Psychology of Sport & Exercise 69 (2023) 102498

Contents lists available at ScienceDirect

Psychology of Sport & Exercise

journal homepage: www.elsevier.com/locate/psychsport

Moderate-to-vigorous intensity cycling exercise immediately after visual learning enhances delayed recognition memory performance

Andrew C. Venezia [a,*], Lauren R. Weiss [b,c], Kristy A. Nielson [d,e], J. Carson Smith [b,c]

[a] Department of Health and Human Performance, The University of Scranton, Scranton, PA, USA
[b] Department of Kinesiology, School of Public Health, University of Maryland, College Park, MD, USA
[c] Program in Neuroscience and Cognitive Science, University of Maryland, College Park, MD, USA
[d] Department of Psychology, Marquette University, Milwaukee, WI, USA
[e] Department of Neurology and the Center for Imaging Research, Medical College of Wisconsin, WI, USA

ARTICLE INFO

Keywords:
Arousal
Acute exercise
Memory
IAPS
Salivary alpha-amylase

ABSTRACT

A single bout of acute aerobic exercise has been shown to improve long-term memory, though it is unclear if exercise before learning or after learning is optimal for memory enhancement. Although some research has demonstrated that exercise before learning is ideal, investigations have consistently shown that acute arousal post-learning is a powerful memory enhancer. Therefore, the purpose of this investigation was to compare the effects of self-perceived hard cycling before or after learning on recognition memory for emotional and neutral images, and examine the relationship between central noradrenergic activity and memory performance. Seventy-two males and females (18–35 years of age) participated in this between-subjects study. Participants were randomly assigned to one of the following groups: exercise before learning, exercise after learning, and control. Participants in the exercise groups engaged in 20 min of cycling at a rating of perceived exertion (RPE) of 15 ("hard") on the Borg RPE scale before or after viewing a series of 90 pleasant, unpleasant, and neutral images (30 each). Participants in the control group engaged in no exercise before or after image viewing. At several time points throughout the experiment, saliva was collected to measure salivary alpha amylase (sAA), a marker of central noradrenergic activity. One-week later, recognition memory was assessed where participants viewed 180 images (90 new) and had to identify which images were previously viewed. Participants in the exercise after learning group had significantly higher recognition memory compared to the control group, but this was not seen with exercise before learning. sAA was not correlated with memory in any group, though it did increase during exercise. These results demonstrate that acute self-perceived hard cycling post-learning, but not pre-learning, improves recognition memory, though this was unrelated to the exercise-induced increase in central noradrenergic activity as measured in saliva.

1. Introduction

Regular and consistent participation in physical activity is important for maintaining optimal brain health. Research in humans and animals supports that chronic physical activity, including exercise training (planned, structured, and goal oriented physical activity), leads to anatomical and functional adaptations in the brain supporting cognitive function and mental health (Hillman et al., 2008; Voss et al., 2013; Won et al., 2021). Long-term memory is one such aspect of cognition that is enhanced following chronic physical activity (Roig et al., 2013; Voss et al., 2019). While there is substantial support for the benefits of regular physical activity for overall cognitive health (Colcombe & Kramer, 2003; Hillman et al., 2008; Prakash et al., 2015), there is a lack of understanding of the impact of single bouts of physical activity on long-term memory, which form the building blocks and stimulate longitudinal adaptations (Callow et al., 2021; Loprinzi, Roig, et al., 2021). If regular and consistent physical activity is known to improve learning and memory performance, it is important to understand the effects of single sessions of physical activity on memory processes, as these bouts of activity can be optimized (e.g. intensity and duration) to enhance learning and memory. One outstanding question concerns the optimal timing of acute physical activity relative to the encoding (creating a memory trace) and consolidation (process of stabilizing the memory trace) of to-be-remembered information.

* Corresponding author. 800 Linden Street; Scranton, PA, 18510, USA
E-mail address: Andrew.venezia@scranton.edu (A.C. Venezia).

https://doi.org/10.1016/j.psychsport.2023.102498
Received 24 March 2023; Received in revised form 12 July 2023; Accepted 24 July 2023
Available online 25 July 2023

Research in stress and emotion has established an important role of arousal in the storage and acquisition of memory (Diamond et al., 2007; Lalumiere et al., 2017; McGaugh, 2013; McGaugh & Roozendaal, 2002). Presented with an immeasurable number of episodes throughout life, humans and animals alike need to prioritize memories, with significant "privileged" events being better remembered than inconsequential episodes (McGaugh, 2013). Although evidence suggests that a moderate level of arousal is optimal for certain complex cognitive tasks (high decision making and/or complex visual discrimination), even extremely high levels of arousal can enhance memory (Diamond et al., 2007). Arousal is characterized by an increase in the release of adrenal stress hormones such as epinephrine, which is associated with increased central noradrenergic activity. Noradrenergic signaling has been identified as an important mechanism by which arousal enhances memory and allows for significant events to be better remembered (Cahill et al., 1994; Lalumiere et al., 2017; van Stegeren et al., 1998). Physical activity of sufficient intensity and duration is a physiologically arousing stimulus (McMorris, 2016; Segal et al., 2012; Weiss et al., 2019).

Research has consistently demonstrated that memory can be enhanced by manipulating arousal during the early consolidation period (for reviews see McGaugh, 2013; McGaugh & Roozendaal, 2002) using various approaches such as pharmacological interventions (Cahill & Alkire, 2003), cold exposure (Cahill, 2003), and arousing videos (Liu et al., 2008; Nielson & Correro, 2017; Nielson et al., 2005). There is also evidence to suggest that increased arousal prior to encoding reduces the threshold for memory formation (Hu et al., 2007), making it easier to remember less stimulating episodes. This indicates that either arousal before or after encoding can improve long-term memory; however, it may be that arousal during both encoding and consolidation is most effective. One approach that researchers have used to manipulate arousal during encoding and consolidation is visual presentation of emotional images as the to-be remembered content followed by a manipulation that further increases arousal during consolidation. This experimental approach of using emotionally charged images has provided evidence that the emotional content of the to-be-remembered information may play a critical role in the effectiveness of post-learning arousal to improve long-term memory. While there is evidence that arousal during consolidation can improve memory for neutral and low-to-moderately arousing content (Nielson et al., 2005; Nielson & Powless, 2007), other studies have indicated that arousal during consolidation improves memory only for emotional content, suggesting that arousal during encoding is important for the memory enhancing effects of arousal during consolidation (Cahill, 2003; Segal & Cahill, 2009).

Although arousal can be manipulated with pharmacological interventions, viewing arousing videos, and the perception of threat, physical activity and exercise are low cost, non-invasive, and reliable approaches to manipulate arousal, and have the additional advantage of being healthy behaviors with very few adverse side-effects. Like acute psychological stressors, physical activity of sufficient intensity and/or duration increases circulating catecholamines and central noradrenergic signaling (McMorris, 2021; Weiss et al., 2019). Indeed, acute physical activity-induced arousal has been shown to be effective at facilitating memory formation (Roig et al., 2016), though differences in study design make it difficult to determine the optimal exercise protocol for enhancing memories of varying emotional or stressful features. Importantly, studies have suggested that high-to maximal-intensity exercise is more effective at improving memory compared to lower-intensity exercise, which may be due to elevated arousal (Etnier et al., 2016; Loprinzi et al., 2019; Winter et al., 2007).

The optimal timing of physical activity and exercise-induced arousal relative to learning/encoding has not yet been conclusively determined. Although exercise before encoding (Coles & Tomporowski, 2008; Etnier et al., 2016; Labban & Etnier, 2018; Winter et al., 2007) and during consolidation (Keyan & Bryant, 2017; Segal et al., 2012; van Dongen et al., 2016; Weinberg et al., 2014) have both been shown to improve long-term memory, studies that have compared 30 min of pre- and post-encoding cycling exercise at a moderate-high intensity reported that exercise prior to encoding is more effective at improving long-term memory (Labban & Etnier, 2011, 2018), though these comparison studies utilized neutral content as the to-be remembered information. Memory for emotional images is improved when exercise of sufficient intensity to increase salivary alpha amylase (sAA), a marker of central noradrenergic signaling (Chatterton et al., 1996; Nater & Rohleder, 2009), is performed shortly after picture viewing (Segal et al., 2012; Weinberg et al., 2014), and this finding is consistent with other investigations manipulating arousal during the post-encoding period using non-exercise interventions (Cahill, 2003; Segal & Cahill, 2009). Therefore, we hypothesize that the ideal timing of exercise relative to learning/encoding may be dependent on the emotional charge of the to-be remembered content, and this has not been thoroughly investigated.

The purpose of the current investigation was to determine the time-dependent effects of moderate-to-vigorous intensity aerobic exercise on long-term episodic memory for pleasant, neutral, and unpleasant images. Moreover, because noradrenergic signaling is important for the memory enhancing effects of acute arousal, we measured sAA at several time points before, during, and after the exercise and cognitive task. Based on the extant literature, we hypothesized that sAA will increase during acute aerobic exercise and that there will be a positive correlation between exercise-induced sAA and recognition memory. We also hypothesized an interaction between picture type and acute exercise timing. Specifically, we predicted that cycling exercise performed prior to encoding would non-selectively improve long-term recognition memory for pleasant, neutral, and unpleasant images; we further hypothesized that the same exercise intervention performed after encoding would selectively improve memory for only the emotionally arousing pleasant and unpleasant images.

2. Material and methods

2.1. Participants

Healthy young adults between the ages of 18 and 35 were recruited through undergraduate courses and listservs at the University of Maryland. A power analysis for a between-subjects mixed analysis of variance was conducted with G*Power using effect sizes from previously published studies comparing the effects of exercise timing on long-term memory. These studies reported η_p^2 values of .16 (Labban & Etnier, 2011) and 0.22 (Labban & Etnier, 2018). Using the more conservative $\eta_p^2 = .16$ generated from a between subjects study design (Labban & Etnier, 2011), the analysis showed that a total sample size of 68 subjects would achieve adequate power (0.8) for both main and interaction effects. Individuals interested in participating completed an online pre-screening questionnaire to determine eligibility. Our goal was to examine the effects of acute aerobic exercise in a healthy and regularly active adult population; therefore, exclusion criteria included: a) a history or current diagnosis of anxiety, depression, or other mood disorder; b) sedentary status defined as self-reported participation in moderate-to-high-intensity physical activity <2 days/week; c) contraindications to moderate-to-high-intensity exercise; or d) participation in previously concluded studies which utilized the same or an overlapping selection of picture stimuli. Participation in a previous study that utilized the same picture stimuli could result in participants recognizing images from the previous investigation. Any individual who scored higher than zero on Question 9 of the Beck Depression Inventory-II (BDI-II), which screens for suicidal ideation, was excluded from further participation and provided with contact information for on-campus mental health and counseling resources.

2.2. Experimental design and procedures

This study utilized a between-subjects experimental design. Eligible

individuals were scheduled for separate study sessions exactly one week apart and typically at the same time of day. Participants were instructed to arrive at the first study session prepared to exercise and to abstain from a) drinking caffeine for 12 h, and b) drinking alcohol or participating in strenuous exercise for 24 h prior to the scheduled visits. Adherence to these instructions was confirmed through self-report at the beginning of each session. Upon enrollment, participants were allocated to exercise-before (ex-before), exercise-after (ex-after), and rest (control) groups based on pre-generated assignment sequences for male and female participants. This approach was designed to ensure a comparable proportion of male and female participants in each experimental group.

Study procedures were approved by the Institutional Review Board at the University of Maryland. At the first study session, participants provided informed consent and completed a health history and demographic questionnaire. Participants also completed the State-Trait Anxiety Inventory Forms Y1–Y2 (STAI-Y1, STAI-Y2; Spielberger, 2010), Beck Depression Inventory II (BDI-II; Beck et al., 1996), Godin Leisure Time Exercise Questionnaire (LTEQ; Godin G & Shephard R.J., 1997), and 7-Day Physical Activity Recall Interview (7-Day PAR; Blair, 1994) to characterize the study sample and ensure eligibility for participation. After completion of questionnaires, the experimenter administered standardized instructions and practice for computerized tasks and self-report scales.

Experimental procedures are depicted in Figure 1. Participants were fitted with a heart rate monitor (Polar® RS800CX, Polar Electro, Kempele, Finland) and completed a 10-min session of quiet seated rest prior to collection of a baseline (T1) saliva sample. The remainder of this study session comprised a pre-encoding interval, encoding task, flanker task, and post-encoding interval. Pre- and post-encoding intervals were completed in accordance with group assignment. Those allocated to the control group completed a seated rest condition during both intervals, while those assigned to ex-before and ex-after groups completed moderate-to-vigorous-intensity cycling exercise during the pre- and post-encoding intervals, respectively. Heart rate (HR) was continuously recorded during baseline quiet seated rest, the exercise and/or rest experimental conditions, the encoding task, and the flanker task procedures. Saliva samples were collected immediately after quiet seated rest (T1), pre-encoding exercise or rest (T2), encoding task (T3), and post-encoding exercise or rest (T4) procedures as depicted in Figure 1.

At the second study session, participants completed the STAI-Y1, STAI-Y2, and 7-Day PAR interview. Participants were fitted with a heart rate monitor and completed another quiet seated rest session prior to receiving standardized instructions and practice on the recognition task. After completion of the recognition task, participants completed a post-experimental questionnaire to assess prior familiarity with the picture stimuli. Participants were then debriefed and fully informed of the complete purpose and hypotheses of the study.

2.3. Acute exercise and rest conditions

The exercise condition consisted of self-regulated cycling on a mechanically braked cycle ergometer (Ergomedic 828E, Monark Exercise AB, Vansbro, Sweden). Participants in the ex-before and ex-after groups completed an acute exercise condition during the pre- and post-encoding intervals, respectively. Participants cycled for a total duration of 24 min comprising a 2-min warm-up, 20-min cycling interval, and 2-min cool down. During the warm-up and cool-down, participants self-selected their cycling speed and resistance. During the exercise interval, participants were instructed to attain and maintain a rating of perceived exertion of 15 ("Hard") on the Borg Rating of Perceived Exertion (RPE) scale, a valid and reliable method for exercise prescription (Dishman, 1994). Pedaling cadence was maintained between 60 and 70 revolutions per minute, while participants adjusted the resistance on the cycle ergometer as needed to maintain the prescribed perception of exertion. We have previously shown that this exercise protocol is effective at elevating sAA, indicating increased noradrenergic signaling (Weiss et al., 2019).

Heart rate and RPE were recorded at baseline, after the warm-up (0-min time point), at 5-, 10-, 15-, and 20-min time points during the exercise interval, and after the cool-down. At these time points, participants provided ratings of affective experience on the Self-Assessment Manikin Valence (SAM-V) and Arousal (SAM-A) dimension scales (Bradley & Lang, 1994) and Borg's Pain Scale (G. Borg, 1998; G. A. Borg, 1982). During the rest condition(s), participants were seated quietly in a chair for 20 min while identical measurements were collected at 0-, 5-, 10-, 15-, and 20-min time points. During both conditions, an

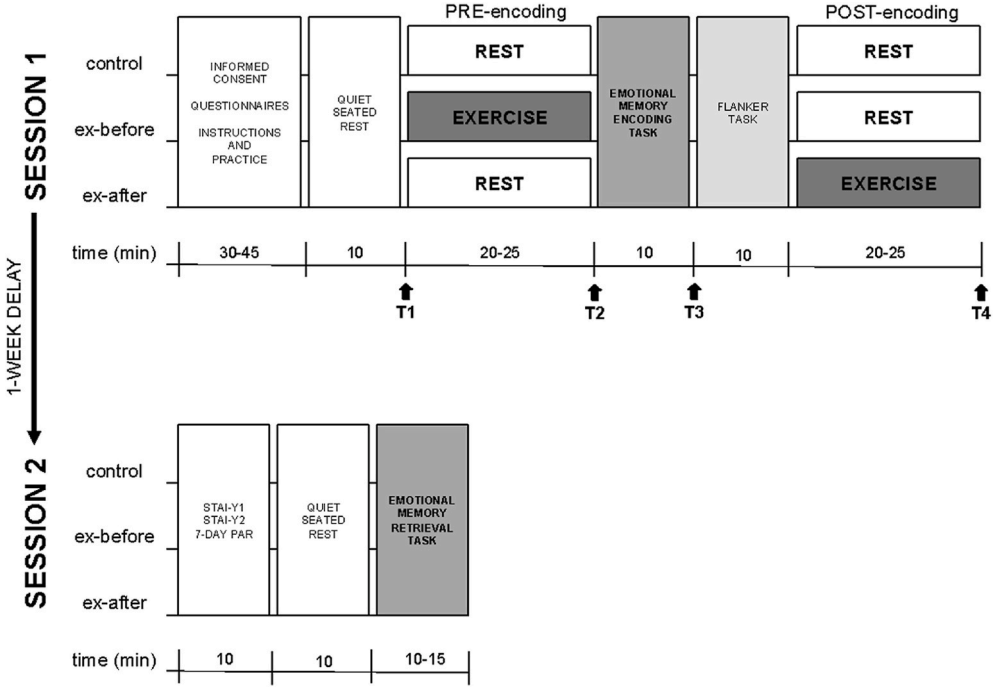

Figure 1. Experimental procedures. Arrows indicate timing of saliva collection. Timing is approximate.

experimenter remained in the room and participants were restricted from technology use, reading, and excessive talking. Water was provided ad libitum, except the 10 min prior to saliva sample collection.

2.4. Salivary alpha-amylase measurement

Saliva samples were obtained using the passive drool method. This method is recommended over the alternative oral swab method as a means of collecting unstimulated whole saliva from adults in a supervised laboratory setting (Rohleder & Nater, 2009). Collected samples were immediately stored on ice and subsequently frozen at −20 °C. Alpha-amylase activity was quantified using a commercially available enzymatic assay (Salivary Alpha-Amylase Kinetic Enzyme Assay Kit, Salimetrics, State College, PA). On the day of the assay, samples were thawed and diluted with the provided alpha-amylase diluent (1:200) and combined with the provided alpha-amylase substrate (37 °C) immediately before absorbance measurement. Absorbance at 1- and 3-min time points was measured with a 405 nm filter on a programmable microplate reader (Synergy H1 Hybrid Multi-Mode Reader, BioTek Instruments, Inc., Winooski, VT) set to incubate at 37 °C. Each sample was analyzed in duplicate during the same absorbance reading cycle. For quality control purposes, high and low concentration controls provided by the manufacturer were included on each plate. Sample duplicates with a coefficient of variation (CV) $< 10\%$ were averaged together for each measurement. Duplicate pairs with a CV $\geq 10\%$ were excluded and re-assessed in up to two subsequent measurements. The detection limit was equivalent to a change in absorbance <0.01. The linearity limit at the given dilution was 400 U/mL. Samples that fell outside this range were excluded from statistical analysis. Only participants with intact data points for all sAA measurements were included in applicable statistical analyses. Samples from 6 participants ($n = 1$ control, $n = 3$ ex-before, $n = 2$ ex-after) were excluded due to: failure to provide a saliva sample of adequate volume ($n = 2$), sAA values exceeding the upper linearity limit ($n = 1$), sAA values below the assay detection limit ($n = 2$), and/or duplicate sAA samples with CV $\geq 10\%$ ($n = 1$).

2.5. Emotional memory task

The emotional memory task utilized a remember-know paradigm (Tulving, 1985) and comprised an encoding procedure and recognition task. The encoding and recognition portions of the memory task were completed at the first and second study sessions, and therefore were separated by one week. Tasks were presented using E-Prime 2.0 Software (Psychology Software Tools, Pittsburgh, PA) on a 15" monitor.

Pictures from the International Affective Picture System (IAPS) were selected as stimuli based on normative valence and arousal ratings from male and female participants (Lang et al., 2008). The complete selection of stimuli included 60 pleasant, 60 neutral, and 60 unpleasant pictures. Images in the emotional (pleasant and unpleasant) categories were defined as those with a normative Self-Assessment Manikin-Arousal (SAM-A) rating ≥6.0 (defined as highly arousing, Lang et al., 2008). From the emotional pictures meeting this criterion, pleasant and unpleasant pictures were selected based on a normative Self-Assessment Manikin-Valence (SAM-V) rating ≥6.0 (i.e., pleasant) or ≤ 4.0 (i.e., unpleasant), respectively. The images selected within the neutral picture category had an arousal rating ≤4.0 (i.e., minimally arousing). The selected stimuli were used to create two encoding task versions each comprising 90 pictures: 30 pleasant, 30 neutral, and 30 unpleasant. The two versions were matched on semantic content (e.g., a comparable number of scenes, people, and animals) and were equivalent on normative valence (SAM-V) and arousal (SAM-A) ratings within pleasant, neutral, and unpleasant categories (Table S1). Encoding task version was counterbalanced across participants.

The encoding task was completed during the first study session. Participants were informed that their memory for the pictures would be tested at the next study session and were instructed to attend to the pictures as they appeared on the screen. During the encoding task, participants passively viewed the pictures as they were presented on the screen. The order of picture presentation within each task version was predetermined at the beginning of the study, and this order was maintained for all participants. The presentation order was pseudo-randomized such that no more than 3 images within pleasant, neutral, or unpleasant categories were presented sequentially. Pictures were presented individually for a duration of 3000 ms. A fixation cross was displayed during the inter-stimulus interval, which lasted for a randomly selected duration of 3000, 3500, or 4000 ms. The duration of the encoding task was approximately 10 min. An experimenter remained in the room for the entirety of the task.

The recognition task was completed during the second study session one week after the encoding procedure was performed (Cahill, 2003; Cahill & Alkire, 2003; Liu et al., 2008; Loprinzi et al., 2022; Segal & Cahill, 2009). Scripted instructions were provided by the experimenter. As each picture was presented on the screen, participants were first asked to indicate whether they had seen that picture during the encoding task. Participants were instructed to indicate that a picture was "old" if it was presented during encoding, and "new" if it had not been presented to them at the first study session. For each "old" response, the task continued to a screen prompting the participant to report if the picture was "remember[ed]" or "familiar." The distinction between responses was described using instructions adapted from (Dudukovic & Knowlton, 2006). Briefly, participants were instructed, "For this test, remembering a picture would signify that the picture evokes specific memories of what was experienced during its presentation, such as how it looked on the screen, the way in which it was presented, or even what you were thinking or doing at the time it was shown. Knowing a picture would signify that you are confident the picture appeared, but cannot recollect any aspects of its presentation." The recognition task included the complete selection of 180 pictures (i.e., from both task versions) presented to all participants in a predetermined order. The order of stimulus presentation was pseudo-randomized such that no more than 3 pictures from a given task version were presented sequentially. The recognition task was self-paced, with a typical duration of approximately 10–15 min.

2.6. Flanker task

Participants performed a flanker task after completion of the encoding procedure. The flanker task was included as a distractor that was consistent across experimental groups. The aim of administering a distractor task was to ensure that participants in the exercise-before and control groups did not have the advantage of perseverating or mentally reciting the encoded pictures immediately upon completion of picture viewing, while the exercise-after group was preparing for and engaging in the exercise bout. The task was presented using E-Prime 2.0 Software (Psychology Software Tools, Pittsburgh, PA) and responses were provided on the button response box. Flanker task duration was approximately 10 min.

2.7. Statistical analyses

Statistical analyses were performed using IBM SPSS Statistics Version 25. An alpha value of 0.05 was set as the threshold for significance. Shapiro-Wilk statistics and Q-Q plots were examined to evaluate deviations of the data from normality. Levene's tests were used to assess homogeneity of variance between independent samples. When assumptions of the parametric test were not satisfied, we utilized non-parametric statistics or transformed data as appropriate. For ANOVA procedures with more than two repeated measures, Huynh-Feldt adjustment was used when Mauchly's test of sphericity met significance. Significant omnibus tests were further examined with pairwise comparisons using independent samples or paired tests as appropriate. We controlled the probability of type I error within each family of tests

using the False Discovery Rate (FDR) at a threshold (q) of 0.05 (Benjamini & Hochberg, 1995); therefore, the threshold for statistical significance was adjusted as a function of the number of tests conducted and unadjusted p values are reported.

Sample characteristics, including psychometric and physical activity measures, were compared between randomly assigned groups using one-way analysis of variance (ANOVA). Trait anxiety scores (STAI-Y2) were averaged across study sessions. We compared repeated measures of state anxiety (STAI-Y1) and physical activity over the past week (7-Day PAR) between study visits using paired t tests. To evaluate the success of our stratified random assignment and counterbalancing procedures, relations of sex and list with group assignment were examined using the chi-square test for independence.

Physiological and psychological measures during exercise and rest conditions were averaged across 5-, 10-, 15-, and 20-min time points to capture the exercise interval and corresponding control (i.e., resting) interval for the conditions, respectively. We compared average HR (HR_{avg}) between pre- and post-encoding intervals using paired t tests *within* each group. Due to the ordinal nature of the RPE (RPE_{avg}), pain ($pain_{avg}$), valence ($SAM\text{-}V_{avg}$) and arousal ($SAM\text{-}A_{avg}$) data, within-group comparisons between pre- and post-encoding intervals were conducted using non-parametric Wilcoxon signed-rank tests. Levene's tests on HR_{avg} indicated inhomogeneity of variance between groups within both pre-encoding ($W(2, 69) = 11.579$, $p < .001$) and post-encoding ($W(2, 69) = 6.843$, $p = .002$) intervals. Therefore, between-group comparisons of HR_{avg}, RPE_{avg}, $pain_{avg}$, $SAM\text{-}V_{avg}$ and $SAM\text{-}A_{avg}$ ratings were conducted using non-parametric Krukal-Wallis H tests. Post hoc comparisons for these measures were conducted using non-parametric Mann-Whitney U tests. Exercise intervals were compared between the ex-before and ex-after group with an independent samples t-test (HR_{avg}) and Mann-Whitney U tests.

Review of Q-Q plots and Shapiro-Wilk statistics suggested that sAA measurements were positively skewed and leptokuric; therefore, we applied a square root transformation ($\sqrt{sAA}$) to these data (Granger et al., 2007). Square root-transformed sAA was compared between groups at baseline using a one-way ANOVA. We examined the change in $\sqrt{}$ sAA over time within each group using repeated measures ANOVAs. To account for the potential impact of sex on $\sqrt{sAA}$, sex was also included in each model as a nominal between-subjects factor. Significant omnibus tests were further deconstructed using paired-samples t tests with baseline ($\sqrt{sAA}_{T1}$) as the comparator for all subsequent time points ($\sqrt{sAA}_{T2}$, $\sqrt{sAA}_{T3}$, $\sqrt{sAA}_{T4}$). We additionally examined whether change in $\sqrt{sAA}$ during exercise ($\sqrt{sAA}_{EX}$) was equivalent between the ex-before and ex-after groups using an independent samples t-test.

Indices of memory performance were calculated from signal detection theory. Signal detection theory provides a method of estimating sensitivity and response bias, where sensitivity (or "discriminability") refers to the ability to discriminate between the presence or absence of a signal (e.g., an encoded memory). These indices are derived from raw counts of a) previously encoded items correctly identified as old ("hit") or incorrectly identified as new ("miss"), and b) novel items correctly identified as new ("correct rejection") or incorrectly identified as old ("false alarm"). The parametric statistic d' reflects both discriminability and response bias and is calculated as the difference between z-scored hit rate and false alarm rate. The d' statistic was calculated using log-linear adjustment for extreme values as recommended by (Hautus, 1995). Recollection and familiarity were assessed by calculating the proportion of hits that were subjectively identified as "remembered." We conducted 3 (group: rest, ex-before, ex-after) × 3 (picture type: pleasant, neutral, unpleasant) mixed-model ANOVAs to determine the effects and interaction of group (between-subjects factor) and picture type (within subjects factor) on d' and the proportion of remembered hits. To determine a relationship between sAA and d', a Pearson's correlation analysis was completed.

3. Results

3.1. Study sample size and characteristics

Eighty-one participants (52F/29M) provided informed consent and were enrolled in the study. Seven participants (5F/2M) did not complete the study procedures and one participant (M) was excluded due to indication of suicidal ideation. The number of participants included in the final analyses was comparable across ex-before (n = 24), ex-after (n = 25), and control (n = 23) groups. Sample demographics and characteristics are summarized in Table 1. There were no significant between-group differences in age, depression symptoms, trait anxiety, or leisure-time exercise. Paired t-tests indicated no significant within-subject differences between state anxiety (STAI-Y2; $t(73) = -0.267$, $p = .790$) or weekly physical activity (7-Day PAR; $t(73) = 0.349$, $p = .728$) measured at the first and second study visits. Between-group comparisons revealed no between-group difference in state anxiety ($F(2, 71) = 0.708$, $p = .496$; $F(2, 71) = 0.886$, $p = .417$) or past-week physical activity ($F(2, 71) = 0.909$, $p = .408$; $F(2, 71) = 0.657$, $p = .521$) measured at either study visit.

3.2. Acute exercise manipulation check

Physiological and psychological measurements collected during the acute exercise and rest conditions are summarized in Table 2. Taken together, these results indicate a successful intervention such that physiological and psychological measures accompanying exercise were significantly different than rest conditions performed by the same participants, and rest conditions performed within the same time intervals.

Table 1
Sample demographics and characteristics. Values reported as mean ± standard deviation. Omnibus between-group comparisons conducted using one-way analysis of variance and chi-square test of independence. GBDI-II, Beck Depression Inventory II; STAI-Y1, State-Trait Anxiety Inventory Form Y1; STAI-Y2, State-Trait Anxiety Inventory Form Y-2; LTEQ, Godin Leisure Time Exercise Questionnaire; 7-Day PAR, 7-Day Physical Activity Recall Interview Questionnaire.

Variable	Group			Between-Group Comparison	Total Sample
	Control	Ex-Before	Ex-After	p value	
N	23	24	25	–	72
Age (years)	21.0 ± 2.2	21.6 ± 4.0	21.6 ± 4.0	0.800	21.4 ± 3.5
Sex	14F, 9M	15F, 9M	17F, 8M	0.863	46F, 26M
Depression symptoms (BDI-II)	6.6 ± 4.3	5.3 ± 4.4	5.3 ± 3.1	0.451	5.7 ± 3.95
Trait anxiety (STAI-Y1)	35.9 ± 7.7	33.9 ± 6.7	34.7 ± 7.7	0.637	34.8 ± 7.3
State anxiety (STAI-Y1), Session 1	30.7 ± 7.9	30.5 ± 6.4	28.4 ± 8.4	0.496	29.8 ± 7.6
State anxiety (STAI-Y1), Session 2	32.1 ± 11.1	28.6 ± 8.7	29.9 ± 7.2	0.417	30.2 ± 9.1
Leisure time physical activity (LTEQ), hrs/wk	93.1 ± 35.2	117.2 ± 61.1	113.4 ± 63.7	0.283	108.2 ± 55.5
Leisure and occupational physical activity (7-Day PAR, kJ/kg/day), Session 1	124.9 ± 17.0	131.2 ± 17.1	131.9 ± 24.1	0.408	129.4 ± 19.7
Leisure and occupational physical activity (7-Day PAR, kJ/kg/day), Session 2	126.8 ± 21.1	132.8 ± 20.0	128.0 ± 16.0	0.521	129.2 ± 19.0

Table 2
Physiological and psychological variables measured during pre-encoding and post-encoding exercise and rest. Values reported as mean ± standard deviation. Omnibus between-group comparisons conducted using Kruskal-Wallis *H* tests. Pairwise comparisons conducted using Mann-Whitney *U* tests. Common superscripts indicate significant within-group differences between pre- and post-encoding intervals revealed by Wilcoxon signed-rank tests. All within-group *p* values < .001. Ex-B, ex-before group; Ex-A, ex-after group; C, control group; HR_{avg} (bpm), average heart rate (beats per minute); RPE_{avg}, average rating of perceived exertion; $Pain_{avg}$, average pain scale rating; SAM-V_{avg}, average Self-Assessment Manikin Valence rating; SAM-A_{avg}, average Self-Assessment Manikin Arousal rating.

Pre-Encoding Interval				Between-Group	Pairwise Comparisons		
	Group			Comparison	Ex-B - C	Ex-A - C	Ex-B - Ex-A
	Control	Ex-Before	Ex-After	*p* value	*p* value	*p* value	*p* value
HR_{avg} (bpm)	68.4 ± 7.2	153.0 ± 19.2[a]	64.5 ± 10.6[b]	**<.001**	**< .001**	.055	**<.001**
RPE_{avg}	6.1 ± 0.5	14.1 ± 0.9[c]	6.1 ± 0.3[d]	**<.001**	**<.001**	.546	**<.001**
$Pain_{avg}$	0.1 ± 0.2	1.4 ± 1.2[e]	0.1 ± 0.4[f]	**<.001**	**<.001**	.749	**<.001**
SAM-V_{avg}	6.1 ± 1.4	6.2 ± 1.3	6.2 ± 1.9	.834	.779	.582	.688
SAM-A_{avg}	1.5 ± 0.8	5.9 ± 1.8[g]	1.9 ± 1.5[h]	**<.001**	**<.001**	.657	**<.001**
Post-Encoding Interval							
HR_{avg} (bpm)	67.3 ± 7.0	74.3 ± 12.2[a]	155.7 ± 16.7[b]	**<.001**	**.037**	**<.001**	**<.001**
RPE_{avg}	6.2 ± 0.5	6.1 ± 0.4[c]	14.1 ± 0.9[d]	**<.001**	.158	**<.001**	**<.001**
$Pain_{avg}$	0.0 ± 0.1	0.2 ± 0.6[e]	1.6 ± 1.1[f]	**<.001**	.927	**<.001**	**<.001**
SAM-V_{avg}	5.6 ± 1.3	6.4 ± 1.9	5.9 ± 1.3	.255	.168	.176	.451
SAM-A_{avg}	1.6 ± 0.9	1.8 ± 1.2[g]	5.9 ± 1.4[h]	**<.001**	.589	**<.001**	**<.001**

3.3. Salivary alpha-amylase

Square root-transformed sAA data are presented in Figure S1 and Table S2. No between-group difference in $\sqrt{sAA}$ was detected at baseline ($\sqrt{sAA}_{T1}$; $F(2, 65) = 0.503$, $p = .607$). Two-way repeated measures ANOVAs revealed significant main effects of time on $\sqrt{sAA}$ in the ex-before ($F(3, 57) = 4.318$, $p = .008$, $\eta_p^2 = 0.158$) and ex-after ($F(3, 63) = 9.707$, $p < .001$, $\eta_p^2 = 0.316$) groups. No significant main effect of time was revealed in the control group ($F(3, 60) = 2.040$, $p = .118$, $\eta_p^2 = 0.093$). No significant main effects of sex or interactions of sex and time on $\sqrt{sAA}$ were revealed. *Post hoc* paired *t* tests were conducted to compare $\sqrt{sAA}$ at baseline (T1) with T2, T3, and T4 measurements within exercise groups. In the ex-before group, $\sqrt{sAA}_{T2}$ was significantly higher than $\sqrt{sAA}_{T1}$ ($t(20) = 3.254$, $p = .004$). Neither $\sqrt{sAA}_{T3}$ ($p = .251$) nor $\sqrt{sAA}_{T4}$ ($p = .296$) significantly differed from $\sqrt{sAA}_{T1}$. In the ex-after group, $\sqrt{sAA}_{T4}$ was significantly higher than $\sqrt{sAA}_{T1}$ ($t(22) = 5.115$, $p < .001$). Neither $\sqrt{sAA}_{T2}$ ($p = .603$) nor $\sqrt{sAA}_{T3}$ ($p = .297$) significantly differed from $\sqrt{sAA}_{T1}$. There was no significant difference in the sAA response to exercise ($\Delta\sqrt{sAA}_{EX}$) between ex-before and ex-after groups ($t(41) = 0.426$, $p = .673$).

3.4. Recognition memory signal detection indices

Analysis of *d'* revealed significant main effects of valence ($F(1.861, 128.387) = 6.993$, $p = .002$, $\eta_p^2 = 0.092$) and group ($F(2, 69) = 4.201$, $p = .019$, $\eta_p^2 = 0.109$). No interaction of valence and group was detected ($p = .785$). *Post hoc* paired *t* tests indicated that *d'* was significantly higher for unpleasant than pleasant ($t(71) = 3.361$, $p = .001$) and neutral ($t(71) = 3.763$, $p < .001$) pictures (see Figure 2). Independent samples *t* tests revealed higher *d'* in the ex-after group relative to the control group ($t(46) = 2.641$, $p = .011$), but no further pairwise differences between groups (see Figure 3).

Analysis of recollection and familiarity revealed a significant main effect of valence on the proportion of remembered hits ($F(2, 138) = 35.796$, $p < .001$, $\eta_p^2 = 0.342$). No main effect of group ($p = .496$) nor interaction of valence and group ($p = .086$) was revealed. *Post hoc* paired *t* tests indicated a higher proportion of remembered hits for unpleasant pictures relative to pictures in the neutral ($t(71) = 7.548$, $p < .001$) and pleasant ($t(71) = 6.010$, $p < .001$) categories. There were no significant correlations between change in salivary alpha amylase and indices of recognition memory (data not shown).

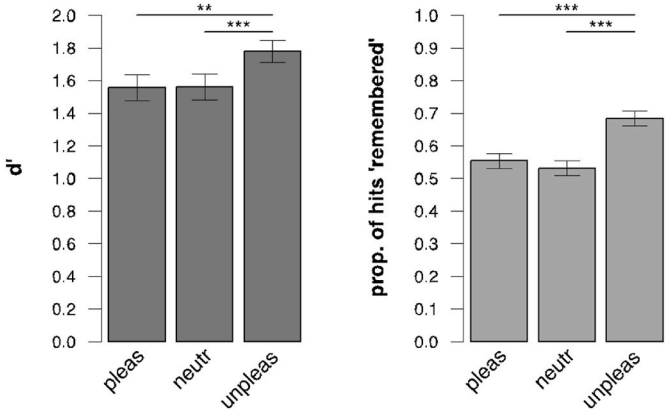

Figure 2. Signal detection indices of memory for pleasant, neutral, and unpleasant picture categories. Columns and error bars represent mean ± standard error of the mean. Asterisks indicate a statistically significant pairwise difference indicated by paired *t*-test corrected for multiple comparisons using FDR; *$p < .05$, **$p < .01$, ***$p < .001$.

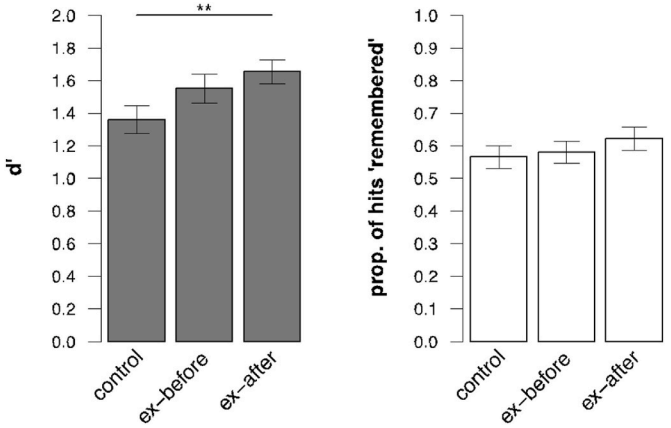

Figure 3. Signal detection indices of memory for control, ex-before, and ex-after groups. Columns and error bars represent mean ± standard error of the mean. Asterisks indicate a statistically significant pairwise difference indicated by independent samples *t*-test corrected for multiple comparisons using FDR; *$p < .05$, **$p < .01$.

4. Discussion

We found that a single bout of moderate-to-vigorous intensity cycling exercise immediately following image viewing (during consolidation) improved long-term recognition memory for images, with no specificity for image valence. This memory enhancing effect of exercise was not observed when exercise was performed before image viewing (pre-encoding). Importantly, this self-perceived "hard" cycling was an exercise exposure of sufficient intensity and duration to elevate salivary alpha amylase, a marker of central noradrenergic signaling, yet there were no significant correlations between change in salivary alpha amylase and recognition memory. These findings suggest that exercise induced arousal during consolidation, but not pre-encoding, improves long-term memory formation, though our data do not support that central noradrenergic signaling is mediating this effect.

4.1. Memory enhanced by physiological arousal, stress, and exercise

The finding that acute exercise during consolidation improved recognition memory is consistent with previous research in stress and arousal. Acute arousal, whether psychological or physical, during the consolidation phase of memory formation is known to improve long-term memory (McGaugh, 2013). In human subjects, a variety of laboratory arousal stimuli and stressors, such as the cold pressor test (Cahill, 2003), the Trier Social Stress Test (Jiang et al., 2019; Preuβ & Wolf, 2009), viewing a video of oral surgery (Nielson & Arentsen, 2012; Nielson et al., 2005; Nielson & Powless, 2007), or performing aerobic exercise (Hötting et al., 2016; Jentsch & Wolf, 2020; Loprinzi et al., 2019; Most et al., 2017; Segal et al., 2012; van Dongen et al., 2016), when induced or performed after encoding, all improve performance on memory tasks. Although physical exercise and psychological arousal and stress differ in many aspects (threat, anxiety, panic, etc.), it has been suggested that the memory enhancing effects of acute exercise are due to elevated arousal and/or circulating stress hormones (McMorris, 2021). Indeed, our RPE-based hard exercise was sufficient to increase sAA, a marker of central noradrenergic signaling, indicating that central noradrenergic activity was increased during and following acute exercise. Regardless of the placement of exercise relative to learning, the exercise stimulus increased sAA, consistent with previous findings (Weiss et al., 2019). However, contrary to our hypothesis, our data suggest that this arousal is effective at improving memory only when experienced during consolidation. An important consideration is that we do not have measurements of sAA during the picture viewing task, so we are unable to determine how long sAA remained elevated in the exercise-before group. It is possible that sAA returned to baseline early in the picture viewing session, and as such noradrenergic activity may not have remained elevated for the duration of the encoding period (Perini et al., 1989). This is an important question to be addressed in future research. Nevertheless, the lack of association between changes in sAA after exercise and long-term recognition memory performance suggests that mechanisms independent of noradrenergic spillover into saliva, such as a delayed exercise-induced elevation in the stress hormone cortisol, may be more important for the observed effects. Unfortunately, we were not able to measure additional stress hormones or obtain blood samples.

4.2. The timing of exercise

Meta-analyses and reviews of literature suggest that acute exercise performed in close temporal proximity to learning, whether before or after, can improve recall and recognition assessed at a later time point (Lambourne & Tomporowski, 2010; Loprinzi et al., 2019; Roig et al., 2016), however studies that have compared exercise before and after learning have found that exercise before learning is more effective at improving memory (Labban & Etnier, 2011, 2018; Salas et al., 2011). For example, Labban and Etnier (2018) reported that 30 min of moderate-intensity cycling prior to performing the learning trials of the Rey Auditory Verbal Learning Task improved memory for the learned words at 60 min and 24 h later. Exercise after the learning trials did not improve memory compared to the no exercise control condition. These results are similar to a study by the same investigators in 2011 that reported recall of a brief story was better when 30 min of exercise was performed prior to auditory exposure to the story (Labban & Etnier, 2011). Again, recall was not better when exercise was performed after exposure to the brief story.

Although studies that have compared exercise performed pre-encoding versus exercise during consolidation have found exercise pre-encoding to be more effective, several studies that have demonstrated a benefit of exercise during consolidation have utilized IAPS stimuli as the to-be remembered content (Segal et al., 2012; Weinberg et al., 2014), or other forms of emotional content (Jentsch & Wolf, 2020; Keyan & Bryant, 2017). This is consistent with other studies that have demonstrated that exposure to an acute stressor during consolidation is effective at improving memory only for emotional content (Cahill, 2003; Segal & Cahill, 2009). Studies that have demonstrated a benefit of exercise before learning, with no benefit of exercise during consolidation, have generally utilized to-be remembered content with low arousal or valence, such as the Rey Auditory Verbal Learning Task or other word lists with neutral valence and arousal. We speculate that some level of arousal during encoding is important for post-learning exercise to be effective at improving memory. Indeed, a recent study by Slutsky-Ganesh et al. (2020) compared 20 min of exercise before learning, 20 min of exercise during consolidation, and a group that performed 10 min of exercise before and 10 min after learning. The to-be remembered content in the study was of low arousal and valence, consistent with previous studies comparing exercise before and exercise after learning. The researchers found that the group performing 10 min of exercise before and after learning had better recall and recognition 24 h later compared to the no exercise group, an effect not seen in the groups that performed 20 min of exercise before or after learning. Recent work by Loprinzi et al. (2021) also demonstrated that a combination of exercise before encoding and after encoding is more effective for improving memory of neutral stimuli compared to exercise occurring either before or after encoding. This further supports the notion that arousal at encoding is important for the memory enhancing effects of exercise during consolidation. Like our current investigation, Segal & Cahill (2012) and Weinberg et al. (2014) showed that acute exercise performed post learning improved memory, and both studies used IAPS images as the to be remembered content. Using this approach, the images themselves provoke arousal during encoding. The fact that the unpleasant pictures were rated as slightly more arousing than the pleasant pictures in our study supports the finding for greater d' and proportion of hits remembered for the unpleasant images compared to pleasant and neutral images. Recently, two studies reported no effect of post-encoding exercise on memory for emotional images (Loprinzi et al., 2022; Smith et al., 2022), though differences in study design may explain the discrepancy between the findings of these studies and the current investigation. Although the exercise in Smith et al. (2022) was a similar intensity as the exercise in our investigation, they utilized a 6-min stepping test as their exercise stimulus and tested recognition memory approximately 1 h after encoding. Loprinzi et al. (2022) utilized 15 min of high-intensity treadmill running. More research is needed to identify the optimal mode and duration of exercise necessary to enhance memory with post-encoding exercise.

Although individuals who performed acute exercise after encoding showed better recognition memory compared to no exercise, there was no effect of exercise on recollection versus familiarity. Participants had higher recollection for unpleasant images compared to neutral or pleasant images, but exercise did not influence recollection or familiarity. Weinberg et al. (2014) also assessed the effect of exercise during consolidation on recollection versus familiarity for emotional images, and similar to the current study, found no significant effect of the

exercise treatment on strength of memories.

4.3. Interactions with valence of affective stimuli

We hypothesized that exercise during consolidation would improve memory of the emotional images (i.e., pleasant and unpleasant) more than memory of neutral images, yet this was not observed. Our encoding stimulus was a collection of mixed images of different subjective valence and arousal ratings, as opposed to blocks of similar images. Potentially, including arousing images intermixed with the neutral images in the image suite leads to carry over arousal that impacts encoding of temporally nearby images. This, however, is not reflected in the sAA levels measured before and after the encoding. Although this suggests that picture viewing was not arousing, it is possible that the sAA assay is not sensitive enough to detect small changes that may be occurring during the picture viewing task. Alternatively, post learning exercise-induced arousal may enhance consolidation of neutral images as effectively as emotional images, which has been shown with word recall of neutral and emotional words learned before watching an arousing video (Nielson & Lorber, 2009).

4.4. Limitations

Our sample consisted of young healthy adults who were undergraduate students at a large public university, which limits the generalizability of our findings. We are not able to determine if these effects would be observed in less educated, less physically active, or middle-aged or older adults. The set of visual stimuli to be remembered were derived from the IAPS, a standardized and widely employed set of affective images; the two versions of stimuli were equivalent in subjective ratings of valence and arousal within each affective category and were counterbalanced between sessions. However, the unpleasant images were rated as more arousing than the pleasant images on average; a common characteristic of IAPS studies, and a minor weakness of our study.

5. Conclusions

A single session of moderate-to-vigorous intensity stationary cycling exercise immediately after the viewing of pleasant, neutral, and unpleasant pictures improved long-term recognition memory one week later for both the emotional and neutral images. This memory enhancing effect of acute exercise was specific to the consolidation period and was not observed when exercise was performed prior to encoding. These findings suggest that exercise may enhance long-term recognition memory for visual stimuli in younger adults, and may have implications for strategies to enhance memory for visual experiences across the lifespan.

Funding

This project was funded by a Graduate Research Initiative Project Award by the Department of Kinesiology at the University of Maryland.

Declaration of competing interest

All authors on this manuscript confirm that they have no conflicts of interest to declare.

Data availability

Data will be made available on request.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.psychsport.2023.102498.

References

Beck, A. T., Steer, R. A., & Brown, G. K. (1996). *Manual for the Beck depression inventory-II*. Psychological Corporation.

Benjamini, Y., & Hochberg, Y. (1995). Controlling the false Discovery rate: A practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society: Series B, 57*(1), 289–300. https://doi.org/10.1111/j.2517-6161.1995.tb02031.x

Blair, S. N. (1994). *How to assess exercise habits and physical fitness* (pp. 424–477). Behavioral Health: A Handbook of Health Enhancement and Disease Prevention.

Borg, G. A. (1982). Psychophysical bases of perceived exertion. *Medicine & Science in Sports & Exercise, 14*(5), 377–381.

Borg, G. (1998). *Borg's perceived exertion and pain scales. Human Kinetics* (pp. 39–43).

Bradley, M. M., & Lang, P. J. (1994). Measuring emotion: The self-assessment manikin and the semantic differential. *Journal of Behavior Therapy and Experimental Psychiatry, 25*(1), 49–59. https://doi.org/10.1016/0005-7916(94)90063-9

Cahill, L. (2003). Enhanced human memory consolidation with post-learning stress: Interaction with the degree of arousal at encoding. *Learning & Memory, 10*(4). https://doi.org/10.1101/lm.62403

Cahill, L., & Alkire, M. T. (2003). Epinephrine enhancement of human memory consolidation: Interaction with arousal at encoding. *Neurobiology of Learning and Memory, 79*(2). https://doi.org/10.1016/S1074-7427(02)00036-9

Cahill, L., Prins, B., Weber, M., & McGaugh, J. L. (1994). β-Adrenergic activation and memory for emotional events. *Nature, 371*(6499), 702–704. https://doi.org/10.1038/371702a0

Callow, D. D., Won, J., Alfini, A. J., Purcell, J. J., Weiss, L. R., Zhan, W., & Smith, J. C. (2021). Microstructural plasticity in the Hippocampus of healthy older adults after acute exercise. *Medicine & Science in Sports & Exercise, 53*(9), 1928–1936. https://doi.org/10.1249/MSS.0000000000002666

Chatterton, R. T., Vogelsong, K. M., Lu, Y., Ellman, A. B., & Hudgens, G. A. (1996). Salivary α-amylase as a measure of endogenous adrenergic activity. *Clinical Physiology, 16*(4), 433–448. https://doi.org/10.1111/j.1475-097X.1996.tb00731.x

Colcombe, S., & Kramer, A. F. (2003). Fitness effects on the cognitive function of older adults. *Psychological Science, 14*(2), 125–130. https://doi.org/10.1111/1467-9280.t01-1-01430

Coles, K., & Tomporowski, P. D. (2008). Effects of acute exercise on executive processing, short-term and long-term memory. *Journal of Sports Sciences, 26*(3), 333–344. https://doi.org/10.1080/02640410701591417

Diamond, D. M., Campbell, A. M., Park, C. R., Halonen, J., & Zoladz, P. R. (2007). The temporal dynamics model of emotional memory processing: A synthesis on the neurobiological basis of stress-induced Amnesia, flashbulb and traumatic memories, and the Yerkes-dodson law. *Neural Plasticity, 1–33*. https://doi.org/10.1155/2007/60803

Dishman, R. K. (1994). Prescribing exercise intensity for healthy adults using perceived exertion. *Medicine & Science in Sports & Exercise, 26*(9), 1087–1094.

van Dongen, E.v., Kersten, I. H. P., Wagner, I. C., Morris, R. G. M., & Fernández, G. (2016). Physical exercise performed four hours after learning improves memory retention and increases Hippocampal pattern similarity during retrieval. *Current Biology, 26*(13), 1722–1727. https://doi.org/10.1016/j.cub.2016.04.071

Dudukovic, N. M., & Knowlton, B. J. (2006). Remember–Know judgments and retrieval of contextual details. *Acta Psychologica, 122*(2), 160–173. https://doi.org/10.1016/j.actpsy.2005.11.002

Etnier, J. L., Wideman, L., Labban, J. D., Piepmeier, A. T., Pendleton, D. M., Dvorak, K. K., & Becofsky, K. (2016). The effects of acute exercise on memory and brain-derived neurotrophic factor (BDNF). *Journal of Sport & Exercise Psychology, 38*(4), 331–340. https://doi.org/10.1123/jsep.2015-0335

Godin, G., & Shephard, R. J. (1997). Godin leisure-time exercise questionnaire. *Medicine & Science in Sports & Exercise, 29*(6s), s36.

Granger, D. A., Kivlighan, K. T., El-Sheikh, M., Gordis, E. B., & Stroud, L. R. (2007). Salivary -amylase in biobehavioral research: Recent developments and Applications. *Annals of the New York Academy of Sciences, 1098*(1), 122–144. https://doi.org/10.1196/annals.1384.008

Hautus, M. J. (1995). Corrections for extreme proportions and their biasing effects on estimated values ofd. *Behavior Research Methods, Instruments, & Computers, 27*(1), 46–51. https://doi.org/10.3758/BF03203619

Hillman, C. H., Erickson, K. I., & Kramer, A. F. (2008). Be smart, exercise your heart: Exercise effects on brain and cognition. *Nature Reviews Neuroscience, 9*(1). https://doi.org/10.1038/nrn2298

Hötting, K., Schickert, N., Kaiser, J., Röder, B., & Schmidt-Kassow, M. (2016). The effects of acute physical exercise on memory, peripheral BDNF, and cortisol in young adults. *Neural Plasticity, 2016*. https://doi.org/10.1155/2016/6860573

Hu, H., Real, E., Takamiya, K., Kang, M.-G., Ledoux, J., Huganir, R. L., & Malinow, R. (2007). Emotion enhances learning via norepinephrine regulation of AMPA-receptor trafficking. *Cell, 131*(1), 160–173. https://doi.org/10.1016/j.cell.2007.09.017

Jentsch, V. L., & Wolf, O. T. (2020). Acute physical exercise promotes the consolidation of emotional material. *Neurobiology of Learning and Memory, 173*. https://doi.org/10.1016/j.nlm.2020.107252

Jiang, A., Tran, T. T., Madison, F. N., & Bakker, A. (2019). Acute stress-induced cortisol elevation during memory consolidation enhances pattern separation. *Learning & Memory, 26*(4). https://doi.org/10.1101/lm.048546.118

Keyan, D., & Bryant, R. A. (2017). Brief exercise enhances intrusive memories of traumatic stimuli. *Neurobiology of Learning and Memory, 141*, 9–13. https://doi.org/10.1016/j.nlm.2017.03.012

Labban, J. D., & Etnier, J. L. (2011). Effects of acute exercise on long-term memory. *Research Quarterly for Exercise & Sport, 82*(4), 712–721. https://doi.org/10.1080/02701367.2011.10599808

Labban, J. D., & Etnier, J. L. (2018). The effect of acute exercise on encoding and consolidation of long-term memory. *Journal of Sport & Exercise Psychology, 40*(6), 336–342. https://doi.org/10.1123/jsep.2018-0072

Lalumiere, R. T., McGaugh, J. L., & McIntyre, C. K. (2017). Emotional modulation of learning and memory: Pharmacological implications. *Pharmacological Reviews, 69*(3), 236–255. https://doi.org/10.1124/pr.116.013474

Lambourne, K., & Tomporowski, P. (2010). The effect of exercise-induced arousal on cognitive task performance: A meta-regression analysis. *Brain Research, 1341*, 12–24. https://doi.org/10.1016/j.brainres.2010.03.091

Lang, P. J., Bradley, M. M., & Cuthbert, B. N. (2008). International affective picture system (IAPS): Affective ratings of pictures and instruction manual. In *Technical report A-8*.

Liu, D. L. J., Graham, S., & Zorawski, M. (2008). Enhanced selective memory consolidation following post-learning pleasant and aversive arousal. *Neurobiology of Learning and Memory, 89*(1). https://doi.org/10.1016/j.nlm.2007.09.001

Loprinzi, P. D., Blough, J., Crawford, L., Ryu, S., Zou, L., & Li, H. (2019). The temporal effects of acute exercise on episodic memory function: Systematic review with meta-analysis. *Brain Sciences, 9*(4). https://doi.org/10.3390/brainsci9040087. MDPI AG.

Loprinzi, P. D., Day, S., Hendry, R., Hoffman, S., Love, A., Marable, S., McKee, E., Stec, S., Watson, H., & Gilliland, B. (2021). The effects of acute exercise on short- and long-term memory: Considerations for the timing of exercise and phases of memory. *Europe's Journal of Psychology, 17*(1), 85–103. https://doi.org/10.5964/ejop.2955

Loprinzi, P., Olafson, D., Scavuzzo, C., Lovorn, A., Mather, M., Frith, E., & Fujiwara, E. (2022). Effects of acute exercise on emotional memory. *Cognition & Emotion, 36*(4), 660–689. https://doi.org/10.1080/02699931.2022.2050890

Loprinzi, P. D., Roig, M., Etnier, J. L., Tomporowski, P. D., & Voss, M. (2021). Acute and chronic exercise effects on human memory: What we know and where to go from Here. *Journal of Clinical Medicine, 10*(21). https://doi.org/10.3390/jcm10214812

McGaugh, J. L. (2013). Making lasting memories: Remembering the significant. *Proceedings of the National Academy of Sciences of the United States of America, 110* (Suppl. 2), 10402–10407. https://doi.org/10.1073/pnas.1301209110

McGaugh, J. L., & Roozendaal, B. (2002). Role of adrenal stress hormones in forming lasting memories in the brain. *Current Opinion in Neurobiology, 12*(2). https://doi.org/10.1016/S0959-4388(02)00306-9

McMorris, T. (2016). Developing the catecholamines hypothesis for the acute exercise-cognition interaction in humans: Lessons from animal studies. In *Physiology and behavior, 165* pp. 291–299). Elsevier Inc. https://doi.org/10.1016/j.physbeh.2016.08.011.

McMorris, T. (2021). The acute exercise-cognition interaction: From the catecholamines hypothesis to an interoception model. *International Journal of Psychophysiology, 170*, 75–88. https://doi.org/10.1016/j.ijpsycho.2021.10.005

Most, S. B., Kennedy, B. L., & Petras, E. A. (2017). Evidence for improved memory from 5 minutes of immediate, post-encoding exercise among women. *Cognitive Research: Principles and Implications, 2*(1). https://doi.org/10.1186/s41235-017-0068-1

Nater, U. M., & Rohleder, N. (2009). Salivary alpha-amylase as a non-invasive biomarker for the sympathetic nervous system: Current state of research. *Psychoneuroendocrinology, 34*(4), 486–496. https://doi.org/10.1016/j.psyneuen.2009.01.014

Nielson, K. A., & Arentsen, T. J. (2012). Memory modulation in the classroom: Selective enhancement of college examination performance by arousal induced after lecture. *Neurobiology of Learning and Memory, 98*(1). https://doi.org/10.1016/j.nlm.2012.04.002

Nielson, K. A., & Correro, A. N. (2017). Post-learning arousal enhances veridical memory and reduces false memory in the Deese-Roediger-McDermott paradigm. *Neurobiology of Learning and Memory, 144*, 198–207. https://doi.org/10.1016/j.nlm.2017.07.009

Nielson, K. A., & Lorber, W. (2009). Enhanced post-learning memory consolidation is influenced by arousal predisposition and emotion regulation but not by stimulus valence or arousal. *Neurobiology of Learning and Memory, 92*(1), 70–79. https://doi.org/10.1016/j.nlm.2009.03.002

Nielson, K. A., & Powless, M. (2007). Positive and negative sources of emotional arousal enhance long-term word-list retention when induced as long as 30 min after learning. *Neurobiology of Learning and Memory, 88*(1), 40–47. https://doi.org/10.1016/j.nlm.2007.03.005

Nielson, K. A., Yee, D., & Erickson, K. I. (2005). Memory enhancement by a semantically unrelated emotional arousal source induced after learning. *Neurobiology of Learning and Memory, 84*(1), 49–56. https://doi.org/10.1016/j.nlm.2005.04.001

Perini, R., Orizio, C., Comandè, A., Castellano, M., Beschi, M., & Veicsteinas, A. (1989). Plasma norepinephrine and heart rate dynamics during recovery from submaximal exercise in man. *European Journal of Applied Physiology and Occupational Physiology, 58*(8), 879–883. https://doi.org/10.1007/BF02332222

Prakash, R. S., Voss, M. W., Erickson, K. I., & Kramer, A. F. (2015). Physical activity and cognitive vitality. *Annual Review of Psychology, 66*, 769–797. https://doi.org/10.1146/annurev-psych-010814-015249

Preuß, D., & Wolf, O. T. (2009). Post-learning psychosocial stress enhances consolidation of neutral stimuli. *Neurobiology of Learning and Memory, 92*(3). https://doi.org/10.1016/j.nlm.2009.03.009

Roig, M., Nordbrandt, S., Geertsen, S. S., & Nielsen, J. B. (2013). The effects of cardiovascular exercise on human memory: A review with meta-analysis. *Neuroscience & Biobehavioral Reviews, 37*(8). https://doi.org/10.1016/j.neubiorev.2013.06.012

Roig, M., Thomas, R., Mang, C. S., Snow, N. J., Ostadan, F., Boyd, L. A., & Lundbye-Jensen, J. (2016). Time-dependent effects of cardiovascular exercise on memory. *Exercise and Sport Sciences Reviews, 44*(2). https://doi.org/10.1249/JES.0000000000000078

Salas, C. R., Minakata, K., & Kelemen, W. L. (2011). Walking before study enhances free recall but not judgement-of-learning magnitude. *Journal of Cognitive Psychology, 23* (4). https://doi.org/10.1080/20445911.2011.532207

Segal, S. K., & Cahill, L. (2009). Endogenous noradrenergic activation and memory for emotional material in men and women. *Psychoneuroendocrinology, 34*(9). https://doi.org/10.1016/j.psyneuen.2009.04.020

Segal, S. K., Cotman, C. W., & Cahill, L. F. (2012). Exercise-induced noradrenergic activation enhances memory consolidation in both normal aging and patients with amnestic mild cognitive impairment. *Journal of Alzheimer's Disease, 32*(4), 1011–1018. https://doi.org/10.3233/JAD-2012-121078

Slutsky-Ganesh, A. B., Etnier, J. L., & Labban, J. D. (2020). Acute exercise, memory, and neural activation in young adults. *International Journal of Psychophysiology, 158*, 299–309. https://doi.org/10.1016/j.ijpsycho.2020.09.018

Smith, V. M., Watson, P., & Most, S. B. (2022). Enhanced recognition of emotional images is not affected by post-exposure exercise-induced arousal. *Quarterly Journal of Experimental Psychology, 75*(6), 1056–1066. https://doi.org/10.1177/17470218211054950

Spielberger, C. D. (2010). State-trait anxiety inventory. In *The Corsini encyclopedia of psychology*. John Wiley & Sons, Inc. https://doi.org/10.1002/9780470479216.corpsy0943.

van Stegeren, A. H., Everaerd, W., Cahill, L., McGaugh, J. L., & Gooren, L. J. G. (1998). Memory for emotional events: Differential effects of centrally versus peripherally acting β-blocking agents. *Psychopharmacology, 138*(3–4), 305–310. https://doi.org/10.1007/s002130050675

Tulving, E. (1985). Memory and consciousness. *Canadian Psychology/Psychologie Canadienne, 26*(1), 1–12. https://doi.org/10.1037/h0080017

Voss, M. W., Soto, C., Yoo, S., Sodoma, M., Vivar, C., & van Praag, H. (2019). Exercise and Hippocampal memory systems. In *Trends in cognitive sciences, 23* pp. 318–333). Elsevier Ltd. https://doi.org/10.1016/j.tics.2019.01.006 (4).

Voss, M. W., Vivar, C., Kramer, A. F., & van Praag, H. (2013). Bridging animal and human models of exercise-induced brain plasticity. In *Trends in cognitive sciences, 17* pp. 525–544). https://doi.org/10.1016/j.tics.2013.08.001 (10).

Weinberg, L., Hasni, A., Shinohara, M., & Duarte, A. (2014). A single bout of resistance exercise can enhance episodic memory performance. *Acta Psychologica, 153*, 13–19. https://doi.org/10.1016/j.actpsy.2014.06.011

Weiss, L. R., Venezia, A. C., & Smith, J. C. (2019). A single bout of hard RPE-based cycling exercise increases salivary alpha-amylase. *Physiology & Behavior, 208*, Article 112555. https://doi.org/10.1016/j.physbeh.2019.05.016

Winter, B., Breitenstein, C., Mooren, F. C., Voelker, K., Fobker, M., Lechtermann, A., Krueger, K., Fromme, A., Korsukewitz, C., Floel, A., & Knecht, S. (2007). High impact running improves learning. *Neurobiology of Learning and Memory, 87*(4). https://doi.org/10.1016/j.nlm.2006.11.003

Won, J., Callow, D. D., Pena, G. S., Gogniat, M. A., Kommula, Y., Arnold-Nedimala, N. A., Jordan, L. S., & Smith, J. C. (2021). Evidence for exercise-related plasticity in functional and structural neural network connectivity. *Neuroscience & Biobehavioral Reviews, 131*, 923–940. https://doi.org/10.1016/j.neubiorev.2021.10.013