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Mind racing: The influence of exercise on long-term memory consolidation

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Over time, regular exercise can lower the risk for age-related decline in cognition. However, the immediate effects of exercise on memory consolidation in younger adults have not been fully investigated. In two experiments, the effects of exercise were assessed on three different memory tasks. These included paired-associate learning, procedural learning and text memory. Results indicate that performance on procedural learning and situation model memory was increased with exercise, regardless of if participants exercised before or after encoding. No benefit of exercise was found for paired-associate learning. These findings suggest that intense exercise may benefit certain types of memory consolidation.

Keywords: Exercise; Consolidation; Procedural memory; Declarative memory; Paired associates.

Memory consolidation is the organisation and strengthening of memories over time to stabilise them. While major aspects of memory consolidation occurs extensively, although not exclusively, at night during sleep (Marshall & Born, 2007; Stickgold, 2005), such consolidation may also be facilitated during wakefulness, especially during emotional events (Cahill & McGaugh, 1998) and exercise (Cotman & Berchtold, 2002; Tomporowski, 2003). However, the psychological and neurological conditions that underlie memory facilitation by exercise have yet to be fully investigated. Thus, the goal of this research project was to investigate the facilitation of memory consolidation as a consequence of exercise.

General exercise benefits

Exercise, in general, is healthy for both the brain and the body. Long-term benefits of regular exercise include improvements in scores on neuropsychological test batteries (Dustman et al., 1984), as well as increased attention and perceptual abilities (Colcombe & Kramer, 2003). Regular exercise, three times a week, results in a 32% reduction in the risk of dementia and may delay the onset of dementia and

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Alzheimer's disease (Larson et al., 2006). This benefit has been attributed to a decrease in brain tissue loss, especially in the hippocampus, during the natural ageing process (van Praag, Shubert, Zhao, & Gage, 2005).

Aside from the evidence that exercise is helpful for maintaining healthy brain functioning, other work has sought to determine more immediate benefits of exercise on cognitive functioning. Most of this research has focused on executive functioning. Acute treadmill running has been associated with a lager P300 amplitude during the Eriksen Flanker Task (Hillman & Snook, 2003), suggesting that exercise can increase neural processing for cognitive tasks. However, this study failed to find any accuracy or response time effects of exercise on the behavioural data. Alternatively, aerobic exercise has been associated with increased performance on the Stroop task, a measure of inhibition control (Ferris, Williams, & Shen, 2007) and the Sternberg working memory task (Pontifex, Hillman, Fernhall, Thompson, & Valentini, 2009). These studies utilised different cognitive tasks but used a similar response time measure as their construct, so at this point, it is difficult to tease apart a cognitive benefit of exercise from a general increase in response speed.

Two meta-analyses on the effects of exercise and cognition (Lambourne & Tomporowski, 2010; Tomporowski, 2003) also emphasised that exercise improves performance on tasks that measure response time per se, although not all response time tasks reviewed showed an exercise benefit, including the Hillman and Snook (2003) study mentioned earlier. It appears that the relationship between exercise and cognition is more complex than a general, overall boost in cognitive or response time performance. In fact, Lambourne and Tomporowski (2010) argue that the influence of exercise on cognition may depend on the type of exercise, its duration and the type of cognitive task being done. In the current study, we explore the influence of exercise on different types of memory tasks.

Neurological effects of exercise

Understanding the biological mechanisms, operating during exercise helps explain how it may facilitate memory consolidation. In general, physical exercise is associated with the release of a number of neurotransmitters that are known to influence memory, including epinephrine, norepinephrine, dopamine, brain-derived neurotrophic factor and β-endorphins (Vaynman, Ying, Gomez-Pinilla, 2004; Winter et al., 2007). The catecholamines, especially dopamine and norepinephrine, are involved in emotion memory formation and reinforcement learning. It has been widely shown that dopamine is involved in learning (Fiorillo, Tobler, & Schultz, 2003; Flöel et al., 2005; Jay, 2003; Knecht et al., 2004; Schultz, 2002; Wise, 2004), and norepinephrine plays a role in consolidating emotional spatial tasks as well as avoidance learning (LaLumiere, Buen, & McGaugh, 2003; Packard, Cahill, & McGaugh, 1994; Packard & Teather, 1998).

Research has shown that both pre-administration and post-administration of epinephrine facilitate learning in rats (Izquierdo & Dias, 1985) although evidence in humans is thus far restricted to post learning administration (Cahill & Alkire, 2003). Along these lines, glucose administration does appear to have both a retroactive and a proactive facilitatory effect on memory in humans (Manning, Parsons, & Gold, 1992; Sünram-Lea, Foster, Durlach, & Perez, 2002). This pattern of data suggests that epinephrine does directly enhance consolidation rather than improving memory because of a general increase in arousal or decrease in interference. This is in contrast to other chemical compounds (i.e., benzodiazepines and alcohol), which only enhance memory if administered after learning, most likely because of decreased interference for new items (Wixted, 2004). Given that catecholamine levels increase during exercise and also facilitate memory formation, it seems plausible that exercise facilitates declarative memory consolidation as well.

Exercise and memory

The influence exercise has on memory consolidation is being investigated in both animal models and humans participants. Research with rats has shown that voluntary wheel running increases performance on the radial arm maze task (Anderson et al., 2000; Neeper, Gomez-Pinilla, Choi, & Cotman, 1996) and increased neurogenesis (Neeper et al., 1996; van Praag, Kempermann, & Gage, 1999). In humans, research on memory consolidation and exercise has mixed results. For example, a study by Winter et al. (2007) studied the effects of exercise on a vocabulary learning paradigm, and they found exercise was associated with faster learning and short term increased accuracy.

However, the effects of exercise on memory consolidation have resulted in conflicting data. For example, Tomporowski, Ellis, and Stephens (1987) failed to find any effects of treadmill running on free recall for a paired-associate learning task, while Coles and Tomporowski (2008) did find memory effects with their exercise paradigm. In that study, people did a series of cognitive tests both before and after 40 minutes of exercise on a cycle ergometer or 40 minutes of a control condition. This included a free recall task, where people studied a list of words and recalled them in order. Note that this recall followed 100 seconds after the end of list presentation, making it less likely that working memory was involved, but more likely long-term memory was. Their results revealed that exercise decreased forgetting in the long-term memory primacy and recency serial positions effects, suggesting that exercise may facilitate memory consolidation. So why did these studies find different results? Perhaps it was the differences in the exercise paradigm used (cycling vs. treadmill running) or the memory tasks used (paired associates vs. list learning). It is difficult to determine what the exact relationship was between exercise and memory consolidation when each study uses a different exercise and a different memory paradigm.

Current study

The goal of the current study is to investigate the effects of exercise on memory using three different memory tasks: a more implicit serial order task, a more explicit paired-associate learning task and a more explicit sentence memory task. One task was a serial order task. This is more of a measure of implicit, procedural memory (Reber & Squire, 1998), and it has been commonly used. This task was chosen for two reasons: (1) the primary dependent variable is response time, and it is important to determine if an increase in processing speed can be replicated and (2) there is some biological evidence suggesting that exercise can facilitate procedural learning, but this type of memory has not been extensively tested with exercise. Studies have shown that procedural memory consolidation involves dopamine in the nigrostriatal pathway, which again links catecholamines with memory consolidation (Packard & Teather, 1998; Owen et al., 1992) and leads to the prediction that exercise may facilitate procedural memory consolidation.

In terms of more explicit forms of memory, people were also given a paired-associate memory task. This was used because it has been widely used in the past as a reliable measure of declarative memory. Although Tomporowski et al. (1987) failed to find any effects using this task, it is possible that the small sample size used (24 in Experiment 1 and 12 in Experiment 2) was too small to detect any effects. Thus, it seemed worthwhile to assess memory using this task again.

Finally, to assess more complex forms of memory, we also included the sentence memory task. This allows us to better assess whether different kinds of declarative memory may be facilitated by exercise. More specifically, we used tasks that allowed us to better separate out memory for the text (i.e., the surface form or text-based) and memory for what the text was about (i.e., the situation model; Johnson-Laird, 1983; van Dijk & Kintsch, 1983; Zwaan & Radvansky, 1998). For the sentence memory task, people read a list of sentences. Afterwards, they were given a recognition task in which they needed to distinguish sentences that were read compared to similar distracters (Bransford, Barclay, & Franks, 1972; Garnham, 1981; Radvansky, Gerard, Zacks, & Hasher, 1990).

Of critical importance for the sentence memory task were two conditions. In the *confusable condition*, the original sentence described the same event as one of the distracters. For example, a sentence such as “Three turtles sat on a log and a fish swam beneath it” can easily be confused with “Three turtles sat on a log and a fish swam beneath them”. To make an accurate memory decision, people need to rely on their surface form or text-based memory of what was actually read. The situation model is not helpful in this case because it cannot be used to distinguish between these two options. Both sentences can be interpreted as referring to the same event. Thus, if exercise has an influence on memory for what was read then memory would be improved by exercise in this condition.

In comparison, in the *non-confusable condition*, the original sentence described a different event than the corresponding distracter even though the sentence had been altered to a similar degree as in the confusable condition. For example, a sentence such as “Three turtles sat next to a log and a fish swam beneath it” describes a different situation than “Three turtles sat next to log and a fish swam beneath them”. Here, people can make accurate decisions using either the surface form/text-based memory or the situation model. Thus, if exercise has an influence on memory for what the text was about, but not memory for the text itself, then exercise would improve memory in the non-confusable condition, but not the confusable condition.

EXPERIMENT 1

The aim of Experiment 1 was to assess the influence of exercise on our three memory tasks (i.e., a serial order response time task, a paired-associate learning task and a sentence memory task) using the approach that has been used in previous research in which exercise occurs first, followed by learning and memory testing.

METHOD

Participants

A total of 136 people (mean age = 19.22, SD = 1.19), 68 in each of two conditions, were recruited from the University of Notre Dame in exchange for partial credit in psychology classes.

Materials

The paired-associate learning task and the serial order task both were presented on E-Prime software. The sentence memory task was done using pen and paper.

For the paired-associate learning task, 20 word pairs were constructed from words from the Medical Research Council (MRC) Psycholinguistic Database that were one or two syllables in length and semantically unrelated to one another (e.g., candy-engine).

Items for the sentence memory task were adapted from studies by Bransford et al. (1972), Garnham (1981) and Jahn (2004). This list consisted of 30 sets of sentences, where each sentence had four different versions. Two of these versions were easily confusable and two were not. For example, the sentence "Three turtles sat on a log and a fish swam beneath it" can be readily confused with "Three turtles sat on a log and a fish swam beneath them" because they both describe the same situation. However, the sentences "Three turtles sat next to a log and a fish swam beneath it" and "Three turtles sat next to a log and a fish swam beneath them" are less likely to be confused because they describe different situations, even though the sentences have been changed in the same way as in the confusable versions. For the study phase, four different versions of the 30 sentences were created by taking one sentence from each of the 30 sets and assigning it to one of the study lists so that each study list got one of the sentences from the 30 sets. Each study list was printed on one sheet of paper, which was randomly assigned across participants. For the recognition test, lists consisting of all of the possible sentences, arranged in groups of four sentences, were constructed. This test was used for both immediate and delayed tests, and every participant was given the same sentences for the test.

Procedure

The experiment involved two sessions. The first session included the exercise, encoding and an immediate test. The second session was done after a one-week delay and included a delayed test. Before coming into the laboratory, people were randomly assigned to either the exercise or the resting condition. After completing the informed consent, people in the exercise conditions were first given 5 minutes to stretch and then began their exercise. The procedure for exercise was modified from Winter et al. (2007). The experimenter timed participants with a stopwatch as they did 2 minutes of sprints, down a hallway of the psychology building, followed by a 3-minute break. No more than three people exercised at a time.

The website www.websudoku.com was used for the resting conditions. People were seated in front of the computer and did 30 minutes of Sudoku puzzles.

Following the exercise, people were given the three immediate memory tests, namely paired-associate learning, sentence memory and serial order. For these tests, people encoded the stimuli and then were immediately tested. To control for order effects, testing order of these tests was pseudo-randomly assigned so that there was an even number of each testing order in the two groups.

For the serial order task, we used a paradigm adapted from Reber and Squire (1998). In this task, a cue (a black asterisk) was presented on a white computer screen in one of four locations: (1) the bottom left corner, (2) the bottom middle left portion, (3) the bottom middle right, and (4) and the bottom right corner. These asterisks were shown in a repeating sequence of eight trials and were displayed one at a time on a screen for a maximum of 2 seconds. People were told that they would see an asterisk randomly appearing at one of four locations and had to hit the "z", "c", "b" or "m" key, using the index and middle fingers from each hand, to indicate the position of the asterisk on the screen. The keyboard was aligned with the computer screen so that the "z" and "m" keys lined up with the leftmost and rightmost asterisk positions. They were first given a demonstration of the four positions and their corresponding keys, followed by 24 practice trials. For the immediate test, people were then given 200 test trials in repeated sequences of eight locations. Response times were recorded as a measure of how well they learned the task.

For the paired-associate task, people were told that they would see two words at a time on the computer screen and to try to remember the two words went together. When they had finished encoding, they were given the immediate test, where they were given one of the words from a pair, and the task was to type in the word that went with it. If they could not remember the target word, they should hit the "enter" key to advance to the next trial. They were given up to 5 seconds for each of the 20 trials, and response accuracy was recorded.

The sentence memory task was done using pencil and paper. For the study portion of this task, people were randomly assigned to one of the four lists of 30 sentences and given up to 10 minutes to complete the task. Participants were then given the immediate memory test, where all four versions of 30 sentences were given on paper, and people were told to circle the sentence they had previously seen.

The first session of the study was composed of the exercise phase and the immediate memory tests, typically lasting about one hour. One week (seven days) after the first session, people returned for the delayed memory test. In this session, they did not engage in any exercise, and they did not get a chance to review the material. Instead, they did the three memory tests in the same order they did them for the immediate test. For serial order task, they were given 10 practice trials before test, so they could remember the mapping between the asterisk position and the keys. They were then given 200 test trials, consisting of the same eight-location sequence from before. For the paired-associate learning task, people were not given the word pairs again but were tested on the 20 words from the pairs that were not given for the immediate test. The delayed sentence memory task was the same as they were given for the immediate task. The second session lasted approximately 30 minutes.

Results

The means and standard deviations for all three of the memory tests are provided in Table 1. In all cases, the data were submitted to 2 (exercise group) × 2 (delay) mixed analyses of variance (ANOVAs), with the first factor being between subjects and the second within.

Serial order task

For the serial order task, response times for correct trials were faster in the exercise condition than the resting condition over both time periods. The ANOVA revealed that the main effect of exercise group was significant, $F(1, 134) = 7.94$, MSE = 20,496, $p = .006$, $\eta_p^2 = .056$, while the main effect of delay, $F(1, 134) = 1.51$, MSE = 3890, $p = 0.22$, $\eta_p^2 = .011$, and the interaction were not, $F(1, 134) = 1.81$, MSE = 3890, $p = .18$, $\eta_p^2 = .013$. This suggests that exercise improves sequence learning over no exercise and that this improvement was sustained over one-week delay. Thus, exercise improved procedural memory.

Paired-associate learning

For the paired-associate learning task, total accuracy was close to 10 (out of 20) on the immediate test and fell to around 2 a week later across all groups. The results of the ANOVA revealed a significant effect of delay, $F(1, 134) = 402.85$, MSE = 14.31, $p < .001$, $\eta_p^2 = .750$, but no other effects were significant (all Fs < 1). This suggests that while, not surprisingly, memory for the paired associates decreased over time, there was no effect of exercise on this task. This replicated the findings of Tomporowski et al. (1987) and also

TABLE 1
Mean accuracy and response times for exercise and rest conditions (standard deviations in parentheses)

	Exercise	*Rest*
Paired 1	0.55 (5.26)	0.53 (5.86)
Paired 2	0.08 (1.78)	0.08 (2.84)
Mean	0.32 (3.15)	0.31 (3.72)
Typing 1	357 (87.52)	416 (135.46)
Typing 2	377 (91.83)	415 (119.49)
Mean	367 (81.39)	416 (117.67)
Sent 1	0.69 (4.24)	0.62 (4.85)
Sent 2	0.57 (5.30)	0.49 (5.18)
Mean	0.63 (4.11)	0.56 (4.72)

suggests that exercise does not have broad-based improvements on memory.

Sentence memory

To assess performance on the text memory task, overall accuracy was determined for the two groups. The exercise group had the higher accuracy than the resting group. Performance also decreased over the delay, but the same pattern was still present across the groups. An ANOVA revealed main effects of exercise group, $F(1, 134) = 7.67$, MSE = 39.19, $p = .006$, $\eta_p^2 = .054$, and delay, $F(1, 134) = 101.59$, $MSE = 9.05$, $p = < .001$, $\eta_p^2 = .431$, but the interaction was not significant, $F < 1$. Overall, this suggests that exercise can facilitate some forms of declarative memory consolidation.

To further assess the nature of the exercise benefit on memory, performance was broken down based on the type of sentence, namely whether they were part of confusable and non-confusable pairs. Again, for confusable sentence pairs, the incorrect version described the same event as the original, whereas for the non-confusable sentence pairs, the incorrect version did not describe a different event. For our purposes, the confusable condition served as a measure of text-based memory because accurate performance must be guided more by a memory of the text itself as both versions of the sentence refer to the same situation model. In comparison, for the non-confusable condition, it was possible to make memory judgements using the situational model level. The mean and standard deviations (in proportion of errors made) for each condition can be seen in Table 2.

Error rates were set to a 2 (exercise group) × 2 (delay) × 2 (condition: confusable vs. non-confusable) mixed ANOVA. The main effect of exercise group was significant, $F(1, 134) = 5.16$, MSE = .022, $p = .025$, $\eta_p^2 = .037$, with people in the rest group making more errors than people in the exercise group. There was also a significant main effect of delay, $F(1, 134) = 194.66$, MSE = 0.39, $p < .001$, $\eta_p^2 = .592$, with errors increasing over the delay, which was not surprising. Moreover, there was a significant main effect of condition, $F(1, 134) = 82.73$, MSE = 0.27, $p < .001$, $\eta_p^2 = .382$, with people committing more confusable than non-confusable errors, as expected. None of the interactions were significant (all Fs < 1), suggesting that there were no differences between the types of errors and that exercise similarly benefits memory at both the text-based and the situation model levels.

TABLE 2
Mean confusable and non-confusable errors for the exercise and rest conditions (standard deviations in parentheses)

	Exercise	*Rest*
Confusable 1	0.22 (0.09)	0.25 (0.10)
Confusable 2	0.29 (0.09)	0.30 (0.10)
Mean	0.25 (0.09)	0.27 (0.10)
Non-confusable 1	0.10 (0.08)	0.13 (0.12)
Non-confusable 2	0.17 (0.13)	0.20 (0.17)
Mean	0.13 (0.11)	0.17 (0.14)

DISCUSSION

Overall, the results of Experiment 1 are consistent with the idea that exercise prior to encoding helps procedural memory and sentence memory but not paired-associate learning. Thus, while there is a benefit of exercise on memory, this benefit is not a general cognitive boost or increase in response speed. One potential issue with Experiment 1, as well as other research that has followed as similar pattern, is that having participants exercise prior to encoding may have simply increased arousal and, therefore, attention capabilities for encoding. This encoding benefit, and not later retention and consolidation, could be producing the observed benefits. However, because epinephrine administration either before or after learning results in improved memory performance, it seems likely that exercise should have a similar affect and thus facilitates consolidation.

EXPERIMENT 2

Experiment 2 used the same materials to test memory, the only difference was that people encoded the material prior to exercising (or resting), and then their memory was tested. This is to address the possibility that the results observed in Experiment 1 were due to increased exercise-induced arousal during the encoding period as a result of having just exercised. In Experiment 2, all participants encoded the materials first, when there was no difference in arousal between the two groups during encoding due to exercise. If the main benefit of exercise on memory is simply from an increase in arousal during encoding then there should be no difference in performance between the two groups. However, if there is a unique benefit of exercise on memory consolidation then people who exercise should outperform those in the resting condition. Again, because three different types of memory tasks were also used in this study, such a benefit can be assessed with regard to a general memory boost or something specific to the type of task. In addition, heart rate was measured several times during the exercise and resting conditions as to ensure that our exercise manipulation sufficiently increased heart rate above the resting condition.

METHOD

Participants

A total of 132 participants (mean age = 19.07, SD = 1.18), 66 in each of two conditions, were recruited from the University of Notre Dame in exchange for partial credit in psychology classes.

Materials

The same materials from Experiment 1 were used in all three of the memory tasks. To monitor heart rate, watch-style heart monitors were used, which gave a digital read-out of heart rate upon button press.

Procedure

The procedure was the same as Experiment 1 but with a few exceptions. The encoding portion of all three memory tasks was done first. For the serial order task, encoding consisted of a brief description of the task, and then 24 practice trials consisting of the eight sequenced positions repeated three times. The average response times for these encoding tasks were recorded by the computer. Encoding for the paired-associate task and sentence learning task followed the same procedure as in Experiment 1. After encoding, all participants put on the heart rate monitors and engaged in either the resting or the exercise conditions. These conditions were exactly the same as the previous experiments, except heart rate was recorded by the experimenter during each of the sprinting breaks in the exercise condition, and once every 10 minutes in the resting condition. After completion of the exercise or rest conditions, participants were tested on the three memory tasks. They also returned one week later to perform the delayed memory tests just as in Experiment 1.

RESULTS

The average heart rate for participants in the resting condition was fairly low (M = 80.11 bmp) compared to the average heart rate of participants in the exercise condition (M = 142.74 bpm), indicating that the sprinting did induce a moderately strenuous amount of exercise.

Memory tests

Table 3 presents the means and standard deviations for the three memory tests. Again, all data were submitted to a 2 (group) × 2 (delay) mixed ANOVA.

Serial order task. No significant difference between groups was found at encoding, $t(127)$ = 1.26 SE = 38.09, p = .21. Just as in Experiment 1, response times for correct trials were faster in the exercise condition than the resting condition. The ANOVA revealed a significant main effect of group, $F(1, 130) = 9.29$, MSE = 5628, $p = .003$, η_p^2= .067, and delay, $F(1, 130) = 210.40$, MSE = 1818, $p < 0.01$, η_p^2= .618, with people being slower after a one-week delay. The interaction was marginally significant, $F(1, 130) = 3.64$, MSE = 1818, $p = .06$, η_p^2= .027, reflecting that the difference between groups was slightly smaller at one-week delay. This was also the case in Experiment 1 although the differences were slightly larger. These results do replicate the finding from Experiment 1 that exercise improves sequence learning over no exercise and that this improvement may decline but is largely sustained over one-week delay.

TABLE 3
Mean accuracy and response times for exercise and rest conditions (standard deviations in parentheses)

	Exercise	*Rest*
Paired 1	0.25 (4.00)	0.24 (4.01)
Paired 2	0.07 (1.46)	0.04 (1.11)
Mean	0.24 (3.99)	0.06 (1.34)
Typing 1	373 (67.89)	411 (68.41)
Typing 2	307 (55.38)	325 (50.35)
Mean	392 (70.53)	316 (53.51)
Sent 1	0.63 (4.09)	0.56 (4.61)
Sent 2	0.55 (4.17)	0.47 (4.55)
Mean	0.59 (4.44)	0.51 (4.49)

Paired-associate learning. No differences in encoding time was found between the two groups, $t(128) = 0.99$, SE = 0.06, $p = 0.32$. Memory performance on the immediate test was lower than in Experiment 1 (presumably because of the 30-minute delay between encoding and test) but was close to the same average as Experiment 1 a week later. The results of the ANOVA revealed a significant effect of delay, $F(1, 128) = 152.20$, MSE = 6.029, $p < .001$, $\eta_p^2 = .543$, while the effect of groups and the interaction were not significant (Fs < 1). These results replicate Experiment 1, where no significant effects of exercise were found for paired-associate learning.

Sentence memory. Due to a computer glitch, data from 11 subjects (from both conditions) were lost, but the analysis was still carried out. For the sentence memory task, the exercise group had a higher overall accuracy than the resting group, and although performance decreased over the delay, the same pattern was still present across the groups. An ANOVA revealed main effects of group, $F(1, 116) = 8.84$, MSE = 31.36, $p = .004$, $\eta_p^2 = .071$, and delay, $F(1, 116) = 57.13$, MSE = 6.52, $p = < .001$, $\eta_p^2 = .330$, and the interaction was not significant, $F < 1$. This replicates the previous experiment and suggests that exercise facilitates text memory.

Performance was again broken down based on the type of sentence, namely whether they were part of confusable and non-confusable pairs. The mean and standard deviations (in proportion of errors made) for each condition are in Table 4. Error rates were subjected to a 2 (group) × 2 (delay) × 2 (condition) mixed ANOVA. There was a significant main effect of group, $F(1, 116) = 6.86$, MSE = .017, $p = .010$, $\eta_p^2 = .056$, with the rest group making a slightly larger proportion of errors than the exercise group. There was also a significant effect of delay, $F(1, 116) = 54.47$, MSE = 0.004, $p < .001$, $\eta_p^2 = .320$, with more errors being made after the one-week delay. Finally, there was a main effect of condition, $F(1, 116) = 94.96$, MSE = 0.022, $p < .001$, $\eta_p^2 = .450$, with participants being more likely to make confusable than non-confusable errors in general. None of the interactions were significant, (all Fs < 1). These data replicate that of Experiment 1 that performance decreased over time. Moreover, people committed more confusable than non-confusable errors in both conditions. Thus, the data are consistent with the idea that people were using their situation models of the described events to make their memory decisions, and that exercise improved the accuracy of memory overall.

TABLE 4
Mean confusable and non-confusable errors for the exercise and rest conditions (standard deviations in parentheses)

	Exercise	*Rest*
Confusable 1	0.27 (0.09)	0.27 (0.09)
Confusable 2	0.30 (0.09)	0.31 (0.09)
Mean	0.29 (0.09)	0.24 (0.09)
Non-confusable 1	0.10 (0.10)	0.16 (0.13)
Non-confusable 2	0.15 (0.11)	0.21 (0.15)
Mean	0.13 (0.11)	0.19 (0.14)

DISCUSSION

Overall, the results of Experiment 2 largely replicate those of Experiment 1 in showing that exercise can improve some kind of later memory, namely procedural memory and sentence memory. Moreover, the exercise came after encoding but showed the same benefit as Experiment 1, suggesting that the memory benefit in this study is due to processes involved in maintaining information over time, and that the results of Experiment 1 was not due to increased arousal at the time of encoding for people who had just exercised.

GENERAL DISCUSSION

The current study aimed to investigate the relationship between exercise and memory consolidation by comparing the performance of an exercise and a rest group on three separate memory tasks. Importantly, the same pattern of results was observed both when the exercise preceded and followed the initial encoding phase. Thus, it seems more likely that the memory benefits that were observed were due to a benefit in the maintenance of information over time. Moreover, given that this exercise benefit was observed a week later, this suggests that it was the processes associated with the consolidation of memories that was affected.

In general, findings support the idea that short periods of intense physical exercise boost memory consolidation over no exercise. This was the case for two of our three memory tasks. One was a serial order task, a measure of motor skill learning, where participants who in the exercise group had the fastest response times. The exercise group also outperformed the rest group in a sentence memory task, specifically demonstrating superior memory on the text-based level relative to the situation model level. Both of these findings were present immediately and one week later, suggesting that long-term memory consolidation is what is being affected by the exercise.

It should also be noted that no benefit of exercise was found for the paired-associate learning task. This finding was somewhat surprising given that it was the most closely related task to the vocabulary task used in Winter et al. (2007). The most likely explanation for this discrepancy involves task and analysis differences. There were a number of task differences between our study and that by Winter et al. (2007). First, our paired-associate learning task had only 20 trials, and people encoded the pairs only once. However, Winter et al.'s study involved a larger set of 120 experimental trials with five encoding sessions per item pair. A greater number of study trials may have led to a more meaningful encoding to allow for exercise to exert an influence. Second, whereas in our experiment participants simply saw the items during study, in the Winter et al. report, people generated responses during encoding. Also, whereas in our study the paired associates were randomly paired words, in the Winter et al. study, novel words were paired with object images, which may have introduced a greater emphasis on word meanings which could then allow encoding to be deep enough to be affected by exercise. It is also important to note that in the Winter et al. study the critical interaction was not significant, which is consistent with our findings here and that their main conclusions regarding a 20% increase in learning with exercise was based on performance curve analysis, which can be heavily influenced by outside factors.

Apart from the paired-associate learning task, this study contributes two novel findings. First, it was clearly demonstrated that exercise does improve memory on a procedural memory motor task. Previous studies on short- and long-term effects of regular exercise in humans have tended to focus on declarative knowledge and general cognitive functioning (Dustman et al., 1984; Larson et al., 2006; Winter et al., 2007). In fact, studies with rats and mice focus on the water maze task (i.e., Ang, Dawe, Wong, Moochhala, & Ng, 2006; van Praag et al., 2005), and this type of memory is often treated as declarative spatial learning (Morris, 1984). Thus, we hope that results of this study will spur further work on the benefits of exercise on procedural knowledge.

The second novel finding comes from the sentence learning task, which measures declarative memory in such a way that performance on different levels of processing can be separated out. In this task, data analysis showed that not only did people in the exercise group perform better overall, but also this improvement was based on superior situation model and text-based memory. This important distinction that exercise benefited declarative memory at the situation level fits well with the findings from Winter et al. (2007) who used paired associates that were more meaningful than the paired associates in the current study. These results suggest that high-impact exercise may be beneficial to declarative memory for meaning and comprehension.

Previous work (Winter et al., 2007) has revealed that memory benefits are more likely to be from high-impact anaerobic exercise compared to lower-impact aerobic exercising. This is mostly likely because the former involves the release of more catecholamines (Fattor, Miller, Jacobs, & Brooks, 2004; Winter et al., 2007), which have a dose-dependent response for memory enhancement in rats (Introinicollison, Ford, & McGaugh, 1995). However, it has also been found that higher doses of epinephrine are associated less of a memory benefit compared to lower dose (Costa-Miserachs, Portell-Cortes, Aldavert-Vera, Torras-Garcia & Morgado-Bernal, 1994) although this study injected rats with epinephrine rather than the studying natural process of production and absorption during exercise. Costa-Miserachs et al. (1994) also did not investigate if the same effect can be found for norepinephrine or dopamine, which was investigated in Introini-Collinson et al. (1995). Directly comparing the effect levels of the different catecholamines on memory consolidation is an important next step.

The current exercise intervention was designed to follow the procedures from Winter et al. (2007), but there are other potential exercise tasks that could be utilised. According to Audiffren (2009), more energetic bouts of exercise, like the one here, has been shown to facilitate perception and motor control of cognition but can actually be harmful to higher-order cognitive function if fatigue becomes an issue. Although the exercise condition was moderately strenuous, we do not believe that it was enough to interfere with cognition because performance on the sentence learning was significantly greater for the exercise condition. However, it will also be important to investigate if these patterns of results are replicated with more long-term sustained exercise activities, as that may also have a differential effect on cognition (Audiffren, 2009).

One potential concern with the current study has to do with the nature of the control condition. One of the concerns that arose during the review process was that the fact that the control groups were engaged in a cognitive demanding task (playing Sudoku), that this may have led to greater retroactive and proactive interference (in Experiments 1 and 2, respectively), thereby lower performance. This may be the case because the control task required significant cognitive resources that the exercise condition did not, which then interfered with consolidation. As such, it may have been better to have something like a control group that engaged in guided relaxation.

While it is possible that the Sudoku task resulted in both proactive and/or retroactive interference in the procedural and sentence memory tasks, such a possibility is unlikely for a number of reasons. First, if the Sudoku tasks were having a generalised interference effect on a broad range of memory task then this should have emerged in the paired-associate learning task and it did not. Second, the Sudoku task is quite unrelated to the primary tasks. There is a literature showing that switching to unrelated tasks, instead of becoming a source of interference, can release a person from interference (e.g., Wickens, 1972). Finally, there is some recent work by Tibi, Eviatar, and Karni (2013) that digit-based tasks, such as math problems, actually enhance procedural memory, which is the opposite of the suggestion that it is producing interference that is driving this observed effects. Moreover, it should be kept in mind that researchers have also stated that it is also important to ensure control participants are not under-aroused to a level that could influence their cognitive capabilities (Audiffren, 2009). At this point, it is difficult to be certain of the right control condition, but we chose a task that mimics working at a computer over something more arousing. The amount of arousal in the control could be taken into consideration for future research designs.

As for the interference issue, while this may be true to some degree, we think that it is unlikely to be a major player, for a number of reasons. To start with, these sorts of interference effects are more prominent when there is an overlap in content. However, none of our experimental tasks involved digits. Moreover, the one task that did involve single-item stimuli was the paired-associate learning task, and this task showed the least amount of influence of exercise. Further along these lines, if the pattern of results that we observed here were due to the nature of the cognitive task engaged in by the control group then it would be expected that this would have a similar influence across all of the experimental tasks and not just some of them. Given this, it seems unlikely that the nature of our control task was playing a primary role in the effects of interest.

A recent study in *Science* by Akers et al. (2014) discovered that exercise after learning in rodents can lead to forgetting from an increase in neurogenesis in the hippocampus that leads to the disruption of recently established memories. This is in contrary to the data presented here, where exercise after encoding lead to higher memory performance in sentence learning, which likely also involves the hippocampus. There are some clear differences between the current study and the Akers et al. study, for example, we used humans while they used rats, and their contextual fear conditioning paradigm is far different from our sentence learning paradigm. However, the findings from Akers et al. (2014) do provide more information about the biological relationship between exercise and memory that merit further empirical investigation.

Overall, this study demonstrated that exercise can improve long-term memory on both declarative and procedural memory tasks. As such, it appears that people can benefit from taking a small break to exercise when learning either a new skill or when trying to comprehend and remember new information. This demonstrates that not only is exercise important for long-term mental and physical health (Kramer & Erickson, 2007), but it is also important for cognitive abilities, such as memory, and could be used in everyday settings.

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