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Endurance exercise selectively impairs prefrontal-dependent cognition

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Abstract

Two experiments are reported that examine the possibility that exercise selectively influences different types of cognition. To our knowledge, these experiments represent the first attempt to study higher-cognitive processes during exercise. Theoretical thinking was guided by the transient hypofrontality hypothesis. In both experiments, athletes who exercised at a sustained, moderate pace were compared to sedentary controls on two neuropsychological tests, one that is generally regarded as heavily dependent on prefrontal cognition and one that is relatively insensitive to prefrontal operation. Results showed that during exercise performance on tests demanding prefrontal-dependent cognition was impaired, while at the same time, cognitive processes requiring little prefrontal activity were unaffected.

Keywords: Mental health; Depression; Anxiety; Cortex; Transient hypofrontality; Executive function

1. Introduction

It has been well documented that exercise in the moderate, aerobic range is beneficial to mental health (for reviews, see Glenister, 1996; Salmon, 2001; Scully, Kremer, Meade, Graham, & Dudgeon, 1998). Researchers have also established that exercise results in a mild enhancement of cognitive function (for reviews see, Colcombe & Kramer, 2003; Etnier et al., 1997; Hall, Smith, & Keele, 2001; Kramer, Hahn, & McAuley, 2000; Tomporowski, 2003).

A careful review of the empirical literature reveals that in most studies cognitive ability was evaluated at least 10–15 min after the exercise bout had ceased, presumably to control for arousal levels as well as a number of other possible physiological confounds (e.g., Magnie et al., 2000). However, neuroimaging studies on a wide spectrum of brain functions show that the pattern of neural activation associated with a particular task, rapidly returns to baseline levels after the cessation of that task. This suggests that a delay of even a few minutes would be sufficient to normalize any exercise-induced changes in neural activity. We found few studies that attempted to test for cognitive functions during exercise (e.g., Arcelin, Delignieres, & Brisswalter, 1998; Brisswalter, Arcelin, Audiffren, & Delignieres, 1997; Fery, Fery, Vom Hofe, & Rieu, 1997; Youngstedt, Dishman, Cureton, & Peacock, 1993; for recent reviews see, Brisswalter, Collardeau, & Arcelin, 2002; Tomporowski, 2003). Collectively, cognitive testing in these studies was limited to either basic choice reaction time and/or visual recognition tasks. These simple tests are not sufficiently selective to evaluate changes in specific higher-cognitive abilities that may occur during exercise.

To account for the effects of acute exercise on mental health, the transient hypofrontality hypothesis has recently been proposed (Dietrich, 2003). Briefly, a cornerstone of cognitive psychology is the concept that the brain has a limited information processing capacity (Broadbent, 1958) and is continuously balancing costs and benefits associated with efficient information processing (Pinker, 1999). Yet, global cerebral blood flow to the brain during exercise, as well as global metabolism and oxygen uptake, is constant (Ide & Secher, 2000). Building on the fundamental principle that processing in

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the brain is competitive (Miller & Cohen, 2001) coupled with the fact that there are no additional metabolic resources available during exercise (Ide & Secher, 2000), the massive and sustained activation of motor and sensory systems during exercise (Vissing, Anderson, & Diemer, 1996) must come at the expense of activity in other neural structures. The transient hypofrontality hypothesis suggests that this results in the temporary inhibition of brain regions that are not essential to performing the exercise, such as areas of the frontal lobe involved in higher-cognitive functions.

Despite considerable physiological evidence in favor of the hypothesis (see Dietrich, 2003), it is not clear how these data correlate with psychological function, particularly cognitive processes supported by the prefrontal cortex such as working memory, sustained and directed attention, response inhibition, and temporal integration. To our knowledge, the present study is the first attempt to examine changes in higher-cognitive functions during an actual exercise bout and thus provide a more direct test of the transient hypofrontality hypothesis. If the hypothesis is correct, an individual's ability to perform tasks that are known to heavily recruit prefrontal circuits should be selectively impaired during endurance exercise. It is common practice in cognitive and clinical neuroscience to use neuropsychological testing to determine functional deficits and link them to specific brain regions. It has been known for many decades that people with prefrontal lesions perform normally on a wide variety of tasks such as conventional intelligence (e.g., Hebb, 1939), memory, perceptual, and verbal tasks. Neuroimaging studies have confirmed that such tasks make minimal demands on prefrontal areas. Using putative neuropsychological tests, it was predicted that endurance exercise produces an impairment selective for prefrontal-dependent cognition as measured by the Wisconsin Card Sorting Task or the Paced Auditory Serial Addition Task while, at the same time, produces no significant decline in cognitive processes that do not make heavy demands on prefrontal activation as measured by the Brief Kaufman Intelligence Test or the Peabody Picture Vocabulary Test.

In Experiment 1, we used two exercise modes, running and cycling, and two well-established neurocognitive tests that are widely used to assess specific functional impairment. The Wisconsin Card Sorting Task (WCST; Heaton, Chelune, Talley, Kay, & Curtis, 1993) is commonly regarded as sensitive to prefrontal impairment (Robinson, Heaton, Lehmen, & Stilson, 1980). Successful performance requires strategic planning, cognitive shifting, and working memory ability (Lezak, 1983). The Brief Kaufman Intelligence Test (K-BIT; Kaufman & Kaufman, 1990) was primarily selected because it is a well-normed and reliable measure of general intelligence with a short administration time. It was also selected because it is a highly demanding task that, if no impairment were to be found, would argue against a general fatigue explanation as well as add to the already existing literature showing that acute exercise is not simply associated with a general decline of cognitive ability (Brisswalter et al., 2002). Although it could be argued that some of the items of the fluid intelligence component of the K-BIT contain a prefrontal component, there is no evidence that the test is sensitive to mild prefrontal impairment (Kaufman & Kaufman, 1990). Exercise duration (50 min) and intensity (70–80% of maximum heart rate) were determined based on literature using "steady-state aerobic exercise" protocols (see Tomporowski, 2003, p. 302).

2. Experiment 1

2.1. Methods

2.1.1. Participants

Twenty-four males (age: 23.7 ± 9.4 years; body mass: 74.5 ± 7.9 kg; height: 183.7 ± 6.2 cm; mean ± SD) volunteered to participate in this study. All subjects were either college students ($n = 16$) or recent college graduates ($n = 8$), who regularly engaged in endurance training. The training criterion for subject selection was >30 min of running or cycling, respectively, on 4 or more days per week for the previous 6 months.

2.1.2. Procedure

The experiment had three test conditions: running ($n = 8$), cycling ($n = 8$), and sedentary controls ($n = 8$). Subjects satisfying the training criterion for running ($n = 12$) were randomly assigned on a 2:1 basis to either the running or control condition, and subjects satisfying the cycling condition ($n = 12$) were similarly assigned to either the cycling or control condition. All subjects gave written informed consent and were paid $15 for participating. The university's Institutional Review Board for the protection of human subjects approved the study protocol.

To decrease variability due to arousal levels, all subjects reported to the laboratory on a day prior to the testing session to meet the investigators and practice on the exercise apparatus (treadmill or cycle ergometer). Information about personal health and exercise training was obtained by questionnaire and followed up by interview. At the end of the familiarization session, pretest instructions were given that asked each subject to not exercise on test day and to not eat or consume caffeinated beverages for at least 3 h prior to reporting. A 24-h history form, which requests information on medications, exercise, diet, sleep, and general feeling of well-being, was completed on test day. All participants were compliant.

The exercise protocol was the same whether the subject was running on the treadmill (Quinton model Q65, Seattle, WA) or pedaling on the electronically braked cycle ergometer (Excalibur Sport, Lode, Netherlands). In a temperature controlled room (mean temperature 22 °C), exercise began with a 5-min warm-up during which the work rate on the treadmill or cycle ergometer was slowly increased to elicit a heart rate in the range of 70–80% of maximum heart rate (~140–160 b/min). This zone was calculated from subjects' individual maximum heart rates, which were known due to prior, unrelated tests. For endurance-trained runners and cyclists this corresponds to a moderate training effort (Borg, 1998), an exercise intensity that is not easy, but not exhausting either. This represents a physiological steady state that a well-trained subject can continue for a prolonged duration.

Once the desired exercise intensity was reached, the subject ran or cycled at this effort for 45 min. For the first 20 min, the subject was instructed "to run (or cycle) within himself and to pay no attention to the investigators." The treadmill and cycle ergometer were oriented so that the subject faced a blank back wall while running or cycling. Lab personnel stayed out of the visual field of the subject, did not speak with the subject, and minimized any conversation with each other.

After 25 min of exercise (5-min warm-up plus 20 min in the heart rate range), administration of the cognitive tests began. Each subject was given the same two tests, the WCST and the K-BIT, by the same investigator. Test order was counterbalanced among subjects within each condition. Test administration lasted approximately 25 min and the subject continued to exercise in the heart rate range until both tests were completed. Total exercise time was ~50 min. Subjects in the control condition were instructed to either stand on the treadmill or sit on the cycle ergometer for 50 min. After 25 min of waiting, they performed the cognitive tests while facing the same blank back wall. To create the same noise condition that existed in the exercising groups, subjects in the control group were exposed to the sound of a running treadmill.

Throughout the test, heart rate was obtained by telemetry using a Polar heart rate monitor (Oulu, Finland) and recorded every 2 min to insure that subjects stayed in the appropriate heart rate range. Unbeknownst to the subjects, the work rate of the treadmill or the cycle ergometer was adjusted as needed if heart rate drifted out of range. In addition to heart rate, the rating of perceived exertion (RPE) scale was used (Borg, 1998). RPE allows the subject to rate overall physical effort using a numerical scale (ranging from 6 to 20) with accompanying adjectives (e.g., 7 = extremely light, 13 = somewhat hard, and 19 = extremely hard) serving as anchors. This scale correlates well with heart rate during endurance exercise in healthy young adults (Borg, 1998). RPE scores were obtained at 6, 25 min, and at the end of the exercise session.

2.1.3. Cognitive assessment

Both cognitive instruments used in this experiment were projected on a blank back wall using a LCD projector (Proxima Ultralight LXI, Wilsonville, OR). The resulting image measured 70 cm × 50 cm and was located, for all three conditions, approximately 1.7 m directly in front of the subject. No subject reported difficulties visually comprehending the projected images. This experimental setup required minor instructional changes from the standard administration of the tests.

To measure prefrontal-dependent cognition, a computerized version of the WCST-64 was administered (Kongs, Thompson, Iverson, & Heaton, 2000). This shortened version of the task was selected due to its significantly decreased administration time while, at the same time, maintaining the task requirements of the WCST (Kongs et al., 2000). The task requires subjects to sort cards on the basis of three sorting rules: color, number, or shape. The particular sorting rule must be discovered empirically on the basis of feedback that appears on the bottom of the screen. After 10 consecutive correct responses, the sorting rule changes and the new rule must be acquired. The standard instructions for the computerized version require the subject to respond by pressing one of four keys on the computer keyboard, each corresponding to one of the four target cards. To accommodate the novel experimental setup, the projected images of the target cards were clearly labeled so that responses could be given orally.

The WCST yields a number of interrelated dependent variables (Heaton et al., 1993). Five of these indexes were analyzed: (1) total number of errors (TE); (2) number of perseverative errors (PE): consecutive responses to the same wrong sorting rule; (3) number of nonperseverative errors (NPE): wrong responses that are not perseverative; (4) number of perseverative responses (PR): perseverative errors plus responses that are perseverative and correct; and (5) conceptual level responses (CLR): correct matches despite coincidental runs during which more than one rule seems to apply.

The Brief Kaufman Intelligence Test (K-BIT; Kaufman & Kaufman, 1990) was administered as an overall assessment of cognitive functioning. It was selected because of its short administration time (~15 min) and because it has well-normed and reliable measures of verbal as well as nonverbal intelligence. The Vocabulary section (consisting of Expressive Vocabulary and Definition subtests) measures school-related skills, while the nonverbal Matrices section evaluates problem-solving skills by assessing the ability to perceive relationships and complete analogies. Both subscores as well as the K-BIT IQ Composite were analyzed. Since the K-BIT relies entirely on oral responses, standard instructions were used

(Kaufman & Kaufman, 1990), with the exceptions that all stimulus items were scanned into the computer and projected in front of the subject as described previously.

2.1.4. Statistical analysis

Dependent measures were analyzed using one-way analysis of variance (ANOVA) with three levels, Control, Running, and Cycling. Since our hypothesis made explicit predictions, the Fisher LSD post hoc test was used for planned comparisons.

2.2. Results

Mean (±SD) exercise time was 49.3 ± 3.7 min. Mean heart rate (151.9 ± 9.3 b/min) and rating of perceived exertion (12.6 ± 1.2) mean were within the prescribed moderate-intensity range. Neither the rating of perceived exertion nor the heart rate measure increased significantly during the testing period. Mean responses for runners and cyclists were similar.

Fig. 1 shows K-BIT and WCST performances for all three groups using raw error scores.

For the K-BIT, the one-way ANOVA for the IQ Composite score was not significant, $F(2,21) = 0.45$, *ns*, indicating that exercise did not affect general intelligence as measured by this instrument. Separate one-way ANOVAs for each of the two subtests also revealed no significant effect for exercise conditions on the Vocabulary Section, $F(2,21) = 0.44$, *ns*, or the Matrices Section, $F(2,21) = 0.27$, *ns*, demonstrating that neither subscore of general intelligence was affected by exercise.

For the WCST, the one-way ANOVA for total error was significant, $F(2,21) = 3.54$, $p < .05$, and further analysis using planned comparisons ($p < .05$) revealed that both exercise groups, runners and cyclists, committed significantly more errors as compared to the control group. One-way ANOVAs for each of the remaining four indexes of the WCST further consolidated these results. ANOVA revealed a significant effect for CLR, $F(2,21) = 4.71$, $p < .05$ and PR, $F(2,21) = 4.22$, $p < .05$ of the WCST. In each case, post hoc comparisons $p < .05$ revealed that the performance of either exercise group was significantly impaired as compared to controls. Although the ANOVA for PE, $F(2,21) = 3.33$, $p = .055$, and NPE, $F(2,21) = 2.39$, $p = .17$, showed the same trend, they were not significant.

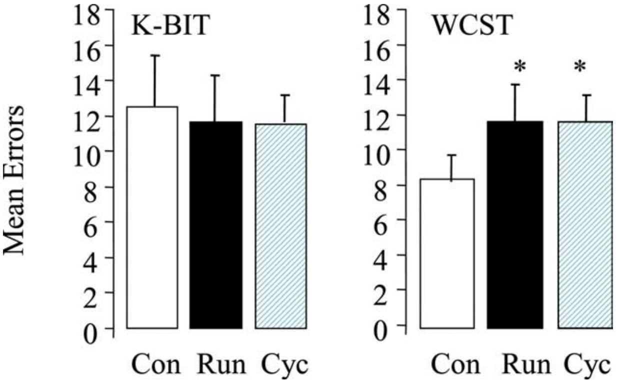

Fig. 1. Performance for each test by condition in Experiment 1. Mean error scores for the Brief Kaufman Intelligence Test (K-BIT) and the Wisconsin Card Sorting Task (WCST) for *control* (Con), running (Run), and cycling (Cyc) conditions. Asterisks represent significant differences.

2.3. Discussion

Results from Experiment 1 showed that exercise resulted in a performance deficit for the WCST but not for the K-BIT. Given the widely accepted interpretations extracted from these neuropsychological measures, it was tempting to conclude that exercise produced deficits that are selective for cognitive function typically ascribed to functional systems that rely on the prefrontal cortex. Indeed, in a clinical setting, this pattern of test results would support a diagnosis of mild and selective prefrontal impairment. However, there was reason to be cautious about drawing such a straightforward conclusion. First, although performance scores for the WCST, but not the K-BIT, were significantly different between the exercising and control conditions, the between-subject design did not allow for a direct comparison of how performance changes in the same individual. Yet, since both testing instruments were administered to exercisers and control subjects alike in a counterbalanced design, this pattern of selective deficit should be most readily attributed to the only manipulated independent variable of the study, namely exercise. Similarly, comparing the performance of the two exercising groups, running and cycling, to the national norm for age, gender, and education (see Heaton et al., 1993; Kaufman & Kaufman, 1990), suggests a selective deficit for WCST but not K-BIT performance.

Second, the two neurocognitive measures might differ in a number of dimensions other than their dependence on prefrontal functioning. For instance, it could be argued that the WCST is simply more difficult or requires more effort. This is unlikely because the K-BIT is a comprehensive and difficult test of general cognitive ability that has a high ceiling and takes an equal amount of time to complete. Also, in post-test informal interview, subjects tended to agree that the K-BIT was a very demanding test. The comparison of performance on both tests in this experiment to the respective national norms also argues against this potential confound.

Third, the two measures might differ merely in a quantitative fashion with regard to prefrontal involvement. Although there is no evidence to suggest that the K-BIT is sensitive to prefrontal deficits, it could be argued that some of the items in the fluid intelligence component of the test, especially the advanced matrix items requiring mental rotation, might depend on prefrontal cognitive processes. However, the WCST depends profoundly on prefrontal cognitive processes such as working memory, sustained attention, and response inhibition. In contrast, the K-BIT does not require significant working memory capabilities or sustained attention because each test item is independent of the next. There is no need to keep in mind information for a longer period of time, as it is the case for the WCST. Additionally, since K-BIT items have no relation to one another, the inhibition of previous responses is not a critical factor in this instrument. In contrast, successful performance on the WCST relies heavily on the inhibition of the previously learned rule, and the resulting measure of perseveration is perhaps the most commonly used indication of prefrontal impairment. Consequently, given the putative usage as well as the specific cognitive requirements of both tests, the pattern of results obtained in Experiment 1 was tentatively interpreted as a selective prefrontal deficit due to acute endurance exercise.

Finally, since the methodology used in this experiment employed a novel and innovative procedure requiring a few adaptations from standardized test administration, a partial replication was deemed highly desirable before more sound conclusions could be drawn.

To address these issues, a second experiment was performed. Experiment 2 used only running exercise and was designed to provide converging evidence for exercise-induced hypofrontality by increasing exercise duration (65 min), employing a within-subject design, which was not possible in Experiment 1 due to the training effects on the WCST and K-BIT, and using two different but equally well-established neurocognitive tests. The tests were selected based on the suitability to accommodate the repeated measures design as well as their sensitivity to prefrontal-dependent cognition. As a frontal-task, the Paced Auditory Serial Addition Task (PASAT; Levin, Benton, & Grossman, 1982), which is sensitive to sustained attention, concentration, working memory, and speed of processing (Diehr, Heaton, Miller, & Grant, 1998), was used. Although overlapping with WCST measures, the PASAT is more commonly used to assess sustained attention. The Peabody Picture Vocabulary Test (PPVT-III; Dunn & Dunn, 1997), a widely used, norm-referenced test, was selected because it measures receptive vocabulary, which is a cognitive ability that is largely prefrontal independent. Additionally, it is, similar to the K-BIT, a difficult test with a high ceiling and a comparable administration time.

3. Experiment 2

3.1. Methods

3.1.1. Participants and procedure

Eight male endurance runners (age: 25.1 ± 6.3 years; body mass: 71.4 ± 7.4 kg; height: 182 ± 7.3 cm; mean ± SD), who satisfied the criterion for running used in Experiment 1, were recruited to participate in this study. Each subject gave written informed consent and was paid $30.

This experiment used a completely within-subject design with all eight participants performing both cognitive tests, the PASAT and the PPVT, in both experimental conditions, running and control. The design was fully counterbalanced for both factors. The procedures followed in Experiment 2 were exactly the same as in Experiment 1 with these modifications: (1) two different cognitive tests were used, the PASAT and the PPVT; (2) the duration of running time in the moderate-intensity range prior to cognitive testing was increased from 20 to 40 min to provide the trained athletes with a more challenging physical situation; (3) the total exercise time was ~65 min; and (4) RPE scores were obtained at 6, 45 min, and at the end of the exercise session.

3.1.2. Cognitive assessment

To measure prefrontal-dependent cognition, the Paced Auditory Serial Addition Task (PASAT; Levin et al., 1982) was administered. The test consists of four series of 50 numbers from 1 to 9 presented at increasing speeds (2.4, 2.0, 1.6, and 1.2 s per digit). Each subject listened to an audiotaped presentation (Diehr et al., 1998) and was asked to add together the two preceding numbers and report the sum out loud. Unlike the PASAT-244, each of the four series in the PASAT-200 version is unique, which results in less of a practice effect (Brittain, La Marche, Reeder, Roth, & Boll, 1991), making this format more suitable for the repeated measures design. The PASAT's standard instructions were sufficient for the experimental setup. The number of errors for each series as well as the number of total errors was analyzed.

To measure prefrontal-independent cognition in Experiment 2, the Peabody Picture Vocabulary Test PPVT-III (Dunn & Dunn, 1997) was administered. The PPVT is a widely used, norm-referenced test that measures receptive vocabulary. The test contains stimulus items that are ordered in increasing difficulty. The subject is shown PicturePlates of 4 pictures while the examiner says one stimulus word. The subject is asked to verbally indicate which picture best represents the stimulus word. Thus, similar to the PASAT, the PPVT has a presentation component that is auditory and responses are verbal. The PPVT was chosen because of its short administration time (~12 min), and because it contains two forms, A and B, making it suitable to the repeated administration required for the within-subject design. Although the alternate-forms reliability coefficient is high, .94 (Dunn & Dunn, 1997), the two forms were also presented in a counterbalanced design. Standard instructions were compatible with our methodology.

3.1.3. Statistical analysis

For the PPVT, the dependent variable total errors was analyzed using dependent-samples *t* tests. For the PASAT, a 2×4 ANOVA with two repeated measures (Exercise Condition and Trials) was used to compare the performance across the increasingly difficult series. Since our hypothesis made explicit predictions, planned comparisons were used for post hoc analysis.

3.2. Results

Mean (±SD) running time was 62.9 ± 1.5 min. As with Experiment 1, mean heart rate (154 ± 5.6 b/min) and rating of perceived exertion (12.8 ± 0.7) were within the prescribed intensity range and neither measure increased significantly during the testing period as compared to the warm-up period.

Fig. 2 shows PPVT and PASAT mean error rates for the running and control conditions.

For the PPVT, the *t* test for total error was not significant, $t(14) = 0.65$, *ns*, showing that running did not affect receptive vocabulary. For the PASAT, the *t* test revealed a significant effect for Exercise Condition, $t(14) = 3.54$, $p < .05$, with runners committing more errors. This indicates that endurance running significantly decreased working memory ability and attentional focus while, at the same time, having no effect on verbal ability.

Fig. 3 shows PASAT performance for each of the four trials of increasing speed (2.4, 2.0, 1.6, and 1.2 s) as well as total errors pooled across trials for the running and control conditions.

A 2×4 ANOVA on PASAT performance revealed a significant effect for Exercise Condition, $F(1,7) = 7$, $p < .05$, showing that runners committed significantly more errors than controls. The ANOVA was also significant for Trials, $F(3,21) = 42.01$, $p < .0001$, verifying that faster presentation speeds increased error rates. The interaction effect of the overall ANOVA was not significant, $F(3,21) = 0.42$, *ns*. This was an expected result because, as can be seen in Fig. 3, performance deteriorated in a similar pattern for both groups. This indicates that runners and controls did not differ with respect to the rate of decline. To determine whether runners and controls differed at each of the four levels of the PASAT, post hoc tests were used despite the overall nonsignificant interaction effect. As depicted in Fig. 3, these comparisons ($p < .05$) demonstrated a significant impairment during running for each of the four trials.

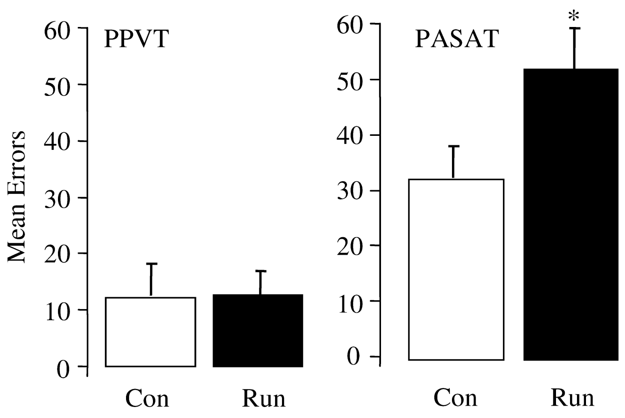

Fig. 2. Performance for each test by Condition in Experiment 2. Mean error scores for the Peabody Picture Vocabulary Test (PPVT) and the Paced Auditory Serial Addition Task (PASAT) for *control* (Con) and running (Run) conditions.

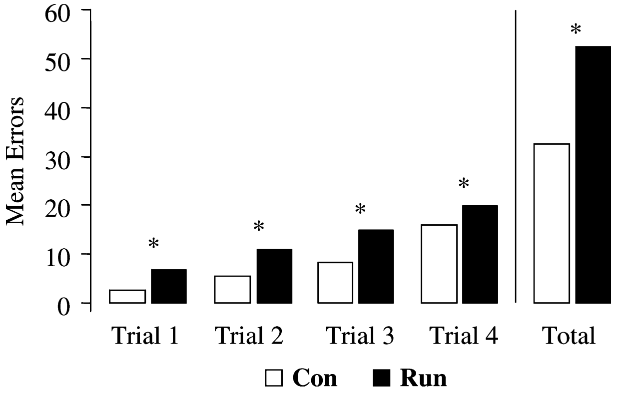

Fig. 3. PASAT performance over Trials PASAT performance for each of the four trials of increasing speed (2.4, 2.0, 1.6, and 1.2 s) as well as total errors pooled across trials for *control* (Con) and running (Run) conditions. Asterisks represent significant differences.

4. Discussion

The results of the two experiments reported here provide convergent evidence consistent with the hypothesis that prolonged exercise might result in a state of transient hypofrontality. In Experiment 1, performance on the WCST, which tests for working memory, perseveration, and the ability to shift cognitive sets, was impaired for runners and cyclists but not controls. Yet, no differences among the three groups were observed in general intelligence as measured by the K-BIT. Using a within-subjects design and two different putative neuropsychological tests, a comparable pattern of impairment emerged in Experiment 2. Performance on the PASAT, which measures sustained attention and working memory ability, was impaired in subjects when running, but not when tested in the control condition. Yet, subjects showed no differences in verbal ability between the conditions.

At the very least, these results indicate that during endurance exercise different cognitive functions are affected to different degrees. However, the converging evidence from several psychometric tests that are widely accepted as indicative of specific cognitive impairments, multiple exercise modes, various exercise lengths, and different experimental designs permit the more advanced conclusion that endurance exercise selectively compromised prefrontal-dependent executive functions such as working memory, sustained attention, and the ability to inhibit habitual responses. In addition, the failure of concomitant deficits on two cognitively taxing prefrontal-independent tasks, coupled with the fact that physiological measures were carefully controlled, argues strongly against a general cognitive decline, general arousal, and/or fatigue explanation. Our methodology also allows us to eliminate another possible confound; that is, exercise merely served to increase the speed of the response at the expense of accuracy. However, with the exception of the PASAT, the cognitive measures used in the present study have no significant time constraints and there was no payoff for reacting faster.

Anecdotal, introspective comments from subjects provide some additional insight to these results. For example, one cyclist remarked about the WCST, "when it [the rule] changed, I would still be thinking about the last cards" and one runner stated, "at the end, I was losing track of what to match up." Similarly, in the PASAT a runner explained: "after about 10 numbers, I could not keep other thoughts from popping into my mind" (all quotes used with permission). To further strengthen our conclusions, other descriptive observations might also be of interest, particularly given the use of the novel approach and methodology. For instance, the decline in PASAT performance in the running condition was instantly noticeable to even the most casual observer and every subject, regardless of counterbalancing, did more poorly when running. In other words, this was not a subtle effect.

The present findings are consistent with physiological data on exercise and brain function and offer a coherent psychological explanation of the EEG data in humans as well as the single cell recording, blood flow, and metabolism data from exercising animals (Dietrich, 2003). Future research will have to address a number of issues related to the finding that endurance exercise selectively and transiently impairs prefrontal-dependent psychological processes. Although several EEG studies have already demonstrated that treadmill running of the same intensity used in the present study reduces prefrontal activity (for a review, see Kubitz & Pothakos, 1997), it would be highly desirable to replicate the present results in a study that also makes use of physiological measures. Additionally, other physiological measures such as optical imaging or ERP combined with other selective neuropsychological measures are needed to further explore the complex interaction between exercise and mental function.

It has been hypothesized that central fatigue might underlie the mental and physical decline in performance associated with maximal exercise (Fery et al., 1997). Indeed, there is very little doubt that with either continued exercise or increased intensity impending exhaustion would ultimately result in a dramatic decline of all types of cognitive performance (Cian et al., 2000; Tomporowski, 2003). It is important to note, however, that the selective impairment seen in the present study occurred under a physical workload that can be sustained for hours by conditioned athletes. Modern brain research conceptualizes cognitive function as hierarchically ordered and the cerebral cortex, and in particular the prefrontal cortex, is at the top of that hierarchy, representing the neural basis of higher-cognitive functions (Markowitsch, 1995). A strain on metabolic resources should, first and foremost, affect the most zenithal higher-order structure followed by a progressive deterioration of brain regions that compute less sophisticated cognitive processes (Dietrich, 2003). The brain's metabolic resources remain constant during exercise (Ide & Secher, 2000). Given that intensity is coded by the rate of neuronal firing, exercise of low intensity might be insufficient to cause metabolic needs in motor and sensory structures that would require a shift of the brain's finite resources from areas that are not essential to the task to areas sustaining the workload. Conversely, exercise of high intensity cannot be maintained long enough by the cardiovascular system to tax the brain's resources. A moderate physical workload on the other hand would be associated with a considerable increase in neuronal firing rates in a large amount of neural tissue that can be sustained for a long period of time. It is suggested that this condition is most conducive to force a reallocation of resources at the expense of higher cognitive and emotional structures such as areas of the prefrontal cortex. In light of these theoretical considerations, the present findings have significant implications for an individual's ability to make complex cognitive judgments, while operating under physical constraints. Future research will have to address the time course of the effects of sustained physical exercise on higher-cognitive functions.

The present findings and the broader theoretical framework have potential implications for the use of exercise in the treatment of depression and anxiety disorders. PET studies have demonstrated that the right ventromedial prefrontal cortex, along with the amygdala and the anterior cingulate gyrus, are hyperactive during depression (see Mayberg, 1997). Neuroimaging studies of individuals with anxiety disorders implicate frontal lobe dysfunction in a similar manner. In obsessive–compulsive disorder for instance, the ventromedial prefrontal cortex exhibits widespread hypermetabolism as well (Baxter, 1990; Baxter et al., 1987). Given the analytical, emotional, and attentional capacities of the prefrontal cortex, the excessive activity is thought to generate a state of hyper-vigilance and hyper-awareness. Exercise may provide relief from stress, anxiety, and negative thinking patterns by running on "safe mode" the very structure that instigates these mental troubles— the prefrontal cortex. Thus, acute exercise might "take the edge off" by neutralizing this circuitry, producing temporary inability to focus on life's worries. On a psychological level, this has been called the distraction hypothesis; that is, exercise provides a "time-out" from life's stress (Bahrke & Morgan, 1978). Unlike other theories, the theoretical framework of transient hypofrontality provides a mechanistic explanation for the clinical data showing that exercise in the moderate, aerobic range is most beneficial to mental health.

The present findings need to be integrated into the literature describing the effects of exercise on cognitive function. First, two recent meta-analyses concluded that the weight of the evidence suggests that exercise produces a slight enhancement of cognitive performance (Colcombe & Kramer, 2003; Etnier et al., 1997). However, both meta-analyses failed to clearly differentiate between post-exercise and during-exercise cognition. As briefly argued above, the temporal resolution of neuroimaging studies provide reasonable grounds to suspect that post-exercise assessment of mental function offer little insight into emotional and cognitive processes during actual exercise. Neural structures are considered to compete for the brain's finite resources (e.g., Miller & Cohen, 2001) and the computational costs of large scale motor output such as in exercise should result in constraints of metabolic recourses available for cognitive functions. Consequently, the finding of the present study that exercise can impair cognitive function does not necessarily run counter to the general conclusions in the literature.

Second, a few studies have reported improved cognitive performance during exercise (Brisswalter et al., 2002). However, the cognitive testing in these studies was limited to either basic choice reaction time and/or visual recognition tasks. These tasks represent comparatively simple decisional paradigms that are not sufficiently selective to evaluate changes in specific higher-cognitive abilities that may occur during exercise. Indeed, these tasks might be simple enough to be positively affected by arousal. With increased task difficulty, such is the case in the present study, arousal is not likely to lead to improved performance. Thus, our results that higher-cognitive functioning is selectively impaired during exercise also do not run counter to the findings that performance on simpler cognitive tasks is enhanced during exercise.

Recent advances in psychology and neuroscience have greatly enhanced our understanding of the contribution of the prefrontal cortex to cognition. In the future, this knowledge will allow exercise scientists to ask more specific questions regarding the effects of exercise on cognition. Using a novel methodology that makes use of this knowledge, our data are the first to show changes in higher-cognitive functions during an actual exercise bout and thus represents a start in that direction.

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