *21*(3), 447–460. https://doi.org/10.1162/jocn.2009.21045

St-Laurent, M., Abdi, H., & Buchsbaum, B. R. (2015). Distributed Patterns of Reactivation Predict Vividness of Recollection. *Journal of Cognitive Neuroscience*, *27*(10), 2000–2018. https://doi.org/10.1162/jocn_a_00839

Taikh, A., & Bodner, G. E. (2022). Pupil dilation during recognition reflects the subjective recollection/familiarity experience at test rather than the level of processing at encoding. *Canadian Journal of Experimental Psychology / Revue Canadienne de Psychologie Expérimentale*, *76*(3), 186–192. https://doi.org/10.1037/cep0000283

Tanaka, K. Z., Pevzner, A., Hamidi, A. B., Nakazawa, Y., Graham, J., & Wiltgen, B. J. (2014). Cortical representations are reinstated by the hippocampus during memory retrieval. *Neuron*, *84*(2), 347–354. https://doi.org/10.1016/j.neuron.2014.09.037

Thakral, P. P., Kensinger, E. A., & Slotnick, S. D. (2016). Familiarity and priming are mediated by overlapping neural substrates. *Brain Research*, *1632*, 107–118. https://doi.org/10.1016/j.brainres.2015.12.008

Thios, S. J., & D'Agostino, P. R. (1976). Effects of repetition as a function of study-phase retrieval. *Journal of Verbal Learning and Verbal Behavior*, *15*(5), 529–536. https://doi.org/10.1016/0022-5371(76)90047-5

Tulving, E. (1982). Synergistic ecphory in recall and recognition. *Canadian Journal of Psychology/Revue Canadienne de Psychologie*, *36*(2), 130–147. https://doi.org/10.1037/h0080641

Tulving, E. (1983). Ecphoric Processes in Episodic Memory. Ecphoric processes in episodic memory. (1983). *Philosophical Transactions of the Royal Society of London. B, Biological Sciences*, *302*(1110), 361–371. https://doi.org/10.1098/rstb.1983.0060

Tulving, E., & Pearlstone, Z. (1966). Availability versus accessibility of information in memory for words. *Journal of Verbal Learning and Verbal Behavior*, *5*(4), 381–391. https://doi.org/10.1016/s0022-5371(66)80048-8

Tulving, E., & Thomson, D. M. (1973). Encoding specificity and retrieval processes in episodic memory. *Psychological Review*, *80*(5), 352–373. https://doi.org/10.1037/h0020071

van der Wel, P., & van Steenbergen, H. (2018). Pupil dilation as an index of effort in Cognitive Control Tasks: A Review. *Psychonomic Bulletin & Review*, *25*(6), 2005–2015. https://doi.org/10.3758/s13423-018-1432-y

Van Strien, J., Verkoeijen, P., Vandermeer, N., & Franken, I. (2007). Electrophysiological correlates of word repetition spacing: Erp and induced band power old/new effects with massed and spaced repetitions. *International Journal of Psychophysiology*, *66*(3), 205–214. https://doi.org/10.1016/j.ijpsycho.2007.07.003

Varazzani, C., San-Galli, A., Gilardeau, S., & Bouret, S. (2015). Noradrenaline and dopamine neurons in the reward/effort trade-off: A direct electrophysiological comparison in behaving monkeys. *Journal of Neuroscience*, *35*(20), 7866–7877. https://doi.org/10.1523/JNEUROSCI.0454-15.2015

Võ, M. L.-H., Jacobs, A. M., Kuchinke, L., Hofmann, M., Conrad, M., Schacht, A., & Hutzler, F. (2008). The coupling of emotion and cognition in the eye: Introducing the pupil old/new effect. *Psychophysiology*, *45*(1), 130–140. https://doi.org/10.1111/j.1469-8986.2007.00606.x

Voss, J. L., Lucas, H. D., & Paller, K. A. (2010). Conceptual priming and familiarity: Different expressions of memory during recognition testing with distinct neurophysiological correlates. *Journal of Cognitive Neuroscience*, *22*(11), 2638–2651. https://doi.org/10.1162/jocn.2009.21341

Voss, J. L., Reber, P. J., Mesulam, M.-M., Parrish, T. B., & Paller, K. A. (2007). Familiarity and conceptual priming engage distinct cortical networks. *Cerebral Cortex*, *18*(7), 1712–1719. https://doi.org/10.1093/cercor/bhm200

Wagner, A. D., Gabrieli, J. D., & Verfaellie, M. (1997). Dissociations between familiarity processes in explicit recognition and implicit perceptual memory. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *23*(2), 305–323. https://doi.org/10.1037/0278-7393.23.2.305

Wagner, A. D., Maril, A., & Schacter, D. L. (2000). Interactions between forms of memory: When priming hinders new episodic learning. *Journal of Cognitive Neuroscience*, *12*(Supplement 2), 52–60. https://doi.org/10.1162/089892900564064

Wais, P. E., Mickes, L., & Wixted, J. T. (2008). Remember/know judgments probe degrees of recollection. *Journal of Cognitive Neuroscience*, *20*(3), 400–405. https://doi.org/10.1162/jocn.2008.20041

Wais, P. E., Wixted, J. T., Hopkins, R. O., & Squire, L. R. (2006). The hippocampus supports both the recollection and the familiarity components of recognition memory. *Neuron*, 49, 459–466.

Wang, W.-C., Ranganath, C., & Yonelinas, A. P. (2014). Activity reductions in perirhinal cortex predict conceptual priming and familiarity-based recognition. *Neuropsychologia*, *52*, 19–26. https://doi.org/10.1016/j.neuropsychologia.2013.10.006

Wickelgren, W. A., & Norman, D. A. (1966). Strength models and serial position in short-term recognition memory. *Journal of Mathematical Psychology*, *3*(2), 316–347. https://doi.org/10.1016/0022-2496(66)90018-6

Wixted, J. T. (2007). Dual-process theory and signal-detection theory of recognition memory. *Psychological Review*, 114, 152–176.

Whittlesea, B. W. A., & Williams, L. D. (1998). Why do strangers feel familiar, but friends don't? A discrepancy-attribution account of feelings of familiarity. *Acta Psychologica*, *98*(2–3), 141–165. https://doi.org/10.1016/s0001-6918(97)00040-1

Xue, G., Mei, L., Chen, C., Lu, Z.-L., Poldrack, R., & Dong, Q. (2011). Spaced learning enhances subsequent recognition memory by reducing neural repetition suppression. *Journal of Cognitive Neuroscience*, *23*(7), 1624–1633. https://doi.org/10.1162/jocn.2010.21532

Yaffe, R. B., Kerr, M. S. D., Damera, S., Sarma, S. V., Inati, S. K., & Zaghloul, K. A. (2014). Reinstatement of distributed cortical oscillations occurs with precise spatiotemporal dynamics during successful memory retrieval. *Proceedings of the National Academy of Sciences of the United States of America*, *111*(52), 18727–18732. https://doi.org/10.1073/pnas.1417017112

Yonelinas, A. P. (2001). Components of episodic memory: The contribution of recollection and familiarity. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *356*(1413), 1363–1374. https://doi.org/10.1098/rstb.2001.0939

Yonelinas, A. P. (2002). The nature of recollection and familiarity: A review of 30 years of research. *Journal of Memory and Language*, *46*(3), 441–517. https://doi.org/10.1006/jmla.2002.2864

Zerbi, V., Floriou-Servou, A., Markicevic, M., Vermeiren, Y., Sturman, O., Privitera, M., von Ziegler, L., Ferrari, K. D., Weber, B., De Deyn, P. P., Wenderoth, N., & Bohacek, J. (2019). Rapid reconfiguration of the functional connectome after chemogenetic locus Coeruleus Activation. *Neuron*, *103*(4). https://doi.org/10.1016/j.neuron.2019.05.034

Zhao, X., Wang, C., Liu, Q., Xiao, X., Jiang, T., Chen, C., & Xue, G. (2015). Neural mechanisms of the spacing effect in episodic memory: A parallel EEG and fmri study. *Cortex*, *69*, 76–92. https://doi.org/10.1016/j.cortex.2015.04.002