

Kent Academic Repository

Loprinzi, Paul, Roig, Marc, Tomporowski, Phillip D., Javadi, Amir-Homayoun and Kelemen, William L. (2022) *Effects of acute exercise on memory: Considerations of exercise intensity, post-exercise recovery period and aerobic endurance.* Memory . ISSN 1532-5946.

Downloaded from <u>https://kar.kent.ac.uk/97954/</u> The University of Kent's Academic Repository KAR

The version of record is available from https://doi.org/10.3758/s13421-022-01373-4

This document version Publisher pdf

DOI for this version

Licence for this version CC BY (Attribution)

Additional information

Versions of research works

Versions of Record

If this version is the version of record, it is the same as the published version available on the publisher's web site. Cite as the published version.

Author Accepted Manuscripts

If this document is identified as the Author Accepted Manuscript it is the version after peer review but before type setting, copy editing or publisher branding. Cite as Surname, Initial. (Year) 'Title of article'. To be published in *Title of Journal*, Volume and issue numbers [peer-reviewed accepted version]. Available at: DOI or URL (Accessed: date).

Enquiries

If you have questions about this document contact <u>ResearchSupport@kent.ac.uk</u>. Please include the URL of the record in KAR. If you believe that your, or a third party's rights have been compromised through this document please see our <u>Take Down policy</u> (available from <u>https://www.kent.ac.uk/guides/kar-the-kent-academic-repository#policies</u>).

Effects of acute exercise on memory: Considerations of exercise intensity, post-exercise recovery period and aerobic endurance

Paul D. Loprinzi¹ · Marc Roig^{2,3} · Phillip D. Tomporowski⁴ · Amir-Homayoun Javadi^{5,6} · William L. Kelemen⁷

Accepted: 6 November 2022 © The Psychonomic Society, Inc. 2022

Abstract

Accumulating research demonstrates that acute exercise can enhance long-term episodic memory. However, it is unclear if there is an intensity-specific effect of acute exercise on long-term episodic memory function and whether this is influenced by the post-exercise recovery period, which was the primary objective of this experiment. Another uncertainty in the literature is whether aerobic endurance influences the interaction between exercise intensity and post-exercise recovery period on long-term episodic memory function, which was a secondary objective of this study. With exercise intensity and post-exercise recovery period occurring as within-subject factors, and fitness as a between-subject factor, 59 participants (M_{age} = 20 years) completed 12 primary laboratory visits. These visits included a 20-min bout of exercise (Control, Moderate, and Vigorous), followed by a recovery period (1, 5, 10, and 15 min) and then a word-list episodic memory task, involving an encoding phase and two long-term recall assessments (20-min and 24-h delayed recall). The primary finding from this experiment was that moderate and vigorous-intensity exercise improved memory function when compared to a non-exercise control. A secondary finding was that individuals with higher levels of aerobic endurance, compared to their lesser fit counterparts, had greater memory performance after exercise (moderate or vigorous) when compared to after a control condition. Additionally, individuals with higher levels of aerobic endurance, compared to their lesser fit on the memory task with longer post-exercise recovery periods. Future research should carefully consider these parameters when evaluating the effects of acute exercise on long-term episodic memory.

Keywords Cognition · Memory context · Physical activity

Introduction

Acute exercise and cognition

Given its implications for improving a variety of daily tasks or endeavors (e.g., academic performance, problem solving), there has been an increased research interest over the last

 Paul D. Loprinzi pdloprin@olemiss.edu
 Marc Roig marc.roigpull@mcgill.ca
 Phillip D. Tomporowski ptomporo@uga.edu
 Amir-Homayoun Javadi a.h.javadi@gmail.com
 William L. Kelemen wkelemen@txstate.edu

¹ Department of Health, Exercise Science and Recreation Management, Exercise & Memory Laboratory, University of Mississippi, MS 38655 Oxford, USA several decades on the effects of acute exercise and the timing (in relation to the cognitive task; Roig et al., 2016) of acute exercise (i.e., a single bout of exercise) on cognitive function (Brisswalter, Collardeau, & Rene, 2002; Chang, Labban, Gapin, & Etnier, 2012; Etnier et al., 2016; Gomez-Pinilla & Hillman, 2013; Ishihara, Drollette, Ludyga, Hillman, & Kamijo, 2021; Labban & Etnier, 2011, 2018; Lambourne & Tomporowski,

- ² Memory and Motor Rehabilitation Laboratory (MEMORY-LAB), Feil and Oberfeld Research Centre, Jewish Rehabilitation Hospital, Montreal Center for Interdisciplinary Research in Rehabilitation (CRIR), Laval, Quebec, Canada
- ³ School of Physical and Occupational Therapy, Faculty of Medicine, McGill University, Montreal, Quebec, Canada
- ⁴ Department of Kinesiology, Cognition and Skill Acquisition Laboratory, University of Georgia, Athens, GA, USA
- ⁵ School of Psychology, University of Kent, Canterbury, UK
- ⁶ School of Rehabilitation, Tehran University of Medical Sciences, Tehran, Iran
- ⁷ Department of Psychology, Texas State University, San Marcos, TX, USA



2010; Loprinzi, Loenneke, & Storm, 2021b; Pyke et al., 2020; Salas, Minakata, & Kelemen, 2011; Tomporowski, 2003; Tomporowski, Ellis, & Stephens, 1987; Voss et al., 2020; Zuniga, Mueller, Santana, & Kelemen, 2019). Empirical work has demonstrated a potential intensity-dependent effect of acute exercise on cognition; moderate-intensity acute exercise may improve prefrontal cortex-dependent higher-order cognition (Chang, Labban, Gapin, & Etnier, 2012), such as executive control, whereas vigorous-intensity acute exercise may improve highly automated behavior (McMorris, 2016). Whether these intensity-dependent effects of acute exercise on global cognition extend to specific cognitive parameters, such as long-term episodic memory (defined as the remembrance of one's own previous experiences; Madan, 2020), is less clear (Loprinzi, Roig, Etnier, Tomporowski, & Voss, 2021e) and requires additional empirical investigation.

Acute exercise and memory: Intensity-specific effects

In 2013, Roig et al. (2013) conducted a comprehensive metaanalysis and reported that acute exercise improves short-term or working memory (ES = 0.26) and long-term memory (ES = 0.52) in approximately 48% and 58%, respectively, of published studies. Their moderation analyses suggested that working memory was enhanced to a greater extent when the exercise duration was less than 20 min and performed at a low intensity. This aligns with a systematic review (Loprinzi, 2018) suggesting that lower-intensity exercise (e.g., light and moderate) may benefit working memory performance, whereas vigorous-intensity acute exercise may benefit more simplistic memory outcomes (e.g., free-recall without dual task or interference) that may be less reliant on cognitive control. As a follow-up to the 2013 meta-analysis by Roig et al., Loprinzi et al. (2019) meta-analyzed the temporal (exercise before, during, or after memory encoding) effects of acute exercise on memory. The results of this meta-analysis demonstrated that acute exercise prior to encoding improved memory performance, but this effect was more pronounced for vigorous-intensity exercise. These meta-analyses, however, only provide initial support for the moderation effects of exercise intensity; a limited number of studies were included in these analyses, and sub-group analyses, as opposed to meta-regression, were employed to evaluate such moderation effects. The present study extends the work included in these prior reviews by experimentally evaluating the moderation effects of exercise intensity.

Acute exercise and memory: Mechanisms

As reviewed by El-Sayes et al. (2019), acute exercise, particularly vigorous-intensity exercise, may improve memory function via neural plasticity-related mechanisms. Acute exercise may alter molecular changes, such as increasing vascular endothelial growth factor and brain-derived neurotrophic factor (Ludyga, Gerber, & Kamijo, 2022). These molecular responses may lead to functional responses (e.g., increased blood flow, glucose and oxygen metabolism, neurotransmitter release, neural/receptor activity), which ultimately may improve memory function, either through encoding and/or consolidation-based mechanisms (Loprinzi, Roig, Etnier, Tomporowski, & Voss, 2021e). In addition to functional responses, acute exercise-related alterations may, in theory, induce structural neuronal changes that subserve memory function. For example, animal work demonstrates that induction of long-term potentiation (sustained excitatory post-synaptic potentiation) via electrical stimulation can induce synaptic changes (e.g., increases in the size of dendritic spines) within a few hours of the stimulus induction (Amaral & Pozzo-Miller, 2009; Bourne & Harris, 2012); speculatively, exercise may induce similar effects (van Praag et al., 2002). Importantly, however, the time course through which these (acute exercise-induced) functional and structural responses influence memory - as well as the extent to which repeated bouts of acute exercise are needed for such effects - needs to be explored in future work. There may, however, be important factors (e.g., cardiorespiratory fitness) that influence the extent to which these mechanisms mediate the effects of acute exercise on memory.

Acute exercise and memory: Fitness-specific effects

Health-related physical fitness includes many components (e.g., cardiorespiratory endurance/fitness, body composition, muscular strength, balance, coordination), but of interest here is the role of cardiorespiratory fitness on memory. Cardiorespiratory fitness involves the ability of the circulatory and respiratory systems to supply oxygen to the body and brain during sustained exercise; it is often measured (from expired gases via indirect calorimetry) by the amount of oxygen an individual can consume and utilize during a maximal graded exercise test. A recent systematic review reported an association between cardiorespiratory fitness and episodic memory performance (Rigdon & Loprinzi, 2019), such that lower fitness is associated with worse memory across multiple memory systems (Pontifex et al., 2014). As suggested by Pontifex et al. (2019), the fitness level of an individual may influence the rate of task acquisition (learning), presumably as a result of fitness moderating the physiological and psychological response to exercise. For example, it has been theorized that cardiorespiratory fitness may prime the underlying neurophysiological mechanisms that are related to exerciseinduced improvements in memory (Pontifex et al., 2019). Importantly, however, recent work reports that aerobic fitness is unrelated to the acquisition of spatial relational memory

(Chandler et al., 2020). Similarly, past meta-regression analyses do not support an association between cardiorespiratory fitness and general cognitive performance (Etnier, Nowell, Landers, & Sibley, 2006). These mixed findings in the literature were the impetus for the present study to evaluate the potential link between fitness/endurance and episodic memory performance. At this point, it is unclear why fitness may, potentially, have a different effect on episodic memory versus other aspects of cognition, but this is plausible as, for example, past meta-analytic work demonstrates that acute exercise may have different effects based on the evaluated cognitive outcome (e.g., executive function, reaction time, attention) (Chang, Labban, Gapin, & Etnier, 2012). In addition to further evaluating this potential moderating role of fitness - to help coalesce the literature - the present study also evaluates whether this potential association is influenced by the post-exercise recovery period.

Acute exercise and memory: Fitness and post-exercise recovery

When exercising (especially vigorous-intensity) and completing a cognitive task at the same time, cognitive resources may be in competition between sustaining the exercise intensity and engaging in cognitive operations when completing the cognitive task (Jung, Ryu, Kang, Javadi, & Loprinzi, 2022). Even after the cessation of exercise and the cognitive task, metabolic resources may be used to facilitate the recovery process at the expense of their use for optimal cognitive processing post-exercise. From a psychological perspective, hypothetically, superior fitness may facilitate a quicker exercise recovery, particularly from higher-intensity acute exercise. This faster post-exercise recovery may allow for greater cognitive resources needed when completing a post-exercise cognitive task; for example, a quicker recovery may help prevent any lingering effects of physical and cognitive fatigue from exercise and may also allow for these additional cognitive resources to help optimize subsequent memory encoding. Interestingly, recent cross-sectional research demonstrates that higher fit individuals display greater attentional processes during a lexical decision task (Chandler, McGowan, Payne, Hampton Wray, & Pontifex, 2019), a finding supported by the broader literature that was inclusive of crosssectional and longitudinal designs (Kao et al., 2020). In addition to these theoretical explanations, empirical work has started to evaluate if cardiorespiratory fitness moderates the effects of acute exercise on memory.

A meta-analysis by Roig et al. (2013) reported that fitness level did not influence the effects of acute exercise on short-term memory. In the same meta-analysis individuals with an average fitness level had the largest effects on long-term memory, but this evidence came from a single study, and thus, should be interpreted with much caution. Rather than focusing specifically on memory, Chang et al. (2012) conducted a meta-analysis evaluating whether fitness moderated the effects of acute exercise on global cognition; a larger number of studies were included in this moderation analysis given that the outcome (global cognition) was more inclusive. Their meta-analysis reported that when cognition was assessed immediately following exercise, acute exercise improved cognition among those with low (d = .169) and high fitness (d = .220), but not those with moderate fitness (d = .029). When cognition was assessed after a delay (> 15 min) following exercise, acute exercise improved cognition among those with moderate (d = .202)and high fitness (d = .331), but not those with low fitness (d = .308). These meta-analytic findings, by themselves, are challenging to interpret. For example, it is uncertain as to why moderately fit individuals would have their longterm memory benefit most from acute exercise. Similarly, it is uncertain as to why moderately fit individuals would not see improvements in global cognition when assessed immediately after exercise, but would see benefits following a delay after exercise. These meta-analytic findings do, however, justify the need for additional work on this topic, as highlighted elsewhere (Pontifex et al., 2019). Further justification for evaluating this in an empirical experiment is that these prior meta-analyses were limited by including relatively few studies - with heterogeneity across studies - in their moderation analyses. It seems reasonable, however, to speculate that the post-exercise recovery duration would interact with fitness level to influence the effect of acute exercise on memory. For example, individuals with a lower fitness level may benefit less from vigorous-intensity acute exercise (due to excessive fatigue), especially if the post-exercise recovery period is short. Of course, if these main effects are substantiated with empirical studies, then additional work will be needed to confirm whether there is any veracity to these speculated mechanisms.

Present experiment

The present experiment systematically manipulates the acute exercise intensity and post-exercise recovery period to evaluate if these factors interact to influence episodic memory, and to what extent these relationships may be influenced by cardiorespiratory fitness/endurance performance. Unlike past meta-analytic work (Chang, Labban, Gapin, & Etnier, 2012), which evaluated whether cognition was improved immediately or > 15 min after exercise, the present experiment systematically evaluates the effects of acute exercise on memory when considering multiple recovery periods within the first 15 min post-exercise; that is, after exercising, participants completed 1-, 5-, 10-, or 15-min periods of rest – watching a video – before starting the encoding phase

of the memory task. We intentionally focused on the first 15 min after exercise for several reasons. Crush and Loprinzi (2017) showed that explicit memory 5 min after moderateintensity exercise, but not 15 or 30 min after exercise, was improved. Recent work by Loprinzi, Lovorn, and Gilmore (2021c) demonstrates that explicit episodic memory function is not improved 30 min after an acute bout of vigorousintensity acute exercise. However, research by Winter et al. (2007) suggested that learning speed and 1-week retention was improved 15 min after high-intensity acute exercise. Thus, the first 15 min after exercise may be an optimal window for episodic memory enhancement to occur.

The primary objective of this study was to evaluate if there is an intensity-specific effect of acute exercise on episodic memory and determine whether this depends on the duration of the post-exercise recovery period. A secondary objective of this study was to evaluate if the fitness level of the individual moderates the potential interaction between acute exercise intensity and post-exercise recovery period on episodic memory function. Regarding our primary objective, we hypothesize that long-term episodic memory will benefit most from vigorous-intensity acute exercise (v moderateintensity or control) and this effect will occur across all post-exercise recovery periods, whereas moderate-intensity acute exercise (v control) will improve episodic memory when coupled with shorter post-exercise recovery periods. Regarding our secondary objective, we anticipate a threeway interaction between exercise intensity, post-exercise recovery period, and fitness. Specifically, we anticipate that vigorous-intensity acute exercise will be optimal in enhancing episodic memory, but this will be restricted to more fit individuals and will occur across all post-exercise recovery periods. We hypothesize, however, that lesser-fit individuals will benefit by having a longer post-exercise recovery period, especially after vigorous-intensity acute exercise.

For these primary and secondary objectives, memory performance was assessed using free recall, as opposed to cued-recall or a recognition task, as free recall may be more sensitive to exercise (Moutoussamy, Taconnat, Pothier, Toussaint, & Fay, 2022). Further, we employed two longterm memory recall assessments, occurring 20 min and 24 h after memory encoding. Although prior work has shown improvements in memory 20 min after exercising (Loprinzi et al., 2020, 2021c), due to a longer period for consolidation to occur, a 24-h delayed assessment might be more sensitive to exercise-induced differences in encoding/consolidation than the 20-min delayed assessment. Notably, empirical work demonstrates that acute exercise may have a greater effect on memory with longer retention intervals (Loprinzi et al., 2021a, 2021b, 2021d, 2021e; Roig, Nordbrandt, Geertsen, & Nielsen, 2013). Thus, including two long-term memory assessments will allow us to determine if the time period post-encoding moderates the effects of acute exercise

on long-term memory performance. Further, this will allow for a somewhat unique investigation as to whether acute exercise may improve long-term memory through increasing the number of item gains over time (e.g., not recalled at the first time period, but recalled at the second time period) or reducing the number of item losses over time (e.g., recalled at the first time period, but not recalled at the second time period) (Sng, Frith, & Loprinzi, 2018).

Methods

Participants

Participant recruitment occurred via a purposive, non-random sampling approach; participants were recruited from undergraduate and graduate courses at the University of Mississippi; sampling occurred across a variety of majors (e.g., public health, exercise science, biology, and psychology). We aimed to sample 60 participants. Notably, this sample size is approximately three times higher than the average sample size among experiments on this topic (see Fig. 9 in Pontifex et al., 2019). Among the 60 recruited participants, one did not start the study, whereas seven participants started the study but failed to complete all 12 conditions (e.g., did not show up for a visit, dropped out of the study), leaving a total of 52 participants with complete data. Among these 52 participants compared to the seven with incomplete data, there were no differences in body mass index, t = .07, df = 57, p = .94, self-reported moderate-to-vigorous physical activity, t = .53, df = 57, p = .60, aerobic endurance, t = .67, df = 57, p = .50, age, t = .50, df = 57, p = .62, or biologicalsex, $\chi^2 = .62$, df = 1, p = .43. We retained all 59 participants in the analyses by using linear mixed models.¹ Linear mixed models are able to accommodate all of the available data for each subject, without having to drop the subject from the analyses if they have a few missing data points (West, 2009).

This study was approved by the ethics committee at the University of Mississippi and all participants provided written consent before participation. Participation was voluntary, with no financial compensation provided.

Eligibility criteria

Similar to other work (Loprinzi, Rigdon, Javadi, & Kelemen, 2021d), participants were excluded from participation (starting the study) if they (1) self-reported as being a

¹ With 12 conditions, including two memory assessments (20-min and 24-h delays), 24 primary data points occurred for each participant. Among the seven participants with incomplete data, six participants each had one missing data point and one participant had 14 missing data points.

daily smoker; (2) self-reported being pregnant; (3) had a concussion or head trauma within the past 30 days; (4) used marijuana or other mind-altering drugs within the past 30 days; (5) were considered a daily alcohol user (> 30 drinks/month for women; > 60 drinks/month for men) or consumed alcohol in the past 12 h, (6) were diagnosed with COVID-19 within the last 2 weeks, (7) were outside the age range of 18–25 years, (8) had a current diagnosis of a psychological disorder, (9) had been diagnosed with a learning disorder, or (10) answered "yes" to any of the seven questions on the Physical Activity Readiness Questionnaire (PAR-Q), suggesting that they should seek medical advice before exercising. These exclusionary criteria were selected as they may influence memory function, and in turn, could potentially confound the effects of acute exercise on memory function.

Study design and procedures

A 3 (*Intensity*: Control, Moderate, Vigorous) \times 4 (*Post-Exercise Recovery*: 1-min Post, 5-min Post, 10-min Post, 15-min Post) factorial design was employed. Both factors (Exercise Intensity, Post-Exercise Recovery) occurred as within-subject factors. See Fig. 1 for an illustration of the study procedures. Prior to all visits, participants were instructed to not exercise within 5 h of each visit and not to consume caffeine within 6 h of each visit.

Allocation concealment occurred by both the researcher and participant not knowing which condition the participant would complete until arriving in the lab. Randomization was performed using a computer-generated algorithm.

Participants completed 13 visits in total. The first visit included a maximal exercise (treadmill) test to determine the participant's maximal heart rate, endurance capacity, and to also familiarize the participant with the memory protocol. The maximum heart rate achieved during the first visit was used in the heart rate reserve formula to set the exercise intensity for the Moderate-intensity and Vigorous-intensity conditions.

Visits 2–13 occurred in a random order, at approximately the same time of day (\pm 2 h) at a within-subject

level (i.e., although variations occurred between subjects, we attempted to minimize variability across visits at the within-subject level), and occurred approximately 24-72 h apart. For these 12 within-subject conditions, the protocol was as follows. The four Control conditions involved no exercise, but included watching a video for 21 min, 25 min, 30 min, and 35 min before starting the memory task (encoding). The four Moderate-intensity conditions involved exercising (treadmill) for 20 min at a moderate intensity and then either resting (video) for 1 min, 5 min, 10 min, or 15 min before starting the memory task (encoding). Lastly, the four Vigorous-intensity conditions involved exercising (treadmill) for 20 min at a vigorous intensity and then either resting (video) for 1 min, 5 min, 10 min, or 15 min before starting the memory task (encoding).

We intentionally chose a 20-min treadmill exercise duration as past work shows that 20 min of treadmill exercise is sufficient in enhancing memory (Loprinzi et al., 2021a, 2021b, 2021d, 2021e). Furthermore, although the timing of their effect in the brain in relation to changes in peripheral concentration is uncertain (see discussion in Skriver et al., 2014), key memory-related neurotrophins, such as brain-derived neurotrophic factor, reach their zenith at this period of acute exercise (Saucedo Marquez, Vanaudenaerde, Troosters, & Wenderoth, 2015). Additionally, as stated in the *Introduction*, key mechanisms (e.g., neurotransmitters) of the exercise-memory relationship are elevated within the first 15 min after exercise (Maddock, Casazza, Fernandez, & Maddock, 2016; Skriver et al., 2014).

Maximal exercise visit (first session)

The first laboratory visit included a maximal treadmillbased assessment. The specific assessment included an individualized protocol (Mier & Gibson, 2004). Participants warmed-up for 3 min by walking at 3.5 miles per hour (mph). Following this, they engaged in a constant speed throughout the test while the grade increased by 2% every 2 min. After the warm-up period, the speed was set, and remained, at 5.5 mph for the entire exercise

20-min of Control, Moderate-intensity or Vigorous-intensity Exercise

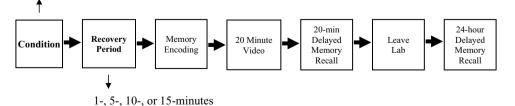


Fig. 1 Experimental study procedures. Participants completed this procedure a total of 12 times, on separate occasions, as both Condition and Recovery Period were within-subject factors

protocol. Due to COVID-19 concerns with researchers being exposed to participant saliva, oxygen consumption (via indirect calorimetry) was not measured, but rather, the exercise duration (seconds) during the maximal exercise test was used as a measure of endurance performance (proxy for cardiorespiratory fitness). Notably, time-to-exhaustion protocols, such as this, are highly correlated with direct measures of oxygen consumption (r = .91-.94) (Pollock et al., 1982).²

During the maximal treadmill test, heart rate (HR) was monitored throughout. Rating of perceived exertion (RPE) was evaluated (6–20 scale) at the conclusion (endpoint) of the bout of exercise; 6 represents "no exertion at all," 9 "very light," 13 "somewhat hard," 15 "hard," 17 "very hard," 19 "extremely hard," and 20 "maximal exertion." The maximal treadmill exercise bout ended when the participant elected to stop exercising due to exhaustion.

Control, moderate-intensity exercise, vigorous-intensity exercise

The Control conditions involved a time-matched cognitive engagement task (self-selected video, e.g., national geographic video). There is experimental evidence suggesting that this type of control task (video viewing) does not prime or enhance memory function (Blough & Loprinzi, 2019). The video was watched without sound to induce a low stimulus condition to prevent boredom (Suwabe et al., 2017). To maintain the same context and posture, the Control conditions involved the participant watching the video while standing on the treadmill.

The exercise conditions involved treadmill exercise for 20 min, followed by either a 1-, 5-, 10-, or 15-min period of rest (standing). During both the exercise and rest periods, participants had a video (sound off) placed in front of the treadmill to match the context of the Control conditions.

Using the participant's maximal heart rate achieved during their maximal exercise bout (visit 1), they exercised at 50% of their HRR (heart rate reserve) for the Moderate-intensity conditions and 80% of their HRR for the Vigorous-intensity conditions (Garber et al., 2011). Heart rate reserve was calculated as ([($HR_{max} - HR_{rest}$) * % target intensity] + HR_{rest}). The resting heart rate measurement occurred after resting quietly for at least 3 min.

At baseline, throughout the acute exercise bout (every 5 min), and during the rest period (1, 5, 10, and 15 min post), heart rate was assessed. Heart rate was measured via

a chest-strap Polar heart rate monitor (H10 model). Rating of perceived exertion (RPE) was measured at the very end of the exercise bout and measured using a 6–20 scale.

Due to concerns with COVID-19, during the entire experimental session (exercise and cognitive testing), participants wore a cloth or surgical facemask (the participant's own mask). This may have had some influence on the data, but if so, we anticipate that it had a minimal effect. For example, even during or after walking exercise, wearing a mask does not appear to influence mood or cognitive performance (Caretti, 1999). Similar findings have been shown for light-intensity cycling (Morris, Piil, Christiansen, Flouris, & Nybo, 2021). Further, even during vigorous-intensity exercise, wearing a facemask does not appear to induce meaningful effects on the work of breathing, blood gases, and other physiological parameters (Hopkins et al., 2020).

Memory assessment

Study list The memory task was programmed in E-Prime (v. 3). Similar to common list-learning paradigms (e.g., Ray Auditory Verbal Learning Test), participants were exposed to five trials, each including 15 words, in black lowercase letters (Calibri typeface, font size 22) on a desktop computer. Notably, this memory protocol has been shown to be sensitive to exercise-related improvements in memory (Loprinzi et al., 2021a, 2021b, 2021d, 2021e). The words were identical across the five trials, but were displayed in a random order, across trials and participants. Separate word lists, occurring in a random order, were used for each of the 12 visits.³ Each word remained on the screen for 1,500 ms and participants read the word aloud as it appeared on the screen (to ensure they were processing the stimuli). A short (3-s) intermittent break occurred between the five trials.

Each word list was created by utilizing the MRC Psycholinguistic Database from the University of Western Australia. The following criteria were set for each word: number of letters (4–10), number of syllables (1–3), familiarity rating (450–700), concreteness rating (450–700), imageability rating (450–700), meaningfulness rating (450–700), and only nouns

 $^{^2}$ The sample in the Pollock et al. article is more heterogeneous than our sample. For example, they had a mean (SD) age of 27.0 years (5.2), whereas our sample was 20.5 years (1.2). Thus, it is possible that the correlation between time-to-exhaustion and oxygen consumption would be even stronger in our sample.

³ With multiple temporal conditions, there is a potential concern with learning or carry-over effects (i.e., participants, over time, get better at recall because of repeated experience with the protocol). Sensitivity analyses, however, did not support this possibility. The mean (SE) proportion of words recalled at the 20-min delay for visits 1–12 (in sequential order) were: 0.56 (0.03), 0.55 (0.03), 0.55 (0.03), 0.55 (0.02), 0.55 (0.03), 0.56 (0.03), 0.54 (0.03), 0.52 (0.03), 0.52 (0.02), 0.58 (0.03), 0.53 (0.03), and 0.53 (0.03). A repeated-measures ANOVA demonstrated that there was not a significant trend across the sequential visits, F(11, 561) = 0.94, p = 0.49, $\eta^2 = .01$.

were used. No two words within each list were semantically related (r < .30) from a latent semantic analysis. Further, a similar proportion of animate words (i.e., animates can act; grow and reproduce; know, perceive, emote, learn and deduce; and made of biological structures that maintain life) appeared in each list (Bonin, Gelin, & Bugaiska, 2014). An ANOVA demonstrated that, across the 12 lists, there was not a statistically significant difference in the number of letters, F(11,(179) = .74, p = .70, M (SE) = 6.04 (.10), number of syllables, F(11, 179) = .65, p = .78, M (SE) = 1.71 (.05), familiarity rating, F(11, 179) = .65, p = .78, M (SE) = 545.99 (3.86), concreteness rating, F(11, 179) = .82, p = .62, M (SE) = 563.76 (3.67), imageability rating, F(11, 179) = 1.13, p = .34, M (SE) = 577.37 (3.18), meaningfulness rating, F(11, 179)= .67, p = .77, M (SE) = 491.56 (2.50), and proportion of animate words, F(11, 179) = .26, p = .99, M (SE) = .21 (.03).

Recall assessment Immediately after encoding the fifth trial, participants watched a video (either The Office or The Big Bang Theory) for 20 min. While viewing the video, participants were asked to draw three small pictures that depict three major scenes from the 20-min video; this was implemented to avoid participants actively rehearsing the words during this 20-min delay period.

After this 20-min delay period, participants free recalled as many words as possible. Twenty-four hours later, participants completed a final free-recall assessment. For both recall assessments (20-min delay and 24-h delay), after the participant recalled their final word, they were encouraged to try and recall at least one more word; this was implemented to avoid minimal effort during memory recall. The subsequent laboratory visit did not occur until after the 24-h free recall assessment had occurred. Further, between the 20-min and 24-h delayed assessments, participants were instructed to not exercise. Also, participants were instructed to not consume caffeine 6 h prior to both of these assessments and to not rehearse the words during the retention intervals (i.e., during the 20-min and 24-h delay periods).

Ultimately, several primary memory outcomes were evaluated, including the number of words recalled at the 20-min delay, the number of words recalled at the 24-h delay, and a proportional difference score. A proportional difference score was calculated to control for individual differences at immediate recall; proportional difference was calculated as (24-h recall / 20-min delay recall). In addition to these outcomes, and using the recall performance at the 20-min and 24-h delay periods, four additional outcomes were calculated: the number of item gains over time (e.g., not recalled at the first time period, but recalled at the second time period), the number of item losses over time (e.g., recalled at the first time period, but not recalled at the second time period), the number of items unrecalled at both time periods, and the number of items recalled at both time periods. On the first visit, various demographic parameters were assessed, including self-report of age and sex, and measured height and weight for determination of body mass index (kg/m²). Additionally, weekly engagement in self-reported moderate-to-vigorous physical activity was assessed using the two item (number of days and average minutes per day) Physical Activity Vital Sign questionnaire (Ball, Joy, Gren, & Shaw, 2016).

Analyses

Our primary aim was to evaluate if there is an intensityspecific effect of acute exercise on episodic memory and determine whether this depends on the duration of the postexercise recovery period. To investigate this primary aim, a 3 (*Exercise Intensity*: Control, Moderate, Vigorous) \times 4 (*Post-Exercise Recovery*: 1 min Post, 5 min Post, 10 min Post, 15 min Post) linear mixed model analysis was employed. Models were computed separately for the different memory outcomes, namely 20-min delayed recall (# of words), 24-h delayed recall (# of words), proportional difference (24-h delay / 20-min delay), gains (# of items), losses (# of items), unrecalled at both time periods (# of items), and recalled at both time periods (# of items).

Our secondary aim was to evaluate if the fitness level of the individual moderates the potential interaction between acute exercise intensity and post-exercise recovery period on episodic memory function. To investigate this secondary aim, a 3 (*Exercise Intensity*) \times 4 (*Post-Exercise Recovery*) \times 2 (*Endurance*: above vs. below median (729 s) level) linear mixed model analysis was computed; separate models were computed for the following outcomes: 20-min delayed recall (# of words), 24-h delayed recall (# of words), and proportional difference.

All linear mixed model analyses were computed in SPSS (v 28) using general guidelines detailed by West (2009). Subject ID (nominal) served as a random effects variable with the inclusion of the intercept; Exercise Intensity (three-level ordinal variable) and Post-Exercise Recovery (four-level ordinal variable) served as fixed effects variables; and Endurance (binary variable) was entered in the model as a covariate (Field, 2015) for the secondary aim. With the inclusion of the random intercept, a scaled identity covariance structure was used given the random effect with only one level. The estimation method used was Maximum like-lihood (ML). For the fixed effects, Type III tests were used for the sum of squares estimation. Degrees of freedom were estimated using Satterthwaite approximation.

Based on a sensitivity analysis, with inputs of an α of 0.05, power of 0.80, 59 participants, 12 measurements/ conditions (three exercise intensities across four recovery

Table 1 Demographic, behavioral, and performance characteristics of the sample (N = 59)

Variable	Point estimate	SE	
Age, mean years	20.5	.16	
Sex, % Female	56.7		
Measured body mass index, mean kg/m ²	24.0	.49	
Physical activity, mean min/week of MVPA	207.0	19.6	
Duration lasted on maximal treadmill test, mean seconds	771.1	30.0	

MVPA moderate-to-vigorous physical activity

periods), and an assumed repeated-measures correlation of 0.50, there was sufficient power to detect a small effect (i.e., effect size f of 0.11; notably, a small- to medium-effect, respectively, range from 0.10 to 0.25). Results of the manipulation checks are shown in the Appendix.

Results

Participant characteristics

Table 1 displays the demographic and behavioral characteristics of the sample. The participants, on average, were 20.5 years of age (SE = .17; range = 18–23), mixed between women (55.8%) and men (44.2%), who were physically active on a regular basis (mean of 210.6 min/week of moderate-to-vigorous intensity physical activity). The target heart rate for the moderate- and vigorous-intensity exercise conditions, respectively, were 50% and 80% of HRR, corresponding to 138.5 bpm and 170.8 bpm in the present sample. Across the four moderate-intensity exercise

 Table 2
 Memory results (estimated marginal means (SD)) across conditions

conditions, the mean heart rates at the endpoint of exercise were 138.7, 138.7, 139.1, and 138.8 bpm. Across the four vigorous-intensity exercise conditions, the mean heart rates at the endpoint of exercise were 168.4, 169.2, 170.2, and 169.9 bpm. The complete set of heart rate responses across all conditions and time points are shown in the Appendix.

Memory performance

Interaction between exercise intensity and post-exercise recovery Table 2 displays the memory results (20-min delay, 24-h delay, and proportional difference) across the conditions. Table 3 shows the memory results for gains, losses, unrecalled at both time periods, and recalled at both time periods.

With memory performance at the 20-min delay as the outcome, a 3 (Exercise Intensity) × 4 (Post-Exercise Recovery) linear mixed model analysis demonstrated that the Type III tests of fixed effects yielded no main effects for Exercise Intensity, F(2, 643.08) = .2.44, p = .09, Post-Exercise Recovery, F(3, 643.04) = .63, p = .60, or an interaction of these factors, F(6, 643.12) = .63, p = .71. Estimates of the fixed effects with Vigorous as referent were as follows; Control, M (95% CI) = .07 (-.71, .85), SE = .40, df = 643.00, t = .17, p = .86; Moderate, M (95% CI) = .07 (-.70, .85), SE = .39, df = 643.06, t = .19, p = .85. Estimates of the fixed effects with the 15-min recovery period as referent were as follows; 1-min rest, M (95% CI) = .33 (-.45, 1.11), SE = .40, df = 643.00, t = .83, p = .41; 5-min rest, M (95% CI) = .41 (-.36, 1.19), SE = .39, df = 643.16, t = 1.05, p = .30;10-min rest, M (95% CI) = .16 (-.62, .93), SE = .39, df = 643.16, t = .40, p = .69.

With memory recall at the 24-h delay as the outcome, the Type III tests of fixed effects yielded a main effect for

Condition	20-min delay	24-h delay	Proportional Difference
Control (20 min) and then 1 min additional rest	7.98 (3.41) (n=59)	5.36 (3.73) (n=59)	.65 (.31) (n=59)
Control (20 min) and then 5 min additional rest	7.71 (3.30) (n=58)	5.45 (3.53) (n=58)	.67 (.32) (n=58)
Control (20 min) and then 10 min additional rest	7.43 (3.35) (n=58)	5.17 (3.46) (n=58)	.66 (.29) (n=58)
Control (20 min) and then 15 min additional rest	8.03 (3.44) (n=58)	5.02 (3.29) (n=57)	.60 (.26) (n=57)
Moderate intensity (20 min) and then 1 min rest	8.05 (3.49) (n=59)	5.90 (3.79) (n=59)	.69 (.28) (n=59)
Moderate intensity (20 min) and then 5 min rest	8.36 (3.88) (n=59)	6.17 (4.31) (n=58)	.67 (.27) (n=58)
Moderate intensity (20 min) and then 10 min rest	8.12 (3.62) (n=58)	5.68 (4.05) (n=57)	.69 (.30) (n=57)
Moderate intensity (20 min) and then 15 min rest	7.98 (3.44) (n=59)	6.12 (3.62) (n=59)	.73 (.29) (n=59)
Vigorous intensity (20 min) and then 1 min rest	8.29 (3.58) (n=58)	6.77 (3.66) (n=57)	.81 (.24) (n=57)
Vigorous intensity (20 min) and then 5 min rest	8.32 (3.59) (n=59)	5.78 (3.74) (n=59)	.68 (.29) (n=59)
Vigorous intensity (20 min) and then 10 min rest	8.07 (3.31) (n=59)	6.44 (3.52) (n=57)	.74 (.23) (n=57)
Vigorous intensity (20 min) and then 15 min rest	7.97 (3.61) (n=58)	6.16 (3.84) (n=56)	.72 (.31) (n=56)

The "20 min" in parentheses represents the duration of the condition (control/exercise). 20-min delay represents the number of words (out of 15 words) recalled 20 min after encoding. 24-h delay represents the number of words (out of 15 words) of words recalled 24 h after encoding. Proportional difference was calculated as (24-h recall / 20-min delay recall)

Table 3 Estimated marginal means (SD) for the item types across condition

	Gains	Losses	Unrecalled both	Recalled both
Control	.19 (.50)	2.68 (2.10)	7.07 (3.40)	5.06 (3.47)
Moderate	.22 (.57)	2.38 (2.09)	6.67 (3.69)	5.74 (3.82)
Vigorous	.24 (.55)	2.18 (2.12)	6.52 (3.57)	6.07 (3.60)

Exercise Intensity, F(2, 635.15) = 10.17, p < .001 (see Fig. 2), but no main effect for Post-Exercise Recovery, F(3,(635.27) = .43, p = .74, or an interaction of these factors,F(6, 635.33) = .91, p = .49. The Sidak-adjusted pairwise comparison demonstrated that Control had a lower memory recall than Moderate, M_{diff} (95% CI) = -.74 (-1.29, -.19), SE = .23, df = 635.15, p = .004, Control had a lower memory recall than Vigorous, M_{diff} (95% CI) = -1.00 (-1.56, -.45), SE = .23, df = 635.10, p < .001, but Moderate was not different than Vigorous, M_{diff} (95% CI) = -.26 (-.82, .29), SE = .23, df = 635.20, p = .59. Estimates of the fixed effects with Vigorous as referent were as follows; Control, M (95% CI) = -1.08 (-2.00, -.17), SE = .47, df = 635.23, t = -2.32, p =.02; Moderate, M (95% CI) = .06 (-.85, .97), SE = .46, df = 635.56, t = .12, p = .90. Estimates of the fixed effects with the 15-min recovery period as referent were as follows; 1 min rest, M (95% CI) = .63 (-.29, 1.54), SE = .47, df = 635.23, t = 1.34, p = .18; 5 min rest, M (95% CI) = -.28 (-1.19, .63),SE = .46, df = 635.56, t = -.61, p = .54; 10 min rest, M (95%) CI) = .30(-.62, 1.22), SE = .47, df = 635.23, t = .64, p = .52.

With proportional difference as the outcome, the Type III tests of fixed effects yielded a main effect for Exercise Intensity, F(2, 635.54) = 7.86, p < .001, but no main

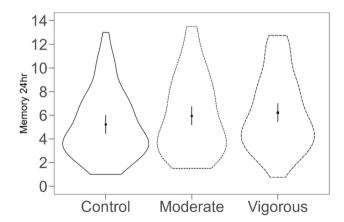


Fig. 2 Violin plot depicting the mean (95% CI) number of words recalled at the 24-h delay period as a function of exercise intensity. Moderate (M = 5.96, SE = .39) and Vigorous (M = 6.22, SE = .39) were different than Control (M = 5.22, SE = .39), p = .004 and p < .001, respectively, but Moderate and Vigorous did not differ from each other, p = .59

effect for Post-Exercise Recovery, F(3, 635.79) = .91, p= .43, or an interaction of these factors, F(6, 635.95) =1.50, p = .17. The Sidak-adjusted pairwise comparison demonstrated that Control had a lower memory recall than Vigorous, M_{diff} (95% CI) = -.09 (-.15, -.04), SE = .02, df = 635.46, p < .001, but Moderate was not different than Vigorous, p = .17, or Control, p = .11. Estimates of the fixed effects with Vigorous as referent were as follows; Control, M (95% CI) = -.12 (-.21, -.02), SE = .05, df = 635.95, t = -2.45, p = .02; Moderate, M (95% CI) =.01 (-.08, .11), SE = .05, df = 635.56, t = .28, p = .78. Estimates of the fixed effects with the 15-min recovery period as referent were as follows; 1 min rest, M (95%) CI = .09 (-.004, .18), SE = .05, df = 635.95, t = 1.87, p = .06; 5 min rest, M (95% CI) = -.04 (-.13, .06), SE = .05, df = 635.56, t = -.74, p = .46; 10 min rest, M (95%) CI) = .03 (-.07, .12), SE = .05, df = 635.95, t = .52, p= .60.

To evaluate if the potential effects of acute exercise on memory are due to item gains or losses, a 3 (Exercise Intensity) × 4 (Post-Exercise Recovery) linear mixed model was computed. With gains as the outcome, the Type III tests of fixed effects demonstrated that there were no main or interactive effects, ps > .37. With losses at the outcome, the Type III tests of fixed effects demonstrated a main effect for Exercise Intensity, F(2, 635.63) = 4.18, p = .01. The Sidakadjusted pairwise comparison demonstrated that Control had more losses than Vigorous, M_{diff} (95% CI) = .51 (.09, .72), SE = .18, df = 635.55, p = .01; no other comparisons were significant, p > .24. With unrecalled at both time periods as the outcome, the Type III tests of fixed effects demonstrated a main effect for Exercise Intensity, F(2, 635.11) = 3.59, p = .028. The Sidak-adjusted pairwise comparison demonstrated that Control had more words that were unrecalled at both time period when compared to Vigorous, M_{diff} (95%) CI) = .51 (.02, .99), SE = .20, df = 635.07, p = .038; no other comparisons were significant, p > .10. Similarly, when recalled at both time periods was the outcome, the Type III tests of fixed effects demonstrated there was a main effect for Exercise Intensity, F(2, 635.15) = 9.93, p < .001. The Sidak-adjusted pairwise comparison demonstrated that Control had fewer words that were recalled at both time period when compared to Moderate, M_{diff} (95% CI) = -.70 (-1.24, -.16), SE = .22, df = 635.15, p = .006; and Vigorous, M_{diff} (95% CI) = -.97 (-1.51, -.43), SE = .23, df = 635.10, *p* < .001; Moderate did not differ from Vigorous, p = .53.

Interaction between exercise intensity, post-exercise recovery, and endurance With memory performance at the 20-min delay as the outcome, a 3 (*Exercise Intensity*) \times 4 (*Post-Exercise Recovery*) \times 2 (*Endurance*) linear mixed model analysis demonstrated that the Type III tests of fixed effects yielded a main effect for Post-Exercise Recovery,

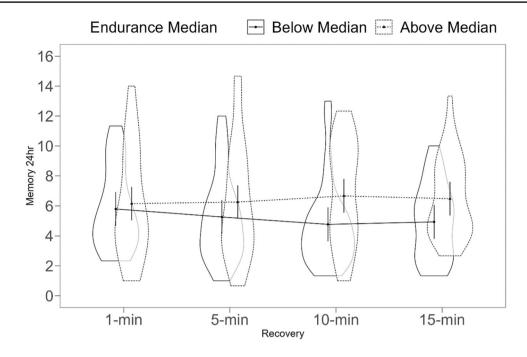


Fig. 3 Violin plot depicting the mean (95% CI) number of words recalled at the 24-h delay period as a function of Post-Exercise Recovery and Aerobic Endurance. At the 1-min, 5-min, and 15-min recovery periods, those with below-median endurance did not differ in their memory performance compared with those with above-

F(3, 643.00) = 2.83, p = .038, and a Post-Exercise Recovery by Endurance interaction, F(3, 643.04) = 2.78, p = .04. No other main or interaction effects were observed, p > .28.

With memory performance at the 24-h delay period serving as the outcome, the Type III tests of fixed effects demonstrated that there was not a three-way interaction, F(6, 635.34) = .78, p = .59, but Post-Exercise Recovery interacted with Endurance, F(3, 635.27) = 3.31, p = .02(Fig. 3). At the 1-min, 5-min and 15-min recovery periods, those with below-median endurance did not differ in their memory performance than those with above-median endurance, p = .66, p = .21, p = .05, respectively. However, at the 10-min recovery period, those with above-median endurance (M = 6.67, SE = .56) had greater memory performance than those with below-median endurance (M = 4.77, SE = .57), p = .01. We also observed an interaction between Exercise Intensity and Endurance, F(2, 635.15) = 3.17, p = .04 (Fig. 4). There was no difference in memory after the Control and Moderate conditions when comparing those below and above the median endurance, p = .48 and p = .05, respectively. However, after Vigorous exercise, those with above-median (M = 6.99, SE = .55) endurance had greater memory performance than those with below-median (M =5.44, SE = .55) endurance, p = .04.

With proportional difference as the outcome, the Type III tests of fixed effects demonstrated that there was not a three-way interaction, F(6, 635.96) = 1.37, p = .22, but

median endurance, p = .66, p = .21, p = .05, respectively. However, at the 10-min recovery period, those with above-median endurance (M = 6.67, SE = .56) had greater memory performance than those with below-median endurance (M = 4.77, SE = .57), p = .01

there was a marginally significant interaction between Exercise Intensity and Endurance, F(2, 635.55) = 2.98, p = .05 (Fig. 5). Those with below-median endurance (M = .64, SE = .03) did not differ in their memory performance than those with above-median endurance (M = .65, SE = .03) after the Control condition, p = .96. However, those with above-median endurance (M = .75, SE = .03) had better memory performance than those with below-median endurance (M = .64, SE = .03) after the Moderate condition, p = .01. Results were somewhat similar when comparing those with above-median endurance (M = .78, SE = .03) to those with below-median endurance (M = .70, SE = .03) after the Vigorous condition, p = .05.

Discussion

Main findings

Past meta-analytic research reports that exercise intensity and post-exercise recovery period may, potentially, influence the effects of acute exercise on cognitive function. However, limited studies within the meta-analyses were included in these moderation analyses. Further, past

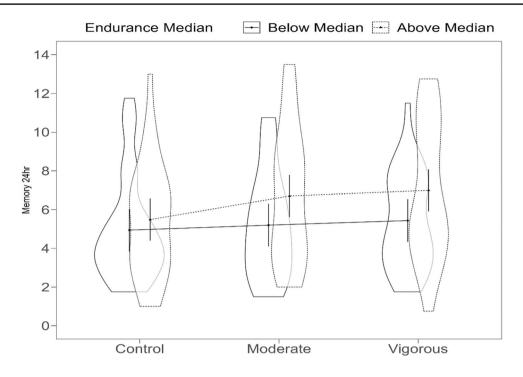


Fig. 4 Violin plot depicting the mean (95% CI) number of words recalled at the 24-h delay period as function of Exercise Intensity and Aerobic Endurance. There was no difference in memory after the control and moderate conditions when comparing those below and

above the median endurance, p = .48 and p = .05, respectively. However, after vigorous exercise, those with above-median (M = 6.99, SE = .55) endurance had greater memory performance than those with below-median (M = 5.44, SE = .55) endurance, p = .04

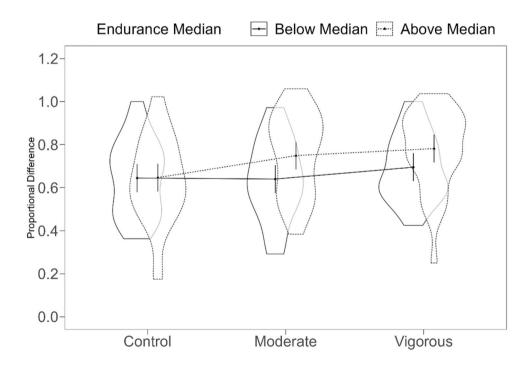


Fig. 5 Violin plot depicting the mean (95% CI) proportional difference results as function of Exercise Intensity and Aerobic Endurance. Those with below-median endurance (M = .64, SE = .03) did not differ in their memory performance compared with those with above-median endurance (M = .65, SE = .03) after the Control condition, p = .96. However, those with above-median endurance (M = .75, SE = .03)

.03) had better memory performance than those with below-median endurance (M = .64, SE = .03) after the Moderate condition, p = .01. Results were somewhat similar when comparing those with above-median endurance (M = .78, SE = .03) to those with below-median endurance (M = .70, SE = .03) after the Vigorous condition, p = .05

work on the association between cardiorespiratory fitness / aerobic endurance on memory performance is mixed. As such, the primary purpose of the present experiment was to evaluate if exercise intensity and post-exercise recovery period moderate the effects of acute exercise on memory. A secondary objective was to evaluate if aerobic endurance is associated with episodic memory and whether the potential interaction between exercise intensity and post-exercise recovery period on the exercisememory relationship is influenced by aerobic endurance. In partial agreement with these objectives, the primary finding from this experiment was that both moderate and vigorous-intensity exercise improved memory function at the 24-h delayed recall period when compared to a non-exercise control. A secondary finding of this experiment was that individuals with higher levels of aerobic endurance, compared to their lesser fit counterparts, had greater memory performance after exercise (at the 24-h delayed period and for the proportional difference metric) when compared to after a control condition. Additionally, individuals with higher levels of aerobic endurance, compared to their lesser fit counterparts, generally performed better on the memory task (at the 24-h delayed) with longer post-exercise recovery periods.

Exercise intensity and memory

The present experiment demonstrated that acute exercise (both moderate and vigorous) improved long-term episodic memory to a greater extent than a non-exercise control condition, an effect observed for the number of words recalled at the 24-h period, proportional difference and the number of items lost over the two time periods. The results of this experiment align with other work showing that both moderate- and vigorous-intensity exercise may enhance episodic memory performance (Loprinzi et al., 2019). When exercising, molecular responses (e.g., upregulation of neurotransmitters) that aid in memory function are increased, and thus, increase the likelihood of observing improvements in memory (Loprinzi, Roig, Etnier, Tomporowski, & Voss, 2021e). Our results suggest that a 20-min bout of exercise, followed by a rest period of up to 15 min, may be sufficient to enhance long-term memory performance.

This temporal period aligns with mechanistic studies in humans showing that, at between 15 and 20 min of post vigorous-intensity exercise (20 min at 80% of heart rate max), a centrally assessed neurotransmitter, glutamate, which is linked with memory (Menard & Quirion, 2012), reach its zenith (Maddock, Casazza, Fernandez, & Maddock, 2016). Further, in humans, Skriver et al. (2014) demonstrated the following temporal responses (relative to baseline) after a 20-min bout of vigorous-intensity exercise: brain-derived neurotrophic factor (BDNF) and insulin-like growth factor-1 (IGF-1) increased immediately after exercise; epinephrine and norepinephrine increased immediately and 5 min postexercise; dopamine increased 5 and 15 min post-exercise; and lastly, lactate levels increased immediately and 5, 10, and 15 min post-exercise. Elevated levels of some of these parameters correlated with procedural memory at different timepoints; higher levels of BDNF immediately after exercise were associated with greater memory retention 1 h and 7 days later; higher levels of norepinephrine were associated with greater memory retention 7 days later; and higher levels of lactate were associated with greater memory 1 h, 24 h, and 7 days later. For details on how exercise-induced changes in these parameters influences memory, the reader is referred elsewhere (Basso & Suzuki, 2017; El-Sayes, Harasym, Turco, Locke, & Nelson, 2019; Loprinzi, Ponce, & Frith, 2018; McMorris, 2021).

Aerobic endurance and memory

In our experiment, we demonstrated that higher fit individuals may have a greater memory performance after a bout of vigorous-intensity exercise, an effect observed for the number of words recalled at the 24-hour period and for the proportional difference metric. As suggested by Pontifex et al. (2019), cardiorespiratory fitness theoretically may prepare underlying exercise-induced neurophysiological mechanisms that are linked to memory improvement. That is, per this cardiovascular fitness hypothesis, higher aerobic endurance is a physiological mediator through which physical exercise may improve cognitive performance (Aberg et al., 2009). Additionally, and as suggested elsewhere (Cole et al., 2020), those with higher cardiorespiratory fitness may have elevated baseline activity of (neurotrophic) pathways (Berchtold, Chinn, Chou, Kesslak, & Cotman, 2005) and processes involved in memory function. In support of this, those with greater cardiorespiratory fitness have faster learning rates in episodic memory when compared to their lesser fit counterparts (Cole et al., 2020).

Exercise intensity, post-exercise recovery, and aerobic endurance

The results from the primary objective demonstrated that acute exercise intensity may influence memory performance. Adding to this finding, the results from the secondary objective suggest that those with higher aerobic endurance may have greater memory performance (proportional difference) after acute exercise. Further, individuals with higher aerobic endurance generally showed greater episodic memory performance when followed by longer recovery periods, an effect observed for the number of words recalled at the 24-h time period. Notably, however, we did not observe a threeway interaction of exercise intensity, recovery period, and aerobic endurance for the 20-min or 24-h delayed memory recall. Thus, the narrative that follows that discusses potential explanations for our observed results depicting an interaction between aerobic endurance and acute exercise, and aerobic endurance with post-exercise recovery, should be interpreted with caution.

Individuals with higher cardiorespiratory fitness have the physiological ability to recover faster post-vigorous exercise (Stanley, Peake, & Buchheit, 2013),⁴ and in turn, may have an enhanced sensitization to the effects of the aforementioned neurotransmitters as compared to individuals that are less fit. In contrast, lesser fit individuals, who recover slower after acute exercise, may have desensitization of the neurotransmitter system (Berchtold, Chinn, Chou, Kesslak, & Cotman, 2005). If these speculations are true, this would suggest that there may be an inverted U-shaped relationship between neurotransmitter / neurotrophin levels and memory, which may be sensitive to the interrelationships between exercise intensity, recovery period, and aerobic endurance (McMorris, 2021).

A more – or equally – likely explanation of this interaction is that the faster post-exercise recovery of aerobically fit individuals may allow for more effective learning/encoding due to enhanced allocation of attentional resources (Audiffren, 2016). The faster post-exercise recovery may allow for greater attentiveness during encoding, as opposed to less effective encoding due to fatigue of the preceding exercise bout. It would be worthwhile for future research to evaluate the extent to which fitness and post-exercise recovery period interact to potentially influence the level of attention at encoding (Audiffren, 2009; Sanders, 1997, 1998). Relatedly, it may be worth exploring whether this change in attentional processes triggers elevated levels of motivation toward performance on the memory task;⁵ for a review on how such effects could increase tonic release of dopamine, and in turn, induce release of norepinephrine to influence memory, the reader is referred to work by McMorris (2021).

Strengths and limitations

Notable strengths of our study include a relatively large sample of 59 participants, the use of a maximal bout of exercise to calculate the heart rate thresholds used for the submaximal exercise intensities, including multiple exercise intensities, incorporating long-term memory assessments out to 24 h, and including multiple within-person observations. A notable limitation is that our aerobic endurance measure was based on how long participants lasted during a maximal treadmill test, as opposed to a direct measurement of cardiorespiratory fitness via indirect calorimetry. Additionally, our findings may only be generalizable to young adults, and thus, future research may wish to evaluate these parameters in other populations. Such work should also carefully consider how certain participant (e.g., intelligence) and behavioral (e.g., sleep quality via Actigraphy) characteristics influence the effect of acute exercise on memory. Lastly, efforts were made to have the primary visit (involving the 20-min recall) occur 24-72 h after the 24-h recall of the preceding condition. However, on occasion, due to scheduling concerns, some participants had their 24-h recall on the same day (but before) as they encoded the new lists of words, potentially leading to proactive interference.

Future work

In addition to the aforementioned recommendations, we see value in future studies targeting potential mechanisms of the exercise-memory relationship. As discussed, acute exercise may enhance long-term memory via encoding and/ or consolidation-based mechanisms (Loprinzi, Roig, Etnier, Tomporowski, & Voss, 2021e). An alternative explanation, however, is that differences in recall as a function of exercise might be due to the ability of subjects to contextually reinstate the original study episode. At longer delays, a subject's ability to recall a list of items may be determined by the extent to which they can reinstate the original encoding context. It may be easier to reinstate the original encoding context when it occurs following exercise (and especially vigorous exercise) than when it occurs without exercise. According to this explanation, exercise might enhance long-term memory not because it improves encoding/consolidation, but because it serves as a cue making it easier for the individual to reinstate the context. This explanation predicts a difference in memory performance more so after 24 h, as opposed to a shorter delay period, such as after 20 min. Indeed, our results demonstrated greater exercise-induced effects on memory performance after 24 h when compared to after 20 min. Additionally, we attempted to further investigate this contextual account by evaluating how often participants failed to recall any items on the 24-h assessment, as such variations across exercise conditions would be consistent with this context account. Our data showed that, collapsed across the four post-exercise recovery periods, the mean (SD) proportion of failing to recall any items on the 24-h assessment for the Control, Moderate, and Vigorous conditions, respectively, were .07 (.13), .04 (.11), and .04 (.11). Although proportions were quantitatively higher for Control compared to the Exercise

⁴ In the Appendix we report the physiological (heart rate) response over the recovery period after vigorous-intensity acute exercise, demonstrating that, within our sample, those with greater aerobic endurance recovered faster than their lesser fit counterparts (see Online Supplementary Material (OSM) Fig. 2).

⁵ It is also equally likely that the other direction of this relationship is occurring, with higher motivation facilitating attentional processes.

conditions, there were no statistically significant differences across conditions, ps > .05.

Future work, however, could more rigorously (experimentally) investigate this context account by giving all participants a salient cue at encoding. This cue should reduce or even eliminate the difference in memory performance as a function of exercise condition on the 24-h delayed assessment. If, however, the exercise effect remains, then this would suggest that exercise-induced differences in memory performance are not driven by differences in contextual reinstatement.

Conclusion

In conclusion, our findings suggest that acute exercise can enhance long-term episodic memory. We also demonstrate evidence that aerobic endurance may interact with the postexercise recovery period and exercise intensity to influence episodic memory. As such, future research should carefully consider these parameters when evaluating the effects of acute exercise on long-term episodic memory. If such findings are replicated, then this may help design tailored protocols to enhance an individual's memory performance based on their fitness and time constraints.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.3758/s13421-022-01373-4.

Acknowledgements Assistance with data collection was provided by Bailey Bass, Anna Case, Caroline Loeb, William Meyers, and Mary Collins West. We thank Dr. Benjamin Storm for feedback on an earlier version of this article. This experiment was not pre-registered.

Declarations

Disclosures None.

References

- Aberg, M. A., Pedersen, N. L., Toren, K., Svartengren, M., Backstrand, B., Johnsson, T., ... Kuhn, H. G. (2009). Cardiovascular fitness is associated with cognition in young adulthood. *Proceedings of the National Academy of Sciences of the United States of America*, 106(49), 20906-20911. https://doi.org/10.1073/pnas.0905307106
- Amaral, M. D., & Pozzo-Miller, L. (2009). The dynamics of excitatory synapse formation on dendritic spines. *Cellscience*, 5(4), 19–25.
- Audiffren, M. (2009). Acute exercise and psychological functions: A cognitive-energetic approach. In T. McMorris, P. Tomporowski, & M. Audiffren (Eds.), *Exercise and cognitive function* (pp. 3–39). Wiley-Blackwell.
- Audiffren, M. (2016). The reticular-activating hypofrontality (RAH) model of acute exercise: Current data and future perspectives. In T. McMorris (Ed.), *Exercise-cognition interaction: Neuroscience perspectives* (pp. 147–166). Elsevier Academic Press.
- Ball, T. J., Joy, E. A., Gren, L. H., & Shaw, J. M. (2016). Concurrent validity of a self-reported physical activity "vital sign" questionnaire with adult primary care patients. *Preventing Chronic Disease*, 13, E16. https://doi.org/10.5888/pcd13.150228

- Basso, J. C., & Suzuki, W. A. (2017). The effects of acute exercise on mood, cognition, neurophysiology, and neurochemical pathways: A review. *Brain Plast*, 2(2), 127–152. https://doi.org/10. 3233/BPL-160040
- Berchtold, N. C., Chinn, G., Chou, M., Kesslak, J. P., & Cotman, C. W. (2005). Exercise primes a molecular memory for brain-derived neurotrophic factor protein induction in the rat hippocampus. *Neuroscience*, 133(3), 853–861. https://doi.org/10.1016/j.neuroscien ce.2005.03.026
- Blough, J., & Loprinzi, P. D. (2019). Experimental manipulation of psychological control scenarios: Implications for exercise and memory research. *Psych*, 1(1), 279–289.
- Bonin, P., Gelin, M., & Bugaiska, A. (2014). Animates are better remembered than inanimates: Further evidence from word and picture stimuli. *Memory & Cognition*, 42(3), 370–382. https:// doi.org/10.3758/s13421-013-0368-8
- Bourne, J. N., & Harris, K. M. (2012). Nanoscale analysis of structural synaptic plasticity. *Current Opinion in Neurobiology*, 22(3), 372–382. https://doi.org/10.1016/j.conb.2011.10.019
- Brisswalter, J., Collardeau, M., & Rene, A. (2002). Effects of acute physical exercise characteristics on cognitive performance. *Sports Medicine*, 32(9), 555–566. https://doi.org/10.2165/00007256-200232090-00002
- Caretti, D. M. (1999). Cognitive performance and mood during respirator wear and exercise. *American Industrial Hygiene Association Journal*, 60(2), 213–218. https://doi.org/10.1080/00028899908984438
- Chandler, M. C., McGowan, A. L., Payne, B. R., Hampton Wray, A., & Pontifex, M. B. (2019). Aerobic fitness relates to differential attentional but not language-related cognitive processes. *Brain and Lan*guage, 198, 104681. https://doi.org/10.1016/j.bandl.2019.104681
- Chandler, M. C., McGowan, A. L., Burles, F., Mathewson, K. E., Scavuzzo, C. J., & Pontifex, M. B. (2020). Aerobic fitness unrelated to acquisition of spatial relational memory in college-aged adults. *Journal of Sport & Exercise Psychology*, 1-8. https://doi.org/10. 1123/jsep.2020-0004
- Chang, Y. K., Labban, J. D., Gapin, J. I., & Etnier, J. L. (2012). The effects of acute exercise on cognitive performance: A meta-analysis. *Brain Research*, 1453, 87–101. https://doi.org/10.1016/j.brain res.2012.02.068
- Cole, R. C., Hazeltine, E., Weng, T. B., Wharff, C., DuBose, L. E., Schmid, P., ... Voss, M. W. (2020). Cardiorespiratory fitness and hippocampal volume predict faster episodic associative learning in older adults. *Hippocampus*, 30(2), 143-155. https://doi.org/10. 1002/hipo.23151
- Crush, E. A., & Loprinzi, P. D. (2017). Dose-response effects of exercise duration and recovery on cognitive functioning. *Perceptual* and Motor Skills, 124(6), 1164–1193. https://doi.org/10.1177/ 0031512517726920
- El-Sayes, J., Harasym, D., Turco, C. V., Locke, M. B., & Nelson, A. J. (2019). Exercise-induced neuroplasticity: A mechanistic model and prospects for promoting plasticity. *Neuroscientist*, 25(1), 65–85. https://doi.org/10.1177/1073858418771538
- Etnier, J., Nowell, P. M., Landers, D. M., & Sibley, B. A. (2006). A meta-regression to examine the relationship between aerobic fitness and cognitive performance. *Brain Research Reviews*, 52(1), 119–130.
- 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
- Field, A. (2015). Discovering Statistics Using IBM SPSS Statistics (5th ed.). Sage.
- Garber, C. E., Blissmer, B., Deschenes, M. R., Franklin, B. A., Lamonte, M. J., Lee, I. M., ... American College of Sports, M. (2011). American College of Sports Medicine position stand.

Quantity and quality of exercise for developing and maintaining cardiorespiratory, musculoskeletal, and neuromotor fitness in apparently healthy adults: guidance for prescribing exercise. *Medicine and Science in Sports and Exercise*, 43(7), 1334-1359. https://doi.org/10.1249/MSS.0b013e318213fefb

- Gomez-Pinilla, F., & Hillman, C. (2013). The influence of exercise on cognitive abilities. *Comprehensive Physiology*, 3(1), 403–428. https://doi.org/10.1002/cphy.c110063
- Hopkins, S. R., Dominelli, P. B., Davis, C. K., Guenette, J. A., Luks, A. M., Molgat-Seon, Y., ... Stickland, M. K. (2020). Facemasks and the cardiorespiratory response to physical activity in health and disease. *Annals of the American Thoracic Society*. https://doi. org/10.1513/AnnalsATS.202008-990CME
- Ishihara, T., Drollette, E. S., Ludyga, S., Hillman, C. H., & Kamijo, K. (2021). The effects of acute aerobic exercise on executive function: A systematic review and meta-analysis of individual participant data. *Neuroscience and Biobehavioral Reviews*, 128, 258–269. https://doi.org/10.1016/j.neubiorev.2021.06.026
- Jung, M., Ryu, S., Kang, M., Javadi, A. H., & Loprinzi, P. D. (2022). Evaluation of the transient hypofrontality theory in the context of exercise: A systematic review with meta-analysis. *Quarterly Journal of Experimental Psychology (Hove)*, 75(7), 1193–1214. https://doi.org/10.1177/17470218211048807
- Kao, S. C., Cadenas-Sanchez, C., Shigeta, T. T., Walk, A. M., Chang, Y. K., Pontifex, M. B., & Hillman, C. H. (2020). A systematic review of physical activity and cardiorespiratory fitness on P3b. *Psychophysiology*, *57*(7), e13425. https://doi.org/10.1111/psyp.13425
- Labban, J. D., & Etnier, J. L. (2011). Effects of acute exercise on long-term memory. *Research Quarterly for Exercise and 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
- Lambourne, K., & Tomporowski, P. (2010). The effect of exerciseinduced arousal on cognitive task performance: a meta-regression analysis. *Brain Research*, 1341, 12–24. https://doi.org/10.1016/j. brainres.2010.03.091
- Loprinzi, P. D. (2018). Intensity-specific effects of acute exercise on human memory function: Considerations for the timing of exercise and the type of memory. *Health Promotion Perspective*, 8(4), 255–262. https://doi.org/10.15171/hpp.2018.36
- Loprinzi, P. D., Ponce, P., & Frith, E. (2018). Hypothesized mechanisms through which acute exercise influences episodic memory. *Physiology International*, 105(4), 285–297. https://doi.org/10. 1556/2060.105.2018.4.28
- 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), 87.
- Loprinzi, P. D., Crawford, L., Moore, D., Blough, J., Burnett, G., Chism, M., & Robinson, G. (2020). Motor behavior-induced prefrontal cortex activation and episodic memory function. *The International Journal of Neuroscience*, 1–21. https://doi.org/10. 1080/00207454.2020.1803307
- Loprinzi, P. D., Day, S., Hendry, R., Hoffman, S., Love, A., Marable, S., ... Gilliland, B. (2021a). The effects of acute exercise on shortand 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. D., Loenneke, J. P., & Storm, B. C. (2021b). Effects of acute aerobic and resistance exercise on episodic memory function. *Quarterly Journal of Experimental Psychology (Hove)*, 74(7), 1264–1283. https://doi.org/10.1177/1747021821994576
- Loprinzi, P. D., Lovorn, A., & Gilmore, J. (2021c). Effects of exercise on explicit memory function: Incidental and intentional encoding

may depend on exercise timing. *Perceptual and Motor Skills, 128*, 865–884.

- Loprinzi, P. D., Rigdon, B., Javadi, A. H., & Kelemen, W. (2021d). EXPRESS: Effects of acute exercise intensity on source episodic memory and metamemory accuracy. *Quarterly Journal of Experimental Psychology (Hove)*, 17470218211069856. https://doi.org/ 10.1177/17470218211069856
- Loprinzi, P. D., Roig, M., Etnier, J. L., Tomporowski, P. D., & Voss, M. (2021e). 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
- Ludyga, S., Gerber, M., & Kamijo, K. (2022). Exercise types and working memory components during development. *Trends in Cognitive Sciences*, 26(3), 191–203. https://doi.org/10.1016/j.tics.2021.12.004
- Madan, C. R. (2020). Rethinking the definition of episodic memory. Canadian Journal of Experimental Psychology, 74(3), 183–192. https://doi.org/10.1037/cep0000229
- Maddock, R. J., Casazza, G. A., Fernandez, D. H., & Maddock, M. I. (2016). Acute modulation of cortical glutamate and GABA content by physical activity. *The Journal of Neuroscience*, 36(8), 2449–2457. https://doi.org/10.1523/JNEUROSCI.3455-15.2016
- McMorris, T. (2016). Developing the catecholamines hypothesis for the acute exercise-cognition interaction in humans: Lessons from animal studies. *Physiology & Behavior*, 165, 291–299. 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
- Menard, C., & Quirion, R. (2012). Group 1 metabotropic glutamate receptor function and its regulation of learning and memory in the aging brain. *Frontiers in Pharmacology*, *3*, 182. https://doi. org/10.3389/fphar.2012.00182
- Mier, C. M., & Gibson, A. L. (2004). Evaluation of a treadmill test for predicting the aerobic capacity of firefighters. *Occupational Medicine* (London), 54(6), 373–378. https://doi.org/10.1093/occmed/kqh008
- Morris, N. B., Piil, J. F., Christiansen, L., Flouris, A. D., & Nybo, L. (2021). Prolonged facemask use in the heat worsens dyspnea without compromising motor-cognitive performance. *Temperature*, 8, 160–165.
- Moutoussamy, I., Taconnat, L., Pothier, K., Toussaint, L., & Fay, S. (2022). Episodic memory and aging: Benefits of physical activity depend on the executive resources required for the task. *PLoS One*, *17*(2), e0263919. https://doi.org/10.1371/journal.pone.0263919
- Pollock, M. L., Foster, C., Schmidt, D., Hellman, C., Linnerud, A. C., & Ward, A. (1982). Comparative analysis of physiologic responses to three different maximal graded exercise test protocols in healthy women. *American Heart Journal*, 103(3), 363–373. https://doi.org/10.1016/0002-8703(82)90275-7
- Pontifex, M. B., Parks, A. C., O'Neil, P. C., Egner, A. R., Warning, J. T., Pfeiffer, K. A., & Fenn, K. M. (2014). Poorer aerobic fitness relates to reduced integrity of multiple memory systems. *Cognitive, Affective, & Behavioral Neuroscience, 14*(3), 1132–1141. https://doi.org/10.3758/s13415-014-0265-z
- Pontifex, M. B., McGowan, A. L., Chandler, M. C., Gwizdala, K. L., Parks, A. C., Fenn, K., & Kamijo, K. (2019). A primer on investigating the after effects of acute bouts of physical activity on cognition. *Psychology of Sport and Exercise*, 40, 1–22.
- Pyke, W., Ifram, F., Coventry, L., Sung, Y., Champion, I., & Javadi, A. H. (2020). The effects of different protocols of physical exercise and rest on long-term memory. *Neurobiology of Learning and Memory*, 167, 107128. https://doi.org/10.1016/j.nlm.2019.107128
- Rigdon, B., & Loprinzi, P. D. (2019). The association of cardiorespiratory fitness on memory function: Systematic review. *Medicina (Kaunas, Lithuania)*, 55(5). https://doi.org/10.3390/medicina55050127

- 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 and Biobehavioral Reviews*, 37(8), 1645–1666. 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), 81–88. https://doi.org/10.1249/JES.000000000 000078
- 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), 507–513.
- Sanders, A. F. (1997). A summary of resource theories from a behavioral perspective. *Biological Psychology*, 45(1-3), 5–18. https:// doi.org/10.1016/s0301-0511(96)05220-9
- Sanders, A. F. (1998). *Elements of human performance: Reaction processes and attention in human skill*. Lawrence Erlbaum Associates Publishers.
- Saucedo Marquez, C. M., Vanaudenaerde, B., Troosters, T., & Wenderoth, N. (2015). High-intensity interval training evokes larger serum BDNF levels compared with intense continuous exercise. *Journal of Applied Physiology (Bethesda, MD: 1985), 119*(12), 1363–1373. https://doi.org/10.1152/japplphysiol.00126.2015
- Skriver, K., Roig, M., Lundbye-Jensen, J., Pingel, J., Helge, J. W., Kiens, B., & Nielsen, J. B. (2014). Acute exercise improves motor memory: Exploring potential biomarkers. *Neurobiology of Learning and Memory*, *116*, 46–58. https://doi.org/10.1016/j.nlm.2014. 08.004
- Sng, E., Frith, E., & Loprinzi, P. D. (2018). Experimental effects of acute exercise on episodic memory acquisition: Decomposition of multi-trial gains and losses. *Physiology & Behavior*, 186, 82–84. https://doi.org/10.1016/j.physbeh.2018.01.014
- Stanley, J., Peake, J. M., & Buchheit, M. (2013). Cardiac parasympathetic reactivation following exercise: Implications for training prescription. *Sports Medicine*, 43(12), 1259–1277. https://doi.org/ 10.1007/s40279-013-0083-4
- Suwabe, K., Hyodo, K., Byun, K., Ochi, G., Yassa, M. A., & Soya, H. (2017). Acute moderate exercise improves mnemonic discrimination in young adults. *Hippocampus*, 27(3), 229–234. https://doi. org/10.1002/hipo.22695

- Tomporowski, P. D. (2003). Effects of acute bouts of exercise on cognition. Acta Psychologica, 112(3), 297–324. https://doi.org/10.1016/ s0001-6918(02)00134-8
- Tomporowski, P. D., Ellis, N. R., & Stephens, R. (1987). The immediate effects of strenuous exercise on free-recall memory. *Ergonomics*, 30(1), 121–129. https://doi.org/10.1080/00140138708969682
- van Praag, H., Schinder, A. F., Christie, B. R., Toni, N., Palmer, T. D., & Gage, F. H. (2002). Functional neurogenesis in the adult hippocampus. *Nature*, 415(6875), 1030–1034. https://doi.org/10. 1038/4151030a
- Voss, M. W., Weng, T. B., Narayana-Kumanan, K., Cole, R. C., Wharff, C., Reist, L., ... Pierce, G. L. (2020). Acute exercise effects predict training change in cognition and connectivity. *Medicine and Science in Sports and Exercise*, 52(1), 131-140. https://doi.org/10. 1249/MSS.00000000002115
- West, B. T. (2009). Analyzing longitudinal data with the linear mixed models procedure in SPSS. *Evaluation & the Health Professions*, 32(3), 207–228.
- Winter, B., Breitenstein, C., Mooren, F. C., Voelker, K., Fobker, M., Lechtermann, A., ... Knecht, S. (2007). High impact running improves learning. *Neurobiology of Learning and Memory*, 87(4), 597-609. https://doi.org/10.1016/j.nlm.2006.11.003
- Zuniga, K. E., Mueller, M., Santana, A. R., & Kelemen, W. L. (2019). Acute aerobic exercise improves memory across intensity and fitness levels. *Memory*, 27(5), 628–636. https://doi.org/10.1080/ 09658211.2018.1546875

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Springer Nature or its licensor (e.g. a society or other partner) holds exclusive rights to this article under a publishing agreement with the author(s) or other rightsholder(s); author self-archiving of the accepted manuscript version of this article is solely governed by the terms of such publishing agreement and applicable law.