

The effect of acute exercise on encoding and consolidation of long-term memory

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Abstract:

Evidence supports that acute exercise benefits long-term memory. However, it is unclear whether these effects are due to benefits to encoding or consolidation. The purpose of this study was to more effectively isolate encoding and consolidation to advance our understanding of the specific nature of the effects of exercise on long-term memory. Using a within-subject design, participants completed a control session (no exercise), an encoding and consolidation condition (exercise prior to exposure to the memory task, E + C), and a consolidation condition (exercise following exposure). The exercise was 30min of moderate-intensity cycling. Memory was assessed using the Rey Auditory Verbal Learning Test with recall assessed at 60 min and recall and recognition assessed at 24 hr. Results showed that the E + C condition had significantly better recall at 60 min and 24 hr than the no-exercise condition. This provides additional evidence that acute exercise benefits encoding more than consolidation.

Keywords: aerobic | cognition | physical activity

Article:

Exercise is generally known to be a healthful activity, with benefits observed for both mental and physiological outcomes. Of interest within the area of mental health is the potential benefit to cognitive function in response to a single bout of exercise. Though results from empirical studies in this area exhibit a great deal of heterogeneity, narrative (Brisswalter, Collardeau, & Rene, 2002; Kashihara, Maruyama, Murota, & Nakahara, 2009; McMorris & Graydon, 2000; Tomporowski, 2003a, 2003b; Tomporowski & Ellis, 1986), and meta-analytic (Chang, Labban, Gapin, & Etnier, 2012; Etnier et al., 1997; Lambourne & Tomporowski, 2010) reviews of the literature converge on the notion that acute exercise can have a positive impact on cognitive performance when the cognitive task is performed after the exercise session.

When reviewing this literature, one important consideration is the particular nature of the cognitive test that is used. Within the acute exercise paradigm, cognitive performance has most commonly been assessed with measures of reaction time and information processing (e.g., Chang & Etnier, 2009; McMorris & Graydon, 2000; Pesce, Cereatti, Casella, Baldari, & Capranica,

2007), executive function (e.g., Emery, Honn, Frid, Lebowitz, & Diaz, 2001; Kubesch et al., 2003; Netz, Argov, & Inbar, 2009), or short-term memory (e.g., Coles & Tomporowski, 2008; Netz et al., 2009; Tomporowski & Ganio, 2006). The dominant assumption within the literature is that changes brought about by acute exercise are transient and, therefore, any resultant changes in cognitive function would also be transient. Indeed, this assumption is supported by the results of a meta-analytic review in which Chang et al. (2012) reported positive overall effects of acute exercise on cognition when assessed within 15 min of exercise cessation, but nonsignificant overall effects when cognition was assessed more than 15 min following exercise cessation. Memory, however, is one cognitive domain for which the effects of acute exercise may be more durable. Long-term memory has been operationalized as memory involving some delay, ranging from minutes to years, between the initial encoding of target material and its retrieval (Baddeley, 1999). Whereas changes to reaction time are not likely to be observed at longer latencies between a bout of exercise and assessment (and so have not historically even been tested at these longer delays), it is conceivable that influences on long-term memory of information learned proximal to an exercise bout could be observable following longer latencies. Such a result would suggest that, specifically, long-term memory processes are sensitive to the effects of acute exercise.

The current body of research testing for an effect of acute exercise on long-term memory (e.g., Coles & Tomporowski, 2008; Labban & Etnier, 2011; Potter & Keeling, 2005; Tomporowski & Ganio, 2006; Winter et al., 2007) has generally supported a positive relationship. In fact, Roig, Nordbrandt, Geertsen, and Nielsen (2013) conducted a meta-analytic review that focused solely on memory outcomes and reported statistically significant positive overall effects of acute exercise on memory. Furthermore, Roig et al. (2013) reported larger effects for measures of long-term memory (standardized mean difference = 0.52) and smaller effects for measures of short-term memory (standardized mean difference = 0.15). More recently, Loprinzi, Frith, Edwards, Sng, and Ashpole (2018) conducted a systematic review of the literature on exercise and memory in young and middle-aged adults and also concluded that acute exercise has beneficial effects for memory. Hence, there is evidence that memory measures are sensitive to acute exercise interventions, and that these effects can be more durable than those observed for other cognitive domains. An important direction for current research is to explore how the timing of the exercise affects memory performance, with a goal of better understanding the extent to which exercise influences encoding and consolidation.

Storage of information into long-term memory can be separated very basically into two processes: encoding and consolidation. Encoding involves the initial attendance to and processing of target material. It is followed by a consolidation period during which information is moved into a more stable and durable state in memory. Consolidation may begin to occur at some point during encoding and continues after encoding of the target material has finished. An as yet unanswered question is whether acute exercise has an effect on encoding, consolidation, or both. The precise nature of this effect may determine the ultimate impact on long-term memory. This question has begun to be explored in recent research.

Labban and Etnier (2011) randomly assigned participants to a control condition or to exercise groups that completed a 30-min bout of exercise either prior to or immediately following exposure to a brief story. Participants were then asked to recount the story 35 min after initial

exposure. Results showed that the group exercising prior to story exposure recalled the story significantly better than did the control group, and there was also a trend for better recall performance as compared with the group that exercised following story exposure ($p = .09$). Salas, Minakata, and Kelemen (2011) randomly assigned participants to exercise or sit prior to exposure to a list of 30 words. Participants were then further assigned to exercise or sit during the consolidation period. Immediately following consolidation, they were asked to recall the words. Results showed that walking prior to exposure resulted in significantly better recall, but that the treatments during consolidation did not significantly influence the results. Frith, Sng, and Loprinzi (2017) randomly assigned young adults to either exercise prior to exposure to the Rey Auditory Verbal Learning Test (RAVLT), after the RAVLT, during the RAVLT, or no exercise (NE). They reported that the exercise prior group performed better on measures of long-term memory (after a 20-min delay and a 24-hr delay) than did the control group. Thus, results from these studies support the benefits of acute exercise for long-term memory and suggest that exercise that occurs prior to both encoding and consolidation results in better long-term memory as compared with exercise at other times or a control condition. However, there are two primary limitations of this past research. First, in all of these studies, the exercise after exposure groups were exercising for almost the entire consolidation period. Furthermore, the exercise immediately preceded recall. Hence, the authors were not able to isolate the effects of the exercise on consolidation, but rather confounded these effects with potential effects on information retrieval. Second, Labban and Etnier (2011) and Frith et al. (2017) used memory protocols in which the participants were asked to both encode and recall targeted material during the exposure period. Thus, again, the effects of exercise were not isolated to encoding but rather might have affected encoding, retrieval, and learning. Because of these limitations, additional research is needed to advance our understanding of whether acute exercise benefits encoding, consolidation, or both.

Thus, the goal of the present study was to more effectively isolate encoding and consolidation periods to further explore whether the effects of exercise on long-term memory operate through the encoding and/or consolidation process(es) of long-term memory formation. Based upon the results from previous research, it was hypothesized that any effects of exercise would operate primarily through benefits to encoding. That is, it was expected that exercising prior to encoding would generally result in better performance on memory tasks relative to the control condition. However, the previous literature does not provide compelling evidence that any differences observed between the encoding and consolidation conditions would achieve statistical significance. Therefore, we did not have an a priori hypothesis relative to the differences between treatment conditions.

Methods

Sample

The sample consisted of 15 students from the university campus. Recruitment was accomplished through the posting of flyers around campus, as well as oral recruitment in individual classes. This sample size was determined by power analyses for a within-subjects design, and on effect sizes based upon the results observed in the study by Labban and Etnier (2011) and from Etnier et al. (2016). These studies were chosen due to the similarities in design and purpose with this

study. Both studies employed verbal memory outcomes for which items recalled—story units and word lists, respectively—were compared across conditions, and both featured delay periods—30 to 35 min—similar to that used in the present study. Large effect sizes were reported by Labban and Etnier (Cohen’s $d = 1.04$) and by Etnier et al. ($\eta_p^2 = .23-.29$), so power analyses were computed using more conservative effect estimates ($\eta^2 = .10-.15$). Results suggested that a sample size of 15 was sufficient to achieve adequate power (.80) at these smaller effect estimates. In keeping with the previously described studies of acute exercise, the sample was limited to healthy participants aged 18–35 years. In addition, these inclusion criteria also perhaps made for a more conservative test of the stated hypotheses, given that a healthy young sample was likely to perform well on cognitive tasks even under control conditions.

Exercise Protocol

The intervention consisted of a 30-min bout of exercise on a recumbent ergometer (Lode Corival, Groningen, The Netherlands). Participants began with a 5-min warm-up, pedaling at 60 revolutions per minute (rpm) with an initial resistance of 25 watts. Participants were asked to pedal at 60 rpm for the entire exercise bout. Resistance was gradually increased and exertion ratings were recorded each minute of the warm-up until a minimum rating of perceived exertion (RPE) of 13 on Borg’s RPE (Borg, 1998) scale had been achieved. Subsequently, RPE was assessed every 3 min for the remainder of the exercise bout, with the resistance level adjusted to keep ratings between 13 and 15. Participants entered a 5-min cool-down phase following the 25-min mark, during which resistance was gradually decreased to the original minimal setting of 25 watts. The use of RPE to determine exercise intensity ensured that each participant was always exercising at a level he or she determined to be “moderate.” The exercise protocol was chosen to be similar in mode, duration, and intensity to that used in the study by Labban and Etnier (2011) and this intensity also matches the middle 5 min of the 15-min ramped protocol used by Frith et al. (2017). For the E + C condition, participants completed the exercise protocol immediately prior to exposure to the word list. For the C condition, exercise began immediately following exposure to the word list. During the NE control condition, participants simply sat quietly at a desk, or read if they so chose, preceding and following exposure to the word list. Participants had free access to water throughout each visit.

Perceived Exertion

Borg’s RPE scale is a widely-accepted measure, possessing acceptable reliability ($\alpha > .90$). Criterion validity, relative to VO_{2max} , is also high when exercise is performed on a cycle ergometer ($r = .83$, 95% confidence interval [2, 46] = .735–.912; Chen, Fan, & Moe, 2002). The scale consists of numbers, ranging from 6 to 20, some of which are paired with verbal descriptors. For example, a rating of 7 is labeled as *very, very light*, whereas a rating of 17 is labeled *very hard*. Participants in this study were instructed to exercise at resistance levels that would elicit ratings between 13 (*somewhat hard*) and 15 (*hard*) on the RPE scale.

Descriptive and Demographic Measures

Potential participants completed a medical screening questionnaire to ensure that it was safe for them to participate in the exercise required for the study. General demographic variables were

also collected, including gender, ethnicity, and education level. Current lifestyle physical activity participation was assessed using the National Health Interview Survey, Part E (Benson & Marano, 1998).

Memory

Memory was assessed using word lists created for the RAVLT (Lezak, Howieson, & Loring, 2004). The word lists used in the present study provided three equivalent memory assessments that were randomized across the three experimental conditions. Each word list consisted of 15 words, and was prerecorded, with words read at a rate of one word per second. During exposure trials, participants heard the word list five times consecutively, with no delay in between trials. Word order was kept the same for each exposure trial. Multiple, consecutive exposure was used in place of the typical multi-trial listen-recall protocol of the RAVLT to maximize encoding opportunity and minimize the opportunity for consolidation through rehearsal. Prior to and following the exposure trials, participants were asked not to mentally rehearse the words. Test instructions and word list readings were administered via electronic recording through over-ear headphones to ensure consistency of administration. Sixty minutes and 24 hr following word list exposure, participants were asked to recount all of the words they could remember from the list. Words that were correctly recalled were counted as “Hits (HT),” with unique HT summed to form 60 min and 24-hr recall scores. The recognition task was administered immediately following the 24-hr recall task, for which participants were asked to identify words from the previous day’s list from a randomly-ordered list of 30 words—all 15 words from the previous day’s list, and 15 distractor words. No feedback regarding recall or recognition was ever provided to participants.

Procedure

The study was conducted using a within-subjects, repeated measures design, requiring three test days for each participant. Participants were instructed not to participate in physical activity, outside of that included in the experimental procedure, on each test day. On the first test day, participants provided informed consent, as well as completion of a medical screening questionnaire and general demographics form. Participants were randomized to condition order at that time. The procedures for each test day were identical except for the presence and timing of the exercise condition.

Depending upon the condition assignment for that day, participants exercised immediately prior to (encoding plus consolidation condition; E + C) or immediately following (consolidation condition; C) exposure to the word list, or NE (see Table 1). The 60-min delay was chosen to provide adequate time during the C condition for exercise completion and recovery so that potential effects of exercise on consolidation would not be confounded by potential effects of exercise on retrieval. Following list exposure, 60 min elapsed (which, depending upon condition, did or did not include exercise) before participants were asked to recount all the words from the list that they could remember, regardless of order. During all rest periods, participants were allowed to pick among a selection of magazines from which they could read quietly. Finally, participants were contacted by phone 24 hr following list exposure; again, asked to recall all the words they could remember, and then given the word recognition task.

Table 1. Protocol for the Study Depicting the Three Conditions and the Timing of Exposure to the Word List and Recall of the Word List Relative to Exercise and Rest

Condition	Preencoding (30 min)	Encoding (~5 min)	Consolidation		60-Min Delay	24-Hr Delay
			30 min	30 min		
Encoding + consolidation	Exercise	List	Rest	Rest	Free recall	Free recall and recognition
Consolidation	Rest	List	Exercise	Rest		
Control	Rest	List	Rest	Rest		

Each test day was separated by a minimum of two days to reduce interference from the previous test day’s word list. Pairing of word lists and conditions was counterbalanced, such that, to the extent possible, word lists were evenly distributed among conditions. Condition order was also counterbalanced and randomly assigned to participants to avoid systematic order effects. The time of day during which testing took place was kept consistent within participants; that is, each participant completed all test days during the same time of day (morning or afternoon), with start times separated by no more than 2 hr.

Data Analysis

Exercise data (HR, RPE, RPM, and workload; Table 2) were compared across the two exercise conditions using repeated-measures analysis of variance to test for any systematic differences in intensity.

Table 2. Objective and Subjective Measures of Exercise Intensity for the Three Conditions, Presented as Mean (SD)

Measure of Exercise Intensity	Encoding and Consolidation	Consolidation	<i>p</i>
RPM	61.5 (1.8)	61.3 (1.5)	.731
Watts	90.5 (21.6)	90.9 (28.7)	.878
Heart rate	139.5 (17.3)	136.2 (18.8)	.265
RPE	13.9 (0.3)	14.1 (0.5)	.166

Note. RPM = revolutions per minute; RPE = rating of perceived exertion.

Memory performances after the 60-min delay and after the 24-hr delay were analyzed separately, with descriptive statistics presented in Table 3. Free recall performance was quantified as the number of words correctly recalled following each delay. Effect sizes for pairwise repeated measures comparisons are presented in the form of Cohen’s d_z (Lakens, 2013). Recognition memory performance was quantified by calculating the discriminability index (d'), which accounts for both correct word recognition as well as errors. To calculate d' , formulas from the RAVLT test manual were followed. Specifically, HT and false alarms (FA) were converted to z -scores and the difference was taken:

$$d' = Z_{HT} - Z_{FA}$$

A bias score (A') was calculated in association with d' to determine whether recognition responses were likely due to chance:

$$A' = \frac{1}{2} + \frac{(HT - FA) \times (1 + HT - FA)}{4 \times HT \times (1 - FA)}$$

A' scores near 1.0 indicate good discriminability; whereas, scores near 0.5 indicate a more random pattern of responses. Descriptive statistics are provided for HT rate, FA, d', and A' (Table 4). Repeated-measures analysis of variances was performed for each outcome measure (60-min recall, 24-hr recall, and 24-hr recognition) to test for differences in long-term memory performance. Planned contrasts, using Tukey's Honestly Significant Difference test, were used to test pairwise differences between conditions. Specifically, these contrasts were conducted to test the hypothesis that exercise prior to encoding would result in greater recall as compared with that observed during the control condition.

Table 3. Outcome Measures: Words Recalled or Recognized Relative to Condition, Presented as Mean (SD)

Condition	60-Min Recall*	24-Hr Recall*	24-Hr Recognition
Encoding + consolidation	7.53 (2.90) ^a	6.57 (3.08) ^a	11.79 (1.63)
Consolidation	6.00 (2.90) ^{a,b}	4.64 (2.56) ^{a,b}	11.21 (2.16)
No exercise	4.93 (2.66) ^b	4.21 (2.58) ^b	10.64 (2.10)

Note. Superscripts that are different denote conditions that were significantly different based on post hoc pairwise comparisons. Those with the same superscript were not significantly different from one another. *Significant omnibus test, $p < .05$.

Table 4. Descriptive Data for 24-Hr Recognition

Condition	Hit Rate	False Alarm Rate	d'	A'
Encoding + consolidation	0.782	0.129	2.308	0.891
Consolidation	0.733	0.204	1.764	0.839
No exercise	0.707	0.187	1.76	0.841

Results

Sample

Participants ($N = 15$) were healthy, regularly active, young adults with a mean age of 22.73 years ($SD = 3.11$). One participant was identified as an outlier due to a failure to recall any words at the 60-min assessment in the C condition. The value of 0 words recalled at the 60-min assessment fell more than two SDs away from the mean for the C condition. Furthermore, this marked a drastic departure from the participant's 60-min recall for the other two conditions (13 and nine words). As such, this participant was excluded from data analysis and an additional participant was recruited to meet the sample size goal of 15. The final sample consisted of five males and 10 females. Multiple ethnicities were represented in the sample, including four African Americans, nine White, one Hispanic, and one Asian. Participants were regularly active (3.6 METs per day) and had completed an average of 3.73 years ($SD = 0.70$) of postsecondary education.

Exercise

Exercise characteristics were similar across the E + C and C conditions. No differences were observed in HR ($F_{1,14} = 1.35, p = .27$), RPE ($F_{1,14} = 2.13, p = .17$), RPM ($F_{1,14} = 0.123, p = .731$), or workload ($F_{1,14} = 0.02, p = .88$) across exercise conditions.

60-Min Recall

Significant differences in word recall were observed at 60 min ($F_{2,28} = 4.30, p = .02, \eta_p^2 = 0.24$). Planned contrasts revealed that, on average, participants recalled significantly ($p = .03, d_z = 0.77$) more words following the E + C condition ($M = 7.53, SD = 2.90$) as compared with the NE condition ($M = 4.93, SD = 2.66$). Differences in the mean number of words recalled following the C condition ($M = 6.00, SD = 2.90$) as compared with E + C or NE conditions did not reach significance ($p = .21, d_z = 0.50$ and $0.66, d_z = 0.28$, respectively).

24-Hr Recall

Data for one participant were removed from this analysis because that participant could not be reached for the 24-hr recall and recognition follow-up to the test day. Therefore, the 24-hr recall and recognition analyses were carried out with a total sample size of 14. Significant differences in word recall were observed following a 24-hr delay ($F_{2,26} = 3.58, p = .04, \eta_p^2 = .22$). Planned contrasts again revealed that, on average, participants recalled significantly ($p = .03, d_z = 0.79$) more words following the E + C condition ($M = 6.57, SD = 3.08$) as compared with the NE condition ($M = 4.21, SD = 2.58$). Differences in the mean number of words recalled following the C condition ($M = 4.64, SD = 2.56$) as compared with E + C or NE conditions did not reach significance ($p = .22, d_z = 0.51$ and $0.97, d_z = 0.12$, respectively).

24-Hr Recognition

No differences in participants' ability to correctly recognize words were observed across conditions ($F_{2,26} = 0.39, p = .68$). In addition, no differences were observed among pairwise comparisons ($p > .05$). Results for A' indicated that recognition responses were not random but showed good discriminability. See Table 4 for mean data.

Discussion

The purpose of this study was to test whether separate processes involved in long-term memory formation would be differently affected by exercise. Specifically, this study design allowed for interpretations to be drawn as to whether acute exercise significantly benefited either encoding or consolidation processes, neither, or both (i.e., if both the E + C and the C conditions yielded results significantly better than those of the NE condition). Participants completed all study conditions (NE, E + C, and C), totaling three test days. During exercise, participants were asked to exercise at a self-determined, moderate intensity. Analyses showed that participants exercised at moderate intensities on both exercise days, with no differences in perceived exertion, HR, RPM, or workload across conditions. Furthermore, mean RPE ratings at all time points fell within the prescribed range of 13–15.

Previous literature in which the timing of exercise relative to different stages of a memory task was manipulated (Frith et al., 2017; Labban & Etnier, 2011; Salas et al., 2011) has reported that, when compared with an NE condition, better recall was observed when exercise preceded encoding rather than followed encoding. The present study's results are consistent with this previous literature in that recall was best when exercise preceded encoding; and also, in that recall when exercise followed encoding was not significantly different from either the NE

condition or from the condition in which exercise preceded encoding. Generally, the pattern of results from previous literature (Frith et al., 2017; Labban & Etnier, 2011; Salas et al., 2011) suggests that encoding, but not consolidation, is sensitive to the effects of acute aerobic exercise. However, the difficulty with this interpretation of the previous studies is that, when exercise has followed encoding, it has occupied the entire delay between encoding and recall. This design limits interpretation regarding long-term memory processes because exercise cessation directly preceded retrieval. A failure to provide an adequate delay between exercise cessation and the recall trial leaves open the likelihood that exercise might have influenced retrieval as well as or instead of consolidation. The current study was designed to minimize these possible confounds by ending exercise 30 min prior to the first recall trial and by including a 24-hr recall. Importantly, results of this study show that exercise prior to encoding benefits recall at 60-min postexercise and at 24-hr postexercise.

Beyond the general study design, the memory assessment protocol used in some previous studies has also limited our ability to decipher, which long-term memory processes are affected by acute exercise. In two of the past studies (Frith et al., 2017; Labban & Etnier, 2011), which have shown that exercise prior to exposure is most beneficial, the exposure phase has actually included encoding, retrieval, and learning because participants were asked to recall the material during the exposure phase. Thus, exercise may have had an effect on the encoding process or exercise may have interacted with retrieval or learning processes that are concomitant with a recall trial. This limitation makes it impossible to know whether exercise benefitted the encoding process or acted upon the consolidation and learning process inherent in immediate recall. Similarly, the results of the study by Salas et al. (2011) are difficult to interpret due to the extended time interval between words during list presentation. In that study, each word was presented for 6 s. This longer latency between words provided greater time for study and mental rehearsal of individual words during list presentation (i.e., consolidation). So again, it is difficult to know which processes (i.e., encoding or consolidation) were impacted by the recently-completed exercise. The present study was designed with these potential confounds in mind, and for this reason, did not include an immediate recall trial or an extended latency between words during list presentation. Again, results confirm that exercise has its greatest benefits when administered prior to the encoding phase.

Consistent with previous studies (Frith et al., 2017; Labban & Etnier, 2011; Salas et al., 2011), there was not a significant difference in the number of words recalled when exercise followed encoding (C condition) versus the NE condition. Thus, again, this seems to suggest that exercise does not benefit consolidation. However, there is still an acknowledged design limitation that makes it impossible to rule out benefits to consolidation completely. In the present study, it could be argued that acute exercise actually did have an impact on consolidation in the E + C condition and that the lack of an effect at 60 min during the C condition stemmed from the lesser amount of time between exercise completion and recall. In other words, in the E + C condition, exercise could potentially have affected encoding, but could also have affected consolidation during the 60 min following exposure; however, in the C condition, exercise could only have affected consolidation for approximately 30 min because participants were exercising for the first 30-min following exposure. Thus, it is possible that exercise affects consolidation, but requires a longer consolidation period for these effects to be observed. Although this is possible, the further observation that after a 24-hr delay, recall results following the C condition were nearly identical

to that of the NE condition, whereas 24-hr recall following the E + C condition remained high, would seem to provide evidence contrary to this argument. Thus, the more plausible conclusion based upon these results is that the effects of acute exercise on memory are a result of effects on encoding and that acute exercise does not directly affect consolidation.

Although the expected difference in measures of long-term recall was observed, no differences in recognition memory were observed. This was somewhat unexpected but may be explained by the modification to the word list RAVLT protocol. That is, because participants were not asked to recall words immediately following each exposure to the list, they had reduced opportunity for learning, which could have led to reduced signal strength at the time of recognition testing. In addition, because only one list per condition was presented to participants in the present study, recognition assessment only included 15 possible HT and 15 possible FA. This is reduced from 30 possible HT and 20 possible FA in the normal recognition assessment protocol of the RAVLT. Such reductions in the potential for both correct responses and mistakes may have served to simplify the assessment to the degree that sensitivity was poor.

The current study does include some limitations. The primary limitation is that the current design still does not eliminate the possibility that exercise completed prior to encoding could also impact consolidation processes. A more complete understanding of the mechanisms and time courses of the effects of acute exercise on long-term memory is likely required to completely address this limitation through design. Related to this concern is the difficulty in interpreting the findings for the consolidation condition. Looking at mean words recalled at 60 min (E + C: M= 7.53; C: M= 6.00; NE: M= 4.93), it is tempting to interpret the results as an indication that exercise benefits both encoding and consolidation; and, that these effects tend to be somewhat cumulative, with greater effects observed when both processes are impacted by exercise. However, future study will be needed to assess the veracity of this hypothesis. Lastly, although this study leverages the strengths of a within-subjects design, the sample size remains relatively small. Replication of these results with larger samples will be helpful in increasing confidence in the magnitude and precision of the effects observed herein.

Though these results help to clarify the relationship between acute exercise and long-term memory, further study is required. First, participants in studies (Frith et al., 2017; Labban & Etnier, 2011; Salas et al., 2011) examining the timing of exercise exposure have mostly been limited to college-aged participants. Additional research on acute exercise and memory needs to be conducted with other age groups. Also, future studies should extend recall delays past 24 hr to determine the duration of the effects of a single session of exercise on long-term memory. These studies could also employ the more traditional learning paradigm (listen-recount) to test whether the effects of acute exercise prior to learning are augmented (magnitude and duration) over those observed with simple exposure (listen only) to the to-be-remembered material.

Furthermore, given the importance of brain-derived neurotrophic factor (BDNF) to learning and memory (Bekinschtein, Cammarota, Izquierdo, & Medina, 2008; Lipsky & Marini, 2007), future studies should explore this mechanistic pathway to further our understanding of how and why acute exercise affects memory. To date, there are relatively few studies with humans in which BDNF has been examined as a potential mechanism to affect memory performance (Etnier et al., 2016; Winter et al., 2007). In contrast to human studies, there is a developing body of animal

literature that supports BDNF as a potential mechanism for the effects of exercise on memory. First, animal research has provided evidence that exercise can increase levels of BDNF in the hippocampus (Cotman & Berchtold, 2002; Vaynman & Gomez-Pinilla, 2005), a region of the brain critical to learning and memory. Secondly, results have suggested that exercise can improve performance on spatial learning and memory tasks via increased BDNF expression (Vaynman & Gomez-Pinilla, 2005). Lastly, and perhaps more compelling, are data that show blockage of exercise-induced increases in BDNF attenuates the improvements to learning and memory (Ang & Gomez-Pinilla, 2007; Cotman & Berchtold, 2007). However, it cannot be assumed that these results would directly translate to human behavior. As such, further study of BDNF as a mediator of the effects of acute exercise on memory is warranted.

The results of this study hold a range of potentially important in vivo implications regarding learning and memory. Demonstration that exercise can positively impact learning and retention of new material could specifically hold implications for the integration of physical education/activity in the school system or in adult training scenarios that typically involve long periods of sedentary behavior. For example, if physical education were offered daily in the schools, there is the potential for students to benefit in terms of their long-term retention of educational material. There could be a similar effect for college-aged students and adult learners who are faced with memory challenges in their education or employment. For these reasons, memory assessment should begin to extend beyond basic assessments, such as simple word lists, to tasks more directly generalizable to real-world applications.

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