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Moderate intensity exercise facilitates working memory

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Objectives: Although the effect of exercise on cognitive functioning has received considerable empirical and theoretical attention, the influence of concurrent exercise on complex cognitive function remains poorly understood. Our research was designed to investigate working memory during a bout of dynamic exercise.
Design: An experimental design was used.
Methods: In two experiments, we examined the impact of moderate intensity exercise on performance of a paced auditory serial addition task (Experiment 1, $N = 24$) and a Sternberg task (Experiment 2, $N = 120$). The tasks were performed at rest and while cycling at different power outputs.
Results: We found that moderate intensity exercise increased the number of correct responses at medium-to-fast stimulus presentation rates during the paced auditory serial addition task and lowered the response latency slopes during the Sternberg task.
Conclusions: Our findings show that working memory is improved by dynamic exercise at moderate intensities and short duration.

Introduction

The influence of exercise on cognitive functioning has attracted considerable empirical and theoretical attention. The benefits of habitual physical activity are now well established (for a recent review see, Smith et al., 2010). For instance, aerobic fitness has been linked to improved executive function (e.g., Themanson & Hillman, 2006; Themanson, Pontifex, & Hillman, 2008). In addition, a large number of studies have reported that cognitive performance is improved after performing exercise (e.g., Kimura & Hozumi, 2012).

The issue concerning the effects of acute exercise on concurrent cognitive performance has attracted considerable research interest. Two quantitative reviews of the literature have systematically interrogated the effects of a bout of dynamic exercise on the performance of a variety of cognitive tasks. An early meta-analysis concluded that exercise had a small ($d = 0.16$) positive effect on cognitive functioning; task difficulty emerged as a moderator, with larger effects for simple than choice reaction times (Etnier et al., 1997). A more recent meta-analysis concluded that acute dynamic exercise has a small ($d = 0.20$) homogeneous positive effect on cognitive function assessed following exercise and a small ($d = -0.14$) albeit heterogeneous negative effect on cognitive functioning assessed during exercise (Lambourne & Tomporowski, 2010). Specifically, this negative effect was moderated by exercise mode (negative for running but positive for cycling), exercise duration (negative for less than and positive for greater than 20 min) and task complexity, with the latter two moderators interacting. This unreliable effect for cognitive functioning during exercise can be attributed, at least in part, to methodological weaknesses of the 21 studies reviewed (e.g., lack of a control group, low reliability of the cognitive function test), with the low statistical power associated with small sample sizes (median = 14, range = 8–41 participants) a notable limitation.

Overall, the findings were interpreted as offering partial support for a number of theoretical accounts, including both attention-based and arousal-based models. Finally, it was concluded that exercise-induced arousal improves performance on rapid decision-making tasks by impacting basic sensorimotor processing during and soon after exercise, and, moreover, that the residual arousal during the post-exercise period also facilitates memory processes (Lambourne & Tomporowski, 2010). It should be noted, however, that a rider tempered this conclusion: relatively few studies have assessed memory in this context. Our research was designed to address this limitation.

Dietrich's (2003, 2006) transient hypofrontality model attempts to explain why complex cognitive processes are impaired during exercise compared to rest and recovery. Assuming that the brain's metabolic resources are limited, the model proposes that exercise

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shifts resources to areas (i.e., sensorimotor cortex) required to monitor and control movements at the expense of non-essential areas (e.g., prefrontal cortex), and, thereby predicts decrements in complex cognitive functioning during but not after exercise. In support of this model, Dietrich and Sparling (2004) found that performance on working memory tasks (paced auditory serial addition task, PASAT and Wisconsin card sorting task) that depended on prefrontal cortex was impaired during prolonged (c. 50–65 min) moderate intensity (c. 70–80% of maximal heart rate) exercise. They also found that concurrent exercise did not influence performance on tasks (intelligence and vocabulary tests) that did not depend on the prefrontal cortex. Lo Bue-Estes et al. (2008) also found that working memory performance was impaired during 20 min of incremental treadmill exercise. Specifically, the ability to add and/or subtract a series of three digits was worse while running at 50% than 25%, 75% and 100% of maximum aerobic capacity which were worse than before and after exercise. However, Lambourne, Audiffren, and Tomporowski (2010) observed no change in performance on the PASAT measured at rest and repeatedly during and after a 40 min bout of moderate intensity cycling. Overall, the results of these studies paint a complex picture of working memory before, during and after exercise.

In the present research we conducted two experiments designed to examine the effects of acute bouts of exercise on working memory performance. In Experiment 1, we used a between-subjects design to compare the effects of moderate intensity exercise on a cycle ergometer and rest on performance of the PASAT (Gronwall, 1977; Tombaugh, 2006). In Experiment 2, we used a mixed design to examine the effects of different levels of exercise intensity on performance of the Sternberg task (Sternberg, 1966). Neuroimaging confirms that prefrontal cortex is activated by the PASAT (Audoin et al., 2005; Lockwood, Linn, Szymanski, Coad, & Wack, 2004) and Sternberg task (Schon, Quiroz, Hasselmo, & Stern, 2009; Wager & Smith, 2003; Wolf, Vasic, & Walter, 2006). The transient hypofrontality model might argue that moderate intensity exercise would impair working memory performance, and therefore we predicted that concurrent exercise on a cycle ergometer would be associated with poorer working memory performance on the PASAT (Experiment 1) and the Sternberg task (Experiment 2).

Experiment 1

With the aim of improving our understanding of the exercise and working memory relationship we investigated PASAT (Gronwall, 1977; Tombaugh, 2006) performance at rest and while cycling. Neuroimaging confirms that prefrontal cortex is activated by the PASAT (Audoin et al., 2005; Lockwood et al., 2004). Based on the transient hypofrontality model, we hypothesised that moderate exercise would impair working memory performance, reflected in decreased accuracy on the PASAT.

Method

Participants

Participants were 24 healthy male students enrolled on a degree course in Sport and Exercise Sciences at a British University with a mean age of 20.50 ($SD = 0.89$) years and body mass index of 23.75 (2.84) kg/m^2. On average, they played sport or exercised mildly, moderately and vigorously for 6.06 ($SD = 3.03$), 4.27 ($SD = 2.14$), and 3.35 ($SD = 2.43$) hours per week. At rest, their mean pulse rate was 76.10 ($SD = 9.10$) beats per minute, mean systolic blood pressure was 128.06 ($SD = 12.50$) mmHg, and mean diastolic blood pressure was 75.40 ($SD = 10.08$) mmHg. The study protocol was approved by the local research ethics committee and all volunteers gave informed consent to participate.

Apparatus

Participants sat on a cycle ergometer (814, Monark). An audiotape player and headphones (Sony) were used to present the instructions and auditory stimuli. Heart rate (bpm) was recorded using a heart rate monitor (Vantage NV, Polar). A coded transmitter was strapped to the participant's chest just below the xiphoid process while a coded receiver was held by the experimenter. The experiment took place in a temperature controlled room.

Paced auditory serial addition task (PASAT)

A version of the PASAT was used to assess working memory. The task consisted of four 2-min blocks of trials. Participants were instructed to add two sequentially presented single digit numbers, while retaining the latter of the two numbers in memory for subsequent addition to the next number presented (Gronwall, 1977; Tombaugh, 2006). Numbers, which ranged from 1 to 9, were presented via an audiotape player and headphones. Participants were instructed to add each number they heard to the previous number and to state the answer out loud. If performance broke down, participants were told to continue with the next number presented. For the control group, the task consisted of four 2-min blocks of 30, 34, 40, and 48 numbers at inter-stimulus intervals of 4.0, 3.5, 3.0, and 2.5 s respectively. These inter-stimulus intervals included the duration (c. 500 ms) of each number. For the exercise group, the task consisted of four 2-min blocks of 28, 33, 37 and 47 numbers; the slight reduction in trials was due to periodic announcements of required changes in pedalling cadence.

Procedure

Participants completed a single testing session while sitting on the cycle ergometer. They relaxed during a 5-min formal rest period while heart rate was measured and then completed 10 practice trials. Participants were tested in a mixed multi-factorial experimental design, with group (experimental, control) as a between-subjects factor and trial block (1, 2, 3, 4) as a within-subjects factor. Participants were randomly assigned to one of two groups. The exercise group ($N = 12$) completed the PASAT while cycling at moderate intensity whereas the control group ($N = 12$) completed the PASAT while sitting at rest on the cycle ergometer. The exercise group was periodically instructed to pedal at a specific number of revolutions per minute, ranging from 60 to 90 ($M = 77$) rpm, intended to generate a power output ranging from 60 to 180 ($M = 146$) Watts. Specifically, the target power outputs (and revolutions per minute) for blocks 1, 2, 3 and 4 of the memory task averaged 95 (63 rpm), 165 (83 rpm), 155 (78 rpm) and 170 (85 rpm) Watts, respectively. This exercise protocol was designed to ecologically simulate the changing demands associated with bicycle races. Heart rate was recorded every minute of the task.

Data reduction

The number of errors (omissions, incorrect responses, late responses) in each block were recorded and used to calculate the percentage of correct responses per block (Tombaugh, 2006). The heart rates measurements were averaged to yield mean heart rate during rest and each block of the task.

Results and discussion

PASAT

A 2 Group (exercise, control) by 4 Block (1, 2, 3, 4) analysis of variance (ANOVA) was performed on the percentage of correct responses. Overall, the exercise group ($M = 89$, $SD = 9$) only tended to outperform the control group (*M* = 82, *SD* = 9), $F(1, 22) = 2.83$, $p = 0.11$, $\eta^2 = 0.11$. However, the analysis yielded effects for block, $F(3, 20) = 8.06$, $p < 0.001$, $\eta^2 = 0.55$, and group by block, $F(3, 20) = 5.06$, $p < 0.01$, $\eta^2 = 0.43$. The scores in each task block for each group are shown in Fig. 1. Polynomial trend analyses confirmed a significant linear trend for block, $F(1, 22) = 20.74$, $p < 0.001$, $\eta^2 = 0.49$, indicating that memory function deteriorated with increasing digit presentation rates. Analyses also revealed a significant group by block quadratic trend, $F(1, 22) = 7.58$, $p < 0.01$, $\eta^2 = 0.26$, with group differences in memory function evident only after the first block of the task.

Heart rate

A 2 Group by 5 Period (rest, block 1, block 2, block 3, block 5) ANOVA yielded effects for group, $F(1, 22) = 49.00$, $p < 0.001$, $\eta^2 = 0.69$, period, $F(4, 19) = 57.49$, $p < 0.001$, $\eta^2 = 0.92$, and group by period, $F(4, 19) = 27.11$, $p < 0.001$, $\eta^2 = 0.85$. The heart rates during rest and while completing each task block for the control and exercise groups are shown in Fig. 2. Significant group by period linear, $F(1, 22) = 112.86$, $p < 0.001$, $\eta^2 = 0.84$, and quadratic, $F(1, 22) = 28.42$, $p < 0.001$, $\eta^2 = 0.56$, trends indicated that that the exercise group's heart rates increased progressively from rest to the last block whereas the control group's heart rates increased from rest to the first block and then remained similarly elevated throughout the remainder of the task. It is worth noting that the exercise group's heart rates during the four blocks of the task were 60 (*SD* = 7), 69 (*SD* = 9), 74 (*SD* = 9), and 77 (*SD* = 10) percent of maximum predicted heart rates, calculated as 220 minus age. In contrast, the control group's corresponding heart rates were only 47 (*SD* = 6), 46 (*SD* = 6), 47 (*SD* = 6) and 48 (*SD* = 6) percent of predicted maximum.

In sum, the results of Experiment 1 indicate that exercise selectively influenced PASAT performance. Specifically, cycling was associated with improved performance compared to rest when the stimuli were presented every two to three seconds whereas this effect was absent when stimuli were presented at a slower rate. It should be noted here that exercise intensity was also greater at the faster presentation rates when performance was improved. Potential limitations need to be considered when interpreting the results of the current experiment. First, the exercise intensity was varied while participants were cycling and therefore this feature of the design may have distracted participants from the memory task performance. Second, the current design confounded presentation rate with elapsed time and level of exertion, and, therefore, these factors (i.e., time, exertion) may partly explain our findings. Finally, the sample size was relatively small and therefore the lack of differences in memory task performance at the slowest stimulus presentation rate may be attributable to low statistical power. The next experiment was designed with these issues in mind.

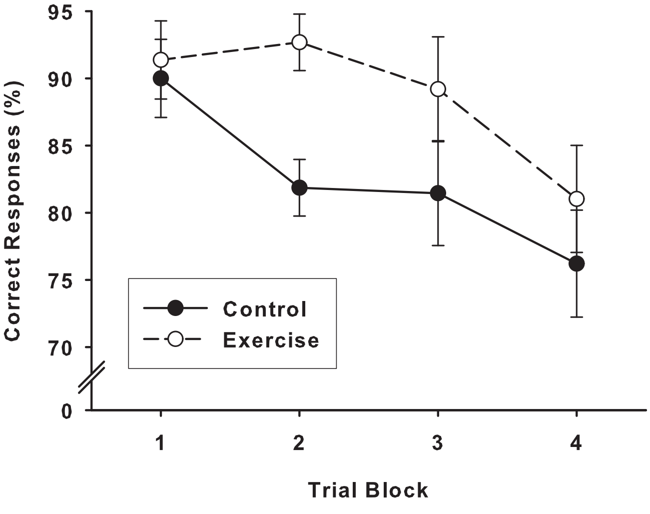

Fig. 1. Mean (*SE*) performance accuracy scores, indexed by the percentage of correct responses, during each two minute block of the PASAT for the non-exercising control group and the exercise group.

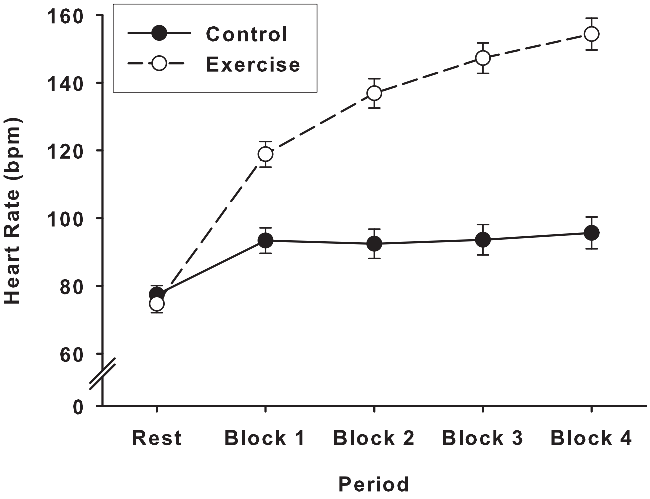

Fig. 2. Mean (*SE*) heart rates at rest and during each two minute block of the PASAT for the non-exercising control group and the exercise group.

Experiment 2

With the aim of further improving our understanding of the exercise and working memory relationship we investigated Sternberg task (Sternberg, 1966) performance at rest and while cycling. Neuroimaging confirms that prefrontal cortex is activated by the Sternberg task (Schon et al., 2009; Wager & Smith, 2003; Wolf et al., 2006). Based on the transient hypofrontality model, we hypothesised that moderate exercise would impair working memory performance, reflected in decreased accuracy on the PASAT and slower processing of information in memory (i.e., a steeper slope) for the Sternberg task.

Method

Participants

Participants were 120 (55 males, 65 females) healthy right-handed students enrolled on a degree course in Sport and Exercise Sciences at a British University with a mean age of 19.57 (*SD* = 0.83) years and body mass index of 22.99 (2.57) kg/m^2. On average, they exercised for 7.07 (*SD* = 3.69) hours per week. At rest, their mean heart rate was 74.94 (*SD* = 12.07) beats per minute, mean systolic blood pressure was 121.68 (*SD* = 9.90) mmHg, and mean diastolic blood pressure was 76.23 (*SD* = 8.87) mmHg. The study protocol was approved by the local research ethics committee and all volunteers gave informed consent to participate.

Apparatus

Participants sat on a cycle ergometer (824E, Monark) with a stimulus box mounted on the front of the ergometer and a response box under their dominant hand. The stimulus box contained a single 40 mm wide by 55 mm high dual-colour (green, red) 7-segment light emitting diode panel that was used for presenting warning, experimental, probe and feedback stimuli. The response box contained two low force microswitch levers (D459-V3LD, Cherry). Heart rate was measured as described in Experiment 1. The experiment took place in a temperature controlled room.

Sternberg task

A version of the Sternberg task (Sternberg, 1966) was used to assess working memory. A computer was programmed in Spike2 to present stimuli and collect responses via a Power1401 (Cambridge Electronic Design). At the start of each of 96 trials, participants were required to depress the two response levers with the index and middle fingers of their dominant hand. The task waited (i.e., no stimuli were presented) until both response levers were depressed. Following a 250 ms delay, the program serially presented a set of either two or six green single-digit numbers ranging from 1 to 9, without any repeats. Each number was presented for 750 ms with a 250 ms interval between numbers. After a 3000 ms delay, a red probe number was presented for 750 ms. Participants were required to decide whether this red number was presented in the previous set of green numbers. If the red number was a match, participants were instructed to lift their middle finger; if it was not a match, participants were instructed to lift their index finger. Participants were then given performance feedback: they were shown a green U if the response was correct and a red U if the response was wrong. Participants were instructed to respond as rapidly as possible while keeping errors to a minimum. The task was divided into blocks of 48 trials, each of which lasted approximately eight minutes. Participants rested for three minutes after each block.

Procedure

Participants completed a single testing session. At the start of the session they completed 24 practice trials. Participants were tested in a mixed multi-factorial experimental design, with condition (control, exercise) as a within-subjects factor and exercise intensity (very low, low, medium) as a between-subjects factor. In the control condition, which was performed first, participants completed the Sternberg task while sitting on the cycle ergometer. In the exercise condition, which was performed second, they completed the Sternberg task while exercising at one of the three randomly assigned intensities. The very low intensity group ($N = 40$) was instructed to pedal at 45 revolutions per minute with no added brake friction, which corresponded to a power output of approximately 5 Watts. The low intensity group ($N = 42$) was instructed to pedal at 50 (women) and 60 (men) revolutions per minute at a power output of 50 Watts (women) and 60 Watts (men). The medium intensity group ($N = 38$) was instructed to pedal at 50 (women) and 60 (men) revolutions per minute at a power output of 75 Watts (women) and 90 Watts (men). In the exercise condition, participants pedalled for two minutes to approach steady state before starting each block of trials of the Sternberg task.

Data reduction

Response latency (ms) was calculated as the time between the onset of the probe stimulus and the release of the switch lever. Responses were discarded if the response latency was less than 100 ms (i.e., anticipation error) or greater than 2250 ms (i.e., inattention error), or if the participant lifted both fingers concurrently (<100 ms apart). The mean response latencies associated with the two-number and six-number sets were used to calculate the slope (ms/digit) and zero intercept (ms) using linear regression (Sternberg, 1966). The heart rate measurements were averaged to yield mean heart rate during control and exercise.

Results and discussion

Sternberg task

A 3 Exercise Intensity Group (very low, low, medium) by 2 Condition (control, exercise) multivariate ANOVA was performed on the slopes and zero intercepts. This yielded multivariate effects for condition, $F(2, 116) = 20.12$, $p < 0.001$, $\eta^2 = 0.26$, and group by condition, $F(4, 232) = 3.55$, $p < 0.01$, $\eta^2 = 0.06$. The performance scores under control and exercise conditions for each intensity group are shown in Fig. 3. To interrogate these effects, a series of 2 Condition (control, exercise) ANOVAs were performed on each group. The slopes were shallower during exercise than control in the low, $F(1, 41) = 11.56$, $p < 0.002$, $\eta^2 = 0.22$, and medium, $F(1, 37) = 9.05$, $p < 0.005$, $\eta^2 = 0.20$, intensity groups but did not differ between conditions in the very low intensity group, $F(1, 39) = 0.67$, $p = 0.42$, $\eta^2 = 0.02$. To further explore this effect, we computed the change in slope (exercise minus control) and compared the change scores of the low ($M = -12.23$ ms/digit) and medium ($M = -11.13$ ms/digit) groups using a 2 Group (low, medium) ANOVA. This analysis indicated that the effect of exercise on memory performance was comparable for these two groups, $F(1, 78) = 0.05$, $p = 0.83$, $\eta^2 = 0.00$. In terms of basic sensorimotor processing speed, the zero intercepts did not differ between conditions for any group: very low, $F(1, 39) = 0.40$, $p = 0.84$, $\eta^2 = 0.00$, low, $F(1, 41) = 0.75$, $p = 0.39$, $\eta^2 = 0.02$, and medium, $F(1, 37) = 1.20$, $p = 0.28$, $\eta^2 = 0.03$.

Heart rate

A 3 Exercise Intensity Group by 2 Condition ANOVA on the heart rates yielded effects for group, $F(2, 114) = 29.21$, $p < 0.001$, $\eta^2 = 0.34$,

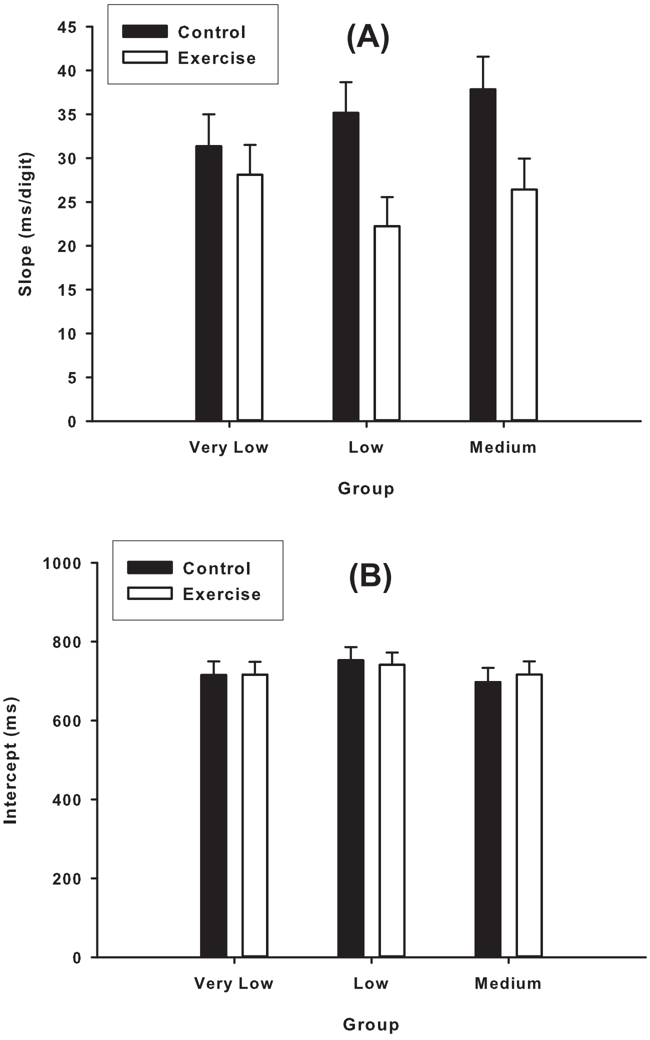

Fig. 3. Mean (*SE*) performance scores on the Sternberg task during control and exercise conditions for the very low, low and medium intensity exercise groups: the slope of the response latencies (A) and the zero intercept of the response latencies (B).

condition, $F(1, 114) = 439.77$, $p < 0.001$, $\eta^2 = 0.79$, and group by condition, $F(1,114) = 90.40$, $p < 0.001$, $\eta^2 = 0.61$. Control and exercise cardiac activity for each group are shown in Fig. 4. To explore these effects, a series of 2 Condition ANOVAs were performed on each variable for each group. The heart rates of all groups increased from control to exercise: very low, $F(1,38) = 6.69$, $p < 0.01$, $\eta^2 = 0.15$, low, $F(1,40) = 263.74$, $p < 0.001$, $\eta^2 = 0.87$, and medium, $F(1,35) = 184.49$, $p < 0.001$, $\eta^2 = 0.85$. A 3 Group ANOVA revealed group differences in the extent of the heart rate reactions to exercise (i.e., exercise value minus control value), $F(2, 114) = 90.40$, $p < 0.001$, $\eta^2 = 0.61$: the cardiac change scores of the medium ($M = 47.7$ bpm) and low ($M = 42.5$ bpm) intensity groups were greater than those of the very low intensity group ($M = 3.0$ bpm). It is noteworthy that the heart rates during the exercise task corresponded to 41 ($SD = 7$), 61 ($SD = 10$) and 64 ($SD = 13$) percent of maximum predicted heart rates for the very low, low and medium intensity groups, respectively.

In brief, the results of Experiment 2 show that exercise selectively influenced Sternberg task performance. Cycling at low to moderate intensities (c. 120–130 bpm corresponding to 60–65% of maximum heart rate) reduced the response latency slopes indicative of improve memory retrieval and scanning processes (Sternberg, 1966). However, exercise did not influence the zero intercept, an index of basic sensorimotor processes. A number of potential limitations need to be considered when interpreting the results of the current experiment. First, the control condition always preceded the exercise condition and therefore the performance during exercise may have been facilitated in part by a learning effect despite the participants practising on the task before the resting control condition performance was formally assessed. Accordingly, the interpretations should be based more strongly on relative control versus exercise comparisons among the three exercise groups. Second, we did not determine each participant's maximum aerobic capacity and then require them to exercise at a proportion of that maximal. Instead our aim was to create different exercise intensities and to recruit a large sample of fit young athletes so that we could first determine whether a brief bout of moderate intensity exercise influenced memory task performance. Our *posterior* computations of workload in terms of relative heart rate, expressed as proportion of maximum predicted heart rate, indicates that the exercise intensities were comparable to previous studies involving moderate intensity exercise. Nonetheless, it should be conceded that future research would do well to more fully characterise the fitness levels of participants and attempt to confirm the current observations.

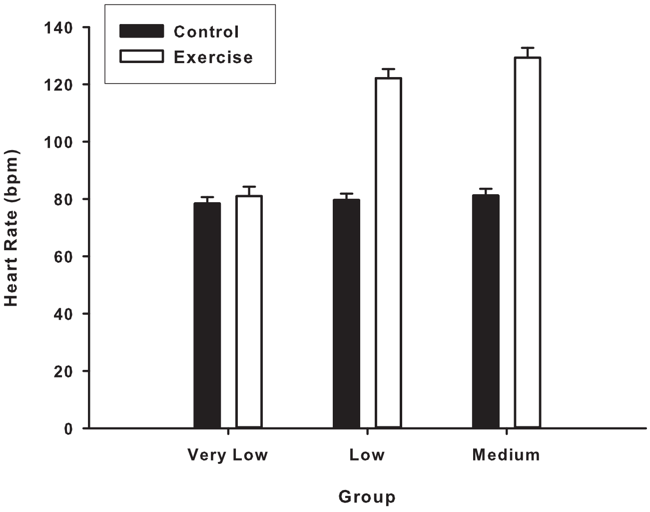

Fig. 4. Mean (*SE*) heart rates while performing the Sternberg task during control and exercise conditions for the very low, low and medium intensity exercise groups.

General discussion

We investigated the influence of dynamic exercise on working memory. We found that moderate intensity cycling increased the number of correct responses in the PASAT at moderate stimulus presentation rates when the task was not too simple (Experiment 1) and reduced the response latency per additional digit in the Sternberg task (Experiment 2). Our findings show that working memory can be improved by aerobic exercise performed at moderate intensities.

Experiment 1 found that exercise selectively influenced PASAT performance. Cycling improved performance compared to rest when the stimuli were presented every two to three seconds whereas the exercise effect was absent when stimuli were presented at slower rates. The finding that overall task performance did not differ significantly is in line with a recent study by Lambourne et al. (2010) who observed no changes in overall PASAT performance before, during and after 40 min of cycling at a similar intensity to our experiment (average heart rates were 143 and 140 bpm, respectively). Their null finding may be attributed to a combination of low power and a ceiling effect due to consistently high performance (with correct responses ranging from 92 to 96%) that was associated with extensive practice and despite individually-tailored stimulus presentation rates of 1.2, 1.6 or 2.0 s.

Importantly, both sets of findings are contrary to the impaired performance reported by Dietrich and Sparling (2004) using the classic version of the task comprising a series of 50 digits at presentation rates of 2.4, 2.0, 1.6 and 1.2 s. Given that exercise intensity (c. 150 bpm corresponding to 70–80% of maximum heart rate) was comparable, the discrepancy may be attributed to differences in exercise mode and duration (cf. Lambourne & Tomporowski, 2010). Specifically, Dietrich and Sparling's (2004) protocol required participants to run on a treadmill for a protracted period (c. 40 min) before commencing the PASAT. Taken together, these results argue that the transient hypofrontality model be revised to consider the mental and physical demands (i.e., complexity, duration, intensity) of the exercise task. This conclusion is similar to the one drawn by Rooks, Thorn, McCully, and Dishman (2010) in their review of the effects of acute exercise on cerebral oxygenation as measured using near-infrared spectroscopy, showing that moderate intensity exercise increased whereas very high intensity exercise decreased the levels of oxygen levels in the prefrontal cortex. Finally, it may be worth noting that elapsed time and level of exertion may also have contributed to the group differences in the memory task performance as a function of block.

Experiment 2 found that exercise selectively influenced Sternberg task performance. Cycling at low to moderate intensities (c. 120–130 bpm corresponding to 60–65% of maximum heart rate) reduced the response latency slopes indicative of improved memory retrieval and scanning processes (Sternberg, 1966). Finally, exercise did not influence the zero intercept, an index of basic sensorimotor processes. Although this latter finding may appear contrary to some previous research indicating that exercise facilitates reaction times (e.g., Etnier et al., 1997), it is worth noting that the zero intercepts, which averaged around 700 ms (i.e., much slower than simple reaction times), indicate that this measure reflects more complex processing demands than simple reaction time. This may help to explain the null effect for the zero intercept observed here. In agreement with the results of experiment 1, our findings confirm that working memory improved during low to moderate intensity exercise. They are also broadly in line with data showing that performance on the Sternberg task is improved immediately and half an hour after exercise (Pontifex, Hillman, Fernhall, Thompson, & Valentini, 2009) and performance on the PASAT is improved similarly after exercise (Tomporowski et al., 2005). Accordingly, this evidence suggests that working memory can be facilitated by modest increases in physiological arousal, both during or after exercise. This pattern of results is compatible with some arousal-based models (and contrary to the transient hypofrontality model as originally specified) of exercise and cognitive functioning (e.g., Kahneman, 1973; Oxendine, 1984; for review see Lambourne & Tomporowski, 2010). Similar improvements in performance with moderate intensity exercise have been noted for other aspects of performance, such as attention (Pesce, Capranica, Tessitore, & Figura, 2002), decision making speed (Davranche & Audiffren, 2004; McMorris et al., 1999) and response preparation (Arcelin, Delignieres, & Brisswalter, 1998). Recent research indicates that memory performance (percent correct) improves with increased arousal and then declines with further increases in arousal (Choi et al., 2012), however, the differences in arousal in our low and medium intensity exercise conditions may not have been sufficiently distinct to test the inverted-U arousal-performance hypothesis (Yerkes & Dodson, 1908). Based on the Yerkes–Dodson Law, arousal-based explanations of the exercise–cognition relationship assume that task performance improves initially at low intensity exercise when arousal increases above basal or resting levels, performance peaks when the intensity of exercise has increased the level of arousal to some optimal level, and then performance declines when exercise-induced arousal continues to rise. In the current research, performance on the memory task improved at low to moderate levels of exercise-induced arousal, however, exercise was never sufficiently intense to cause any deterioration in performance. Accordingly, it would seem that executive functions can be facilitated by relatively low to medium levels of arousal.

In conclusion, the current findings, which were based on relatively medium-to-large samples using well validated tasks and sophisticated experimental designs and recording equipment, revealed medium-to-large effect sizes (Cohen, 1992) for the influence of exercise on working memory. Nevertheless, they need to be replicated by other groups and using other tasks, and, ideally using a multi-measure approach in which behavioural measures of performance are supplemented by physiological measures of brain function.

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References

Arcelin, R., Delignieres, D., & Brisswalter, J. (1998). Selective effects of physical exercise on choice reaction processes. *Perceptual & Motor Skills, 87*, 175–185. http://dx.doi.org/10.2466/pms.1998.87.1.175.

Audoin, B., Ibarrola, D., Au Duong, M. V., Pelletier, J., Confort-Gouny, S., Malikova, I., et al. (2005). Functional MRI study of PASAT in normal subjects. *Magnetic Resonance Materials in Physics, Biology & Medicine, 18*, 96–102. http://dx.doi.org/10.1007/s10334-004-0098-9.

Choi, M.-H., Min, Y.-K., Kim, H.-S., Kim, J.-H., Yeon, H.-W., Choi, J.-S., et al. (2012). Effects of three levels of arousal on 3–back working memory task performance. *Cognitive Neuroscience*. http://dx.doi.org/10.1080/17588928.2011.634064.

Cohen, J. (1992). A power primer. *Psychological Bulletin, 112*, 155–159. http://dx.doi.org/10.1037//0033-2909.112.1.155.

Davranche, K., & Audiffren, M. (2004). Facilitating effects of exercise on information processing. *Journal of Sports Sciences, 22*, 419–428. http://dx.doi.org/10.1080/02640410410001675289.

Dietrich, A. (2003). Functional neuroanatomy of altered states of consciousness: the transient hypofrontality hypothesis. *Consciousness & Cognition, 12*, 231–256. http://dx.doi.org/10.1016/S1053-8100(02)00046-6.

Dietrich, A. (2006). Transient hypofrontality as a mechanism for the psychological effects of exercise. *Psychiatry Research, 145*, 79–83. http://dx.doi.org/10.1016/j.psychres.2005.07.033.

Dietrich, A., & Sparling, P. B. (2004). Endurance exercise selectively impairs prefrontal-dependent cognition. *Brain & Cognition, 55*, 516–524. http://dx.doi.org/10.1016/j.bandc.2004.03.002.

Etnier, J. L., Salazar, W., Landers, D. M., Petruzzello, S. J., Han, M., & Nowell, P. (1997). The influence of physical fitness and exercise upon cognitive functioning: a meta-analysis. *Journal of Sport & Exercise Psychology, 19*, 249–277.

Gronwall, D. M. (1977). Paced auditory serial-addition task: a measure of recovery from concussion. *Perceptual & Motor Skills, 44*, 367–373. http://dx.doi.org/10.2466/pms.1977.44.2.367.

Kahneman, D. (1973). *Attention and effort*. Englewood Cliffs, NJ: Prentice-Hall.

Kimura, K., & Hozumi, N. (2012). Investigating the acute effect of an aerobic dance exercise program on neuro-cognitive function in the elderly. *Psychology of Sport and Exercise, 13*, 623–629. http://dx.doi.org/10.1016/j.psychsport.2012.04.001.

Lambourne, K., Audiffren, M., & Tomporowski, P. D. (2010). Effects of acute exercise on sensory and executive processing tasks. *Medicine & Science in Sports & Exercise, 42*, 1396–1402. http://dx.doi.org/10.1249/MSS.0b013e3181cbee11.

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

Lo Bue-Estes, C., Willer, B., Burton, H., Leddy, J. J., Wilding, G. E., & Horvath, P. J. (2008). Short-term exercise to exhaustion and its effects on cognitive function in young women. *Perceptual & Motor Skills, 107*, 933–945. http://dx.doi.org/10.2466/pms.107.3.933-945.

Lockwood, A. H., Linn, R. T., Szymanski, H., Coad, M. L., & Wack, D. S. (2004). Mapping the neural systems that mediate the paced auditory serial addition task (PASAT). *Journal of the International Neuropsychological Society, 10*, 26–34. http://dx.doi.org/10.1017/S1355617704101045.

McMorris, T., Myers, S., MacGillivary, W. W., Sexsmith, J. R., Fallowfield, J., Graydon, J., et al. (1999). Exercise, plasma catecholamine concentrations and decision-making performance of soccer players on a soccer-specific test. *Journal of Sports Sciences, 17*, 667–676. http://dx.doi.org/10.1080/026404199365687.

Oxendine, J. B. (1984). *Psychology of motor learning*. Englewood Cliffs, NJ: Prentice-Hall.

Pesce, C., Capranica, L., Tessitore, A., & Figura, F. (2002). Effects of a sub-maximal physical load on the orienting and focusing of visual attention. *Journal of Human Movement Studies, 42*, 401–420.

Pontifex, M. B., Hillman, C. H., Fernhall, B., Thompson, K. M., & Valentini, T. A. (2009). The effect of acute aerobic and resistance exercise on working memory. *Medicine & Science in Sports & Exercise, 41*, 927–934.

Rooks, C. R., Thom, N. J., McCully, K., & Dishman, R. K. (2010). Effects of incremental exercise on cerebral oxygenation measured by near-infrared spectroscopy: a systematic review. *Progress in Neurobiology, 92*, 134–150. http://dx.doi.org/10.1016/j.pneurobio.2010.06.002.

Schon, K., Quiroz, Y. T., Hasselmo, M. E., & Stern, C. E. (2009). Greater working memory load results in greater medial temporal activity at retrieval. *Cerebral Cortex, 19*, 2561–2571. http://dx.doi.org/10.1093/cercor/bhp006.

Smith, P. J., Blumenthal, J. A., Hoffman, B. M., Cooper, H., Strauman, T. A., Welsh-Bohmer, K., et al. (2010). Aerobic exercise and neurocognitive performance: a meta-analytic review of randomized controlled trials. *Psychosomatic Medicine, 72*, 239–252. http://dx.doi.org/10.1097/PSY.0b013e3181d14633.

Sternberg, S. (1966). High-speed scanning in human memory. *Science, 153*, 652–654. http://dx.doi.org/10.1126/science.153.3736.652.

Themanson, J. R., & Hillman, C. H. (2006). Cardiorespiratory fitness and acute aerobic exercise effects on neuroelectric and behavioral measures of action monitoring. *Neuroscience, 141*, 757–767. http://dx.doi.org/10.1016/j.neuroscience.2006.04.004.

Themanson, J. R., Pontifex, M. B., & Hillman, C. H. (2008). Fitness and action monitoring: evidence for improved cognitive flexibility in young adults. *Neuroscience, 157*, 319–328. http://dx.doi.org/10.1016/j.neuroscience.2008.09.014.

Tombaugh, T. N. (2006). A comprehensive review of the paced auditory serial addition test (PASAT). *Archives of Clinical Neuropsychology, 21*, 53–76. http://dx.doi.org/10.1016/j.acn.2005.07.006.

Tomporowski, P. D., Cureton, K., Armstrong, L. E., Kane, G. M., Sparling, P. B., & Millard-Stafford, M. (2005). Short-term effects of aerobic exercise on executive processes and emotional reactivity. *International Journal of Sport & Exercise Psychology, 3*, 131–146. http://dx.doi.org/10.1080/1612197X.2005.9671763.

Wager, T. D., & Smith, E. E. (2003). Neuroimaging studies of working memory: a meta-analysis. *Cognitive, Affective & Behavioral Neuroscience, 3*, 255–274. http://dx.doi.org/10.3758/CABN.3.4.255.

Wolf, R. C., Vasic, N., & Walter, H. (2006). Differential activation of ventrolateral prefrontal cortex during working memory retrieval. *Neuropsychologia, 44*, 2558–2563. http://dx.doi.org/10.1016/j.neuropsychologia.2006.05.015.

Yerkes, R. M., & Dodson, J. D. (1908). The relation of strength of stimulus to rapidity of habit-formation. *Journal of Comparative Neurology and Psychology, 18*, 459–482.