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Neuroelectric and behavioral indices of interference control during acute cycling

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Abstract

Objective: This study examined the effects of in-task, moderate-intensity aerobic exercise on neuroelectric and behavioral indices of interference control, one component of executive control.
Methods: Forty-one participants completed a $\dot{V}O_2$ max test to determine maximal heart rate (HR). On a separate day, event-related brain potentials and task performance were measured during the counterbalanced conditions of upright cycling at 60% of maximal HR and rest while performing congruent and incongruent trials of a flanker task.
Results: Exercise resulted in reduced response accuracy for incongruent trials relative to rest; an effect not found for congruent trials. Decreased N1 amplitude was observed during exercise at parietal sites and globally for N2. Exercise also resulted in increased amplitude for the P2 at frontal and central sites, and for the P3 at frontal and lateral sites. Further, longer N2 and P3 latencies were observed during exercise relative to rest.
Conclusion: These findings suggest that the need to allocate attentional resources toward the large-scale bodily movements inherent in exercise may relate to inefficiency of neural resource allocation, resulting in decreased interference control.
Significance: These data indicate general and selective exercise-induced decrements in cognitive processing while performing acute aerobic exercise.

Keywords: Acute exercise; In-task exercise; Executive control; Cognitive function; Event-related brain potentials (ERPs); P3

1. Introduction

A growing body of research has examined acute exercise effects on cognition, with results failing to provide consensus regarding the nature of this relationship. Tomporowski and Ellis (1986) reviewed the extant literature and suggested that the inconsistent relationship between acute exercise and cognition was related to methodological factors regarding the nature of the cognitive processes examined, as well as the intensity and duration of the exercise bout. A further methodological factor responsible for the inconsistent findings relates to the time at which cognition is evaluated relative to the acute exercise bout. Dietrich and Sparling (2004) indicated that the point at which cognitive evaluation occurs is particularly important because neural activation associated with exercise rapidly returns to baseline levels following the cessation of exercise. The vast majority of research has examined changes in cognition following an acute bout of exercise (see Brisswalter et al., 2002; Tomporowski, 2003 for reviews) in an effort to control for changes in physiological arousal (Hillman et al., 2003); while a relatively smaller literature-base has examined changes in cognition during exercise.

There is a further lack of consensus with regard to the direction of cognitive change during acute exercise. Although the majority of studies have employed aerobic exercise of moderate intensity, conflicting findings remain.

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For example, several studies have found a facilitation of cognitive performance on decision-making tasks (Arcelin et al., 2001; Davranche and Audiffren, 2004; Paas and Adam, 1991), whereas others have observed an impairment of cognitive performance on perceptual (Paas and Adam, 1991) and executive control (Dietrich and Sparling, 2004) tasks. Executive control refers to a subset of processes involved in the selection, scheduling, and coordination of computational processes that are responsible for perception, memory, and action (Meyer and Kieras, 1997; Norman and Shallice, 1986).

One likely source for the inconsistent relationship between in-task exercise and cognition is the neural structures that mediate various cognitive processes. As such, Dietrich (2003) proposed the transient hypofrontality hypothesis to account for changes in cognition during exercise. This hypothesis draws from earlier frameworks (e.g., Broadbent, 1958; Keele, 1973) that indicate limited availability of information processing resources in the brain. During exercise there is an increase in the demand placed upon available resources due to the organization and control of gross bodily movements and accompanying physiological systems, without a concomitant increase in available metabolic resources (Ide and Secher, 2000). Accordingly, the allocation of resources necessary for exercise is provided at the expense of other demands (i.e., cognitive) placed upon the information processing system. The transient hypofrontality hypothesis proposes that this reallocation of resources results in the temporary inhibition of neural networks (e.g., frontal lobe) minimally involved with exercise-related movement. Thus, processes subserved by the frontal lobe (i.e., executive control processes) would be expected to exhibit impairment during exercise.

Two studies have examined changes in frontally mediated executive control functions during exercise, and support for the transient hypofrontality hypothesis is mixed. Specifically, Dietrich and Sparling (2004) observing selective impairment for tasks involving extensive amounts of executive control (i.e., Wisconsin Card Sorting Task, Paced Auditory Serial Addition Task) during exercise, with no change in performance on tasks requiring minimal executive control (i.e., Kaufman Brief Intelligence Test, Peabody Picture Vocabulary Test III). Alternatively, Pesce et al. (2002) used a task that examined attentional orienting and cognitive flexibility and observed general improvements in executive control performance during acute cycling. Thus, a further test of the transient hypofrontality hypothesis using measures that examine specific aspects of executive control is warranted. The Eriksen flanker task (Eriksen and Eriksen, 1974) is a paradigm used to manipulate interference control, one aspect of executive control. Variable amounts of interference control are required based on the compatibility of the target and flanking letters. The congruent condition (e.g., HHHHH) elicits faster and more accurate responses than the incongruent condition (e.g., HHSHH; Eriksen and Schultz, 1979), since the latter results in greater response competition between the target and flanker letters (Kramer et al., 1994; Spencer and Coles, 1999).

The evaluation of event-related brain potentials (ERPs) has provided additional insight into the underlying mechanisms involved in cognitive function beyond that of behavioral measures. ERPs reflect patterns of voltage change in ongoing neuroelectric activity that occurs in response to, or in preparation for, a stimulus or response. The ERP is characterized by a succession of positive and negative components, which are constructed according to their direction and the relative time that they occur (Hruby and Marsalek, 2003). Earlier components (N1, P2) of the stimulus-locked potential relate to aspects of selective attention, while later components (N2 and P3 [also known as the P300 or P3b]) relate to various aspects of cognitive function (e.g., response inhibition, attentional resource allocation). Following acute bouts of aerobic exercise increases in P3 amplitude and decreases in P3 latency have been observed (Hillman et al., 2003; Magnié et al., 2000), suggesting greater allocation of attentional resources during stimulus encoding and faster cognitive processing speed, respectively. However, we have been unable to locate any published research examining the relationship between acute exercise and earlier components of an ERP (e.g., N1, P2, and N2).

To date, relatively few studies have attempted to examine ERPs to assess underlying changes in cognitive function during acute exercise. One reason for the paucity of research in this area may be the gross bodily movement inherent in exercise, which introduces artifact into the collected neuroelectric signal. Yagi et al. (1999) used a recumbent cycle ergometer to reduce movement artifact during auditory and visual oddball paradigms in which participants cycled at a rate equivalent to 65–75% of their age-predicted maximum heart rate. During exercise, smaller P3 amplitude and shorter P3 latency was observed for both the auditory and visual oddball tasks, relative to pre and post exercise measures, suggesting a reduction in the allocation of available attentional resources, but faster cognitive processing speed during exercise relative to rest. Further, Grego et al. (2004) examined the neuroelectric responses of trained cyclists using an auditory oddball task during exercise at approximately 66% of $\dot{V}O_2$ max. Specifically, the P3 component was measured at regular intervals during a 180 min cycling session (i.e., 3, 36, 72, 108, and 144 min from the beginning of the acute bout). P3 amplitude was found to increase significantly after the first hour of exercise (72 and 108 min) and remained elevated through the 144th minute. In addition, P3 latency was found to increase steadily during the course of exercise, and was significantly longer at 108 and 144 min following the start of the acute bout. These findings indicate an increase in the allocation of attentional resources, but slower cognitive processing speed during prolonged aerobic exercise (Grego et al., 2004). It is not readily apparent why opposing findings were observed between the two studies for P3 amplitude and latency given that both used similar stimulus discrimination paradigms. Several methodological factors relating to the prescribed exercise intensity, the duration of the acute bout, the small sample size (Grego et al., 2004), and the limited electrode array (Yagi et al., 1999) may be potential sources for the inconsistent findings. Accordingly, there is a further need to examine this relationship using a protocol that exerts control over both the exercise stimulus and the cognitive task.

In the present study, several hypotheses were tested within the context of a modified flanker task. First, it was examined whether in-task aerobic exercise would influence behavioral performance (i.e., RT, response accuracy) during a task requiring variable amounts of interference control. Second, it was examined whether in-task aerobic exercise would influence neuroelectric concomitants of cognition. It was hypothesized that ERP measures, and the P3 component in particular, would exhibit greater sensitivity to in-task exercise than measures of task performance (see Hillman et al., 2004). That is, ERP components are selectively sensitive to a subset of processes that occur between stimulus encoding and response production. As such, it was predicted that the various components (i.e., N1, P2, N2, and P3) would be more sensitive to the effects of in-task exercise relative to the behavioral measures. In the present study, P3 amplitude and latency were specifically examined to better determine the relationship between in-task exercise and attentional resource allocation and cognitive processing speed during performance of congruent and incongruent flanker trials. As discussed above, previous research has been equivocal with respect to the direction of P3 amplitude and latency modulation during exercise (Grego et al., 2004; Yagi et al., 1999) and no data exists for earlier ERP components. Lastly, it was hypothesized that in-task exercise would have a larger effect on incongruent trials compared to congruent trials, supporting previous research indicating that the relationship between exercise and cognition is disproportionately larger for tasks requiring extensive amounts of executive control (Colcombe and Kramer, 2003; Hillman et al., 2003).

2. Method

2.1. Participants

Forty-one right-handed undergraduate students (26 females, age = 20.2 ± 1.6 years) served as participants and receive extra course credit for their participation. All participants provided written informed consent that was approved by the Institutional Review Board of the University of Illinois at Urbana-Champaign and completed the Physical Activity Readiness Questionnaire (PAR-Q), a physical and mental health history questionnaire, the Edinburgh handedness inventory (Oldfield, 1971), and reported normal or corrected to normal vision based on the minimal 20/20 standard. See Table 1 for participants' demographic and fitness data.

Table 1

Mean values ± SD for demographic, cardiorespiratory fitness, and exercise data

Measure	Mean (all)	Mean (female)	Mean (male)
Sample size	41	26	15
Age (years)	20.2 ± 1.6	20.2 ± 1.7	20.0 ± 1.3
Age range (years)	18–24	18–24	18–22
Height (cm)	172.6 ± 8.5	167.8 ± 5	180.9 ± 6.9
Weight (kg)	66.8 ± 11.4	61.3 ± 8.5	76.4 ± 9.5
BMI (kg/m^2)	22.3 ± 2.1	21.7 ± 2.2	23.3 ± 1.7
Days between testing sessions	6.4 ± 7.6	6.7 ± 9.4	5.9 ± 3.0
Heart rate baseline (bpm)	77.0 ± 6.0	77.4 ± 6.4	76.0 ± 4.8
Heart rate max (bpm)	190.7 ± 8.6	187.6 ± 8.0	196.0 ± 6.8
Age-predicted heart rate max (bpm)	199.8 ± 1.6	199.8 ± 1.7	199.9 ± 1.3
RPE max	17.3 ± 1.6	17.0 ± 1.8	17.7 ± 1.1
$\dot{V}O_2$ max (ml/kg/min)	38.3 ± 7.0	35.8 ± 5.0	42.7 ± 7.0

2.2. Procedure

Participants came to the laboratory on two separate occasions ($M = 6.4 \pm 7.7$ days apart). On the first visit, participants completed an informed consent and the PAR-Q to screen for any previous health issues that may be exacerbated by acute exercise. Participants were then fitted with a Polar heart rate monitor (Model A1, Polar Electro, Finland) and had their height and weight measured using a stadiometer and a Tanita BWB-600 digital scale, respectively. A $\dot{V}O_2$ max test was then administered using a cycle ergometer. Prior to the start of the $\dot{V}O_2$ max test, the cycle ergometer was adjusted to accommodate each participant's height and the participant was then prepared for testing on the metabolic cart. Participants sat quietly on the cycle ergometer for 2 min before beginning the 2 min warm up portion of the $\dot{V}O_2$ max test. Upon completion of the warm up period, participants exercised at an increasing workload until volitional exhaustion occurred. Following the $\dot{V}O_2$ max test participants were given a cool down period and waited for their heart rate to return to within 10 beats per minute (bpm) of their resting heart rate prior to leaving.

On the second visit, participants completed a health history and demographics questionnaire and an Edinburgh handedness inventory (Oldfield, 1971) before being prepared for neuroelectric testing, which was conducted in a sound attenuated room. A Polar Heart Rate monitor (Model A1, Polar Electro, Finland) and a 32-channel Quik-cap (Compumedics Neuroscan, El Paso, TX) were applied to each participant. Participants were read the task instructions and given 10 practice trials before the task began. Participants were then counterbalanced into two different experimental conditions such that half the participants received the rest condition prior to the exercise condition, and the other half received the exercise condition prior to the rest condition. The flanker task was also counterbalanced across the two experimental conditions. In the exercise condition, participants cycled at a self-selected pace on a mechanically braked Monark Ergomedic 828E cycle ergometer until steady-state cycling occurred ($M = 5.3 \pm 0.9$ min, range = 3.8–7.3 min) that corresponded with 60% of their heart rate maximum as obtained during their $\dot{V}O_2$ max test. When steady-state was achieved, participants were instructed to continue cycling at their steady-state pace throughout the duration of the flanker task (approximately 6.5 min) until instructed to stop by the experimenter following completion of the task. Heart rate was monitored throughout the flanker task and recorded once per minute. In the rest condition participants sat for 5 min before the flanker task began. For those participants in which the rest condition occurred following the exercise condition, seated rest was performed until heart rate returned to pre-exercise baseline level ($M = 6.3 \pm 1.0$ min, range = 5.0–8.3 min). Upon completion of the last condition, all electrodes were removed and the participant was briefed on the purpose of the experiment.

2.3. Recording conditions

2.3.1. Cardiorespiratory fitness assessment

Cardiorespiratory fitness was measured as relative peak oxygen consumption during a $\dot{V}O_2$ max test on a Monark Ergomedic 828E cycle ergometer with a protocol beginning at 70 W and increasing by 15 W every 2 min. A computerized indirect calorimetry system (ParvoMedics True Max 2400) collected 30 s averages for oxygen uptake (VO_2) and respiratory exchange ratio (RER). A Polar heart rate monitor (Model A1, Polar Electro, Finland) measured heart rate throughout the test and a rating of perceived exertion (RPE; Borg, 1970) was taken at the end of every 2 min stage. RPE allows participants to rate their perceived physical effort on a numerical scale ranging from 6 to 20, with a score of seven indicating "very, very light" intensity and a score of 19 indicating "very, very hard" intensity. RPE has been found to correlate with HR during exercise in healthy young adults (Borg, 1998). Relative peak oxygen consumption was expressed in ml/kg/min, and was based on a maximal effort when the participants achieved three of the following four criteria: (1) reached a plateau in oxygen consumption corresponding to an increase of less than 2 ml/kg/min despite an increase in workload; (2) achieved a heart rate that was within 10 beats per minute (bpm) of age-predicted maximum (220-age); (3) produced a respiratory exchange ratio greater or equal to 1.10; or (4) reported a RPE greater than or equal to 17. See Table 1 for cardiorespiratory fitness data from the $\dot{V}O_2$ max test.

2.3.2. Electroencephalogram

Electroencephalographic (EEG) activity was recorded at Fz, FCz, Cz, CPz, Pz, POz, Oz, F3/4, F7/8, FC3/4, FT7/8, C3/4, T7/8, CP3/4, TP7/8, P3/4, P7/8, and O1/2 electrode sites of the International 10–20 system (Jasper, 1958) using a Neuroscan Quik-cap. Data were referenced to averaged mastoids (A1, A2) with AFz serving as the ground electrode and impedance <10 kΩ. Additional electrodes were placed above and below the left orbit and on the outer canthus of each eye to monitor bipolar electro-oculographic (EOG) activity. Continuous data were digitized at a sampling rate of 500 Hz, amplified 500× with a DC to 70 Hz filter, and a 60 Hz notch filter was applied using a Neuroscan Synamps amplifier.

Continuous data were corrected offline for EOG activity using a spatial filter (Compumedics Neuroscan, 2003). Epochs were created from −100 to 1000 ms around the stimuli, and baseline corrected using the 100 ms pre-stimulus period. Data were then filtered using a zero phase shift 30 Hz (24 dB/octave) low pass filter and a linear detrend was applied across the entire epoch to control for DC drift by plotting a "line of best fit" to the waveform, calculating the slope of the line, and then removing that slope from the waveform. Trials with a response error or artifact exceeding ±100 μV were rejected (see Table 2 for the number of trials included per condition). The N1 and N2 components were defined as the largest negative-going peaks occurring within a 50–150 ms and a 150–300 ms latency window, respectively. The P2 and P3 components were defined as the largest positive-going peaks occurring within a 150–300 ms and a 300–600 ms latency window, respectively. Amplitude was measured as a change score from the prestimulus baseline and peak latency was defined as the time point corresponding to the maximum amplitude. Peak data were outputted in ASCII format and analyzed using SPSS 13.0.

2.3.3. Flanker task

A modified flanker task (Hillman et al., in press; Posthuma et al., 2002), which incorporated arrays of arrows, was used to manipulate interference control. The congruent trials consisted of the target arrow being flanked by other arrows that faced the same direction (e.g., <<<<< or >>>>>). The incongruent trials consisted of the target arrow being flanked by other arrows that faced the opposite directions (e.g., <<><< or >><>>). Participants performed a button press with their left thumb when the target arrow (regardless of condition) faced to the left (e.g., '<') and a button press with their right thumb when the target arrow faced to the right (e.g., '>'). One block of 120 trials, randomized across task conditions, was presented during the exercise and rest conditions. Each block consisted of 60 congruent and 60 incongruent trials with

Table 2
Mean values ± SD for the total number of trials that comprised each ERP average

Measure	Mean
Rest all trials	114.6 ± 6.6
Rest congruent trials	57.9 ± 3.4
Rest incongruent trials	56.7 ± 4.0
Exercise all trials	103.8 ± 14.3
Exercise congruent trials	53.0 ± 7.7
Exercise incongruent trials	50.8 ± 7.4

left and right target arrows occurring with equal probability. The stimuli were 7.62 cm tall white arrows, which were presented focally for 200 ms on a black background with a response window of 1500 ms and an inter-stimulus interval of 1500 ms. Total task duration was approximately 6.5 min.

2.4. Statistical analysis

Statistical analyses were performed using 25 electrode sites (five coronal sites within each of five regions). Omnibus analyses were conducted separately for each ERP component and for amplitude and latency data. ERP component values for each participant were submitted to a 2 (Condition: Exercise, Baseline) × 2 (Task Congruency: Congruent, Incongruent) × 5 (Region: Frontal, Fronto-Central, Central, Centro-Parietal, Parietal) × 5 (Site: 7, 3, z, 4, 8) repeated measures MANOVA. RT and response accuracy data were analyzed using a 2 (Condition) × 2 (Task Congruency) repeated measures MANOVA. All analyses with three or more within-subjects levels used the Wilks' Lambda statistic. Post hoc univariate ANOVAs with Bonferroni corrected *t* tests were used to decompose significant effects when appropriate. A significance level of $p = .05$ was used for all analyses prior to Bonferroni correction.

3. Results

3.1. Condition order

Preliminary analyses were performed to test whether the Condition Order (i.e., rest, exercise vs. exercise, rest), which was counterbalanced across participants, had an effect on the behavioral (i.e., RT, response accuracy) or neuroelectric (N1, P2, N2, P3 amplitude and latency) variables. Findings revealed no significant main effect or interaction involving Condition Order for any variable, with two exceptions. A Condition Order × Task Congruency interaction was observed for N1 and P2 component amplitudes, F's $(1, 39) \geqslant 4.3$, $p < .05$, $\eta^2 \geqslant .10$. Decomposition of these interactions did not reveal any significant findings, t's $(40) \leqslant 1.7$, $p \geqslant .09$. Given that significant Task Congruency effects were not observed for the N1 or P2 component amplitude analyses reported below, all further analyses were collapsed across Condition Order.

3.2. Heart rate response

Confirmatory analyses were performed to test whether HR prior to the rest condition differed as a function of whether the participant received the rest condition before ($M = 76.8 \pm 6.3$ bpm) or after ($M = 77.0 \pm 4.9$ bpm) the exercise condition to reduce the possibility that changes in cognitive function were related to general cardiovascular arousal. Findings did not reveal significant differences in HR prior to the resting condition as a function of Condition Order, $t(39) = 0.14$, $p = .9$. In addition, no differences in HR were observed before ($M = 77.0 \pm 5.3$ bpm) or after ($M = 76.1 \pm 5.3$ bpm) the rest condition, $t(40) = 1.9$, $p = .07$. Lastly, confirmatory analyses were performed on HR during the exercise condition to demonstrate that participants cycled at a steady-state. HR did not differ across the 6 min exercise session, $F(5, 36) = 0.2$, $p = .96$, $\eta^2 = .03$ (see Table 3).

3.3. Task performance

3.3.1. RT

The omnibus analyses revealed a main effect of Task Congruency, $F(1, 44) = 180.7$, $p < .001$, $\eta^2 = .82$, with shorter RT latency for congruent ($M = 409.5$, SE = 8.4) relative to incongruent ($M = 484.9$, SE = 11.0) trials. No Condition effect, $F(1, 40) = 0.004$, $p = .95$, $\eta^2 < .001$, or Condition × Congruency interaction, $F(1, 40) = 0.13$, $p = .72$, $\eta^2 = .003$, was observed.

3.3.2. Response accuracy

Analyses revealed main effects of Condition, $F(1, 40) = 14.1$, $p = .001$, $\eta^2 = .26$, and Task Congruency, $F(1, 40) = 18.4$, $p < .001$, $\eta^2 = .32$, which were superseded by a 2-way interaction of Condition × Task Congruency, $F(1, 40) = 9.0$, $p = .005$, $\eta^2 = .18$. Post hoc Bonferroni corrected *t* tests of Task Congruency within each Condition indicated a significant decrease in response accuracy for incongruent trials during exercise compared to rest, $t(40) = 4.7$, $p < .001$. No such effect was found for congruent trials, $t(40) = 0.9$, $p = .4$ (see Fig. 1).

3.4. ERP component amplitude

3.4.1. N1 amplitude

The omnibus analyses revealed a main effect of Condition, $F(1, 40) = 4.1$, $p = .05$, $\eta^2 = .09$, with smaller amplitude during exercise compared to baseline. In addition, main effects of Region, $F(4, 37) = 8.0$, $p < .001$, $\eta^2 = .47$, and Site, $F(4, 37) = 9.9$, $p < .001$, $\eta^2 = .52$, were observed, which were superseded by Condition × Region, $F(4, 37) = 2.5$, $p = .05$, $\eta^2 = .22$, and Region × Site, $F(16, 25) = 2.7$, $p = .01$, $\eta^2 = .63$, interactions. Decomposition of the Condition × Region interaction examined differences in Condition within each Region and revealed smaller N1 amplitude during exercise relative to rest at the parietal region, $t(40) = 3.5$, $p = .001$ (see Figs. 2–4). Decomposition of the Region × Site interaction examined Site within each Region and revealed significant differences between sites within all five regions, F's $(4, 37) \geqslant 3.8$, p's $\leqslant .01$, $\eta^2 = .29$. Post hoc Bonferroni *t* tests indicated that lateral electrode sites exhibited smaller amplitude than medial electrode sites in all regions, t's $(40) \geqslant 3.1$, $p < .005$.

3.4.2. P2 amplitude

Analyses revealed main effects of Condition, $F(1, 40) = 23.0$, $p < .001$, $\eta^2 = .37$, Region, $F(4, 37) = 12.0$,

Table 3
Mean values ± SD for steady-state heart rate (HR) during the exercise condition

	Min 1	Min 2	Min 3	Min 4	Min 5	Min 6	Mean
HR (bpm)	114.6 (4.9)	114.5 (5.6)	114.5 (5.4)	114.4 (5.3)	114.4 (5.3)	114.4 (5.3)	114.4 (5.2)

$p < .001$, $\eta^2 = .57$, and Site, $F(4, 37) = 4.7$, $p < .005$, $\eta^2 = .33$, which were superseded by three 2-way interactions of Condition × Region, $F(4, 37) = 3.5$, $p < .02$, $\eta^2 = .27$, Condition × Site, $F(4, 37) = 3.5$, $p < .02$, $\eta^2 = .28$, and Region × Site $F(16, 25) = 2.5$, $p = .02$, $\eta^2 = .62$. Decomposition of the Condition × Region interaction examined differences between exercise and rest within each of the five scalp regions. Bonferroni corrected t tests indicated that P2 amplitude was increased during exercise compared to rest at the frontal, fronto-central, and central regions, t's (40) $\geqslant 4.1$, $p < .001$ (see Figs. 3 and 4). This effect was largest at the frontal region and decreased in magnitude parietally. No such effect was observed at the centro-parietal or parietal regions, $t(40) \leqslant 2.3$, $p \geqslant .03$. Decomposition of the Condition × Site interaction examined differences between exercise and rest within each of the five electrode sites (7, 3, z, 4, 8). Bonferroni corrected t tests indicated that P2 amplitude was increased for exercise compared to rest at all electrode sites, t's (40) $\geqslant 2.6$, $p \leqslant .01$, with the exception of the right mid-lateral leads, which was marginal, $t(40) = 2.1$, $p = .04$ (see Fig. 3). Decomposition of the Region × Site interaction examined differences between Sites within each Region. Post hoc tests indicated that the sites differed only at the fronto-central and central regions, F's (4, 37) = 3.0, $p \leqslant .03$, $\eta^2 = .24$. Post hoc Bonferroni corrected t tests indicated that FCz exhibited larger amplitude than FT7, and Cz had greater amplitude than T7, C3, and C4, t's (40) $\geqslant 3.0$, $p < .005$.

3.4.3. N2 amplitude

Analyses revealed main effects of Condition, $F(1, 40) = 10.2$, $p = .003$, $\eta^2 = .2$, with exercise resulting in smaller amplitude than rest (see Fig. 3); Task Congruency, $F(1, 40) = 7.3$, $p = .01$, $\eta^2 = .2$, with congruent trials resulting in smaller amplitude than incongruent trials; Region, $F(4, 37) = 16.4$, $p < .001$, $\eta^2 = .64$; and Site, $F(4, 37) = 6.6$, $p < .001$, $\eta^2 = .42$; which were superseded by a 2-way interaction of Region × Site, $F(16, 25) = 3.6$, $p = .002$, $\eta^2 = .7$. Decomposition of the Region × Site interaction examined differences between electrode sites within each Region. Post hoc tests indicated that electrode sites differed at the frontal, $F(4, 37) = 5.4$, $p = .002$, $\eta^2 = .4$, central, $F(4, 37) = 3.2$, $p = .025$, $\eta^2 = .25$, centro-parietal, $F(4, 37) = 6.0$, $p = .001$, $\eta^2 = .4$, and parietal, $F(4, 37) = 9.5$, $p < .001$, $\eta^2 = .5$, regions, with no effect for the fronto-central region, $F(4, 37) = 2.3$, $p = .08$, $\eta^2 = .2$. Bonferroni corrected t tests indicated frontal differences with Fz exhibiting larger amplitude than F7 and F8, t's (40) $\geqslant 3.1$, $p \leqslant .004$; central differences with C3 exhibiting larger amplitude than T7, $t(40) = 3.1$, $p = .003$; centro-parietal differences with CP3 and CP4 exhibiting larger amplitude than TP7, CPz, and TP8, t's (40) $\geqslant 3.1$, $p \leqslant .004$; and parietal differences with P3 and P4 exhibiting larger amplitude than P7, Pz, and P8, t's (40) $\geqslant 3.9$, $p < .001$.

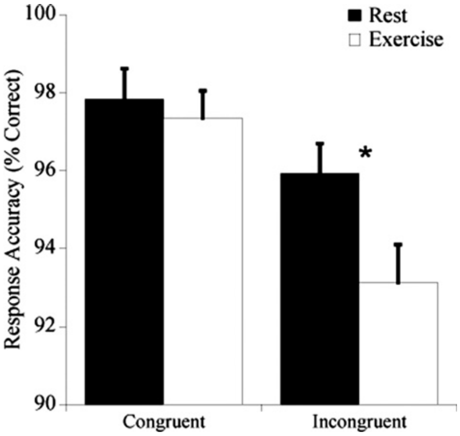

Fig. 1. Average response accuracy during exercise and rest for congruent and incongruent trials of the flanker task.

3.4.4. P3 amplitude

Analyses revealed main effects of Condition, $F(1, 40) = 6.5$, $p < .02$, $\eta^2 = .14$; Region, $F(4, 37) = 6.5$, $p < .001$, $\eta^2 = .41$; and Site, $F(4, 37) = 20.7$, $p < .001$, $\eta^2 = .7$; which were superseded by four 2-way interactions of Condition × Region, $F(4, 37) = 5.2$, $p = .002$, $\eta^2 = .36$, Task Congruency × Region, $F(4, 37) = 3.5$, $p < .02$, $\eta^2 = .28$, Condition × Site, $F(4, 37) = 10.9$, $p < .001$, $\eta^2 = .54$, and Region × Site, $F(16, 25) = 4.7$, $p < .001$, $\eta^2 = .76$. Decomposition of the Condition × Region interaction examined differences between Condition within each Region. Post hoc tests reveled differences in Condition only at the frontal and fronto-central regions, t's (40) $\geqslant 3.1$, $p < .005$, with larger amplitude for exercise relative to rest (see Figs. 3 and 4). No such effect was observed at the central, centro-parietal, or parietal regions, t's (40) $\leqslant 1.1$, $p \geqslant .26$. Decomposition of the Task Congruency × Region interaction examined differences between Task Congruency within each Region. Post hoc tests indicated that congruent trials resulted in larger amplitude than incongruent trials only at the frontal region, $t(1, 40) = 2.8$, $p < .01$. Decomposition of the Condition × Site interaction examined differences between Condition at each Site. Post hoc tests indicated that exercise resulted in larger amplitude at lateral sites (7's and 8's) compared to rest, t's (40) $\geqslant 3.4$, $p \leqslant .002$ (see Fig. 3).

Decomposition of the Region × Site interaction examined differences between electrode sites at each Region. Post hoc tests indicated that electrode sites differed within

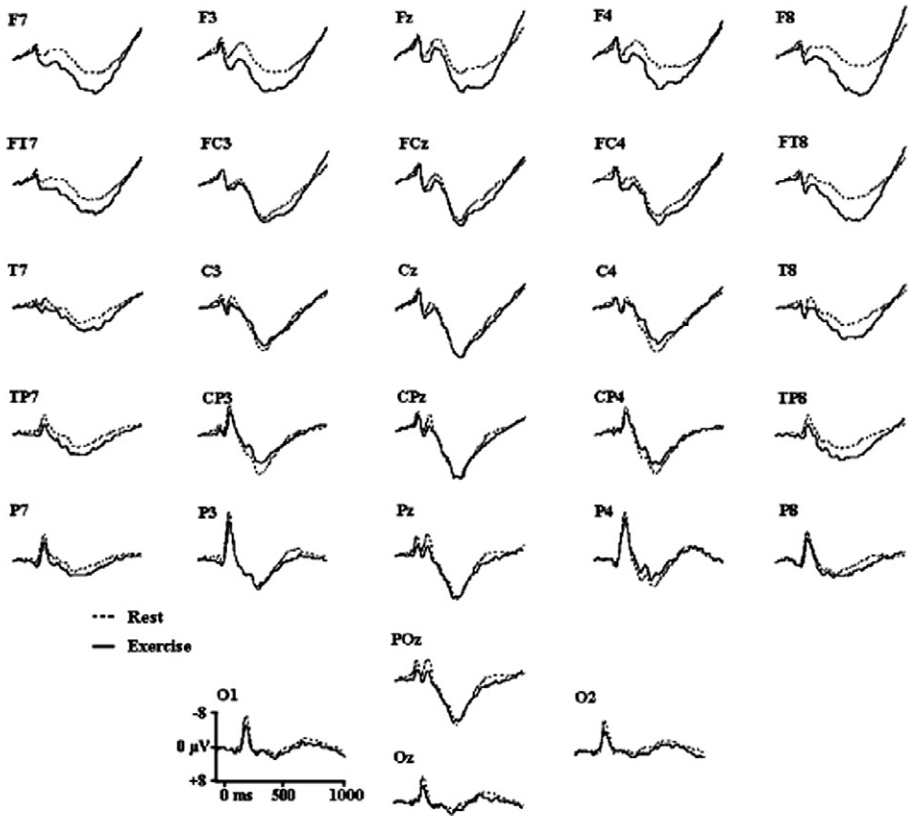

Fig. 2. Grand average waveform for exercise (solid line) and rest (dashed line) at each electrode site.

the fronto-central, central, centro-parietal, and parietal regions, $F(4, 37) \geqslant 9.1$, $p < .001$, $\eta^2 \geqslant .5$; while no differences were observed at the frontal region, $F(4, 37) = 1.0$, $p = .44$, $\eta^2 = .1$. Bonferroni corrected t tests indicated the largest amplitude over midline sites with smaller amplitude observed over lateral sites for all regions, t's $(40) \geqslant 3.0$, $p \leqslant .005$.

3.5. ERP component latency

3.5.1. N1 latency

Analyses revealed main effects of Region, $F(4, 37) = 19.4$, $p < .001$, $\eta^2 = .68$; and Site, $F(4, 37) = 8.1$, $p < .001$, $\eta^2 = .5$; which were superseded by two 2-way interactions of Task Congruency × Site, $F(4, 37) = 3.1$, $p < .03$, $\eta^2 = .3$; and Region × Site, $F(16, 25) = 3.5$, $p = .003$, $\eta^2 = .7$. Decomposition of the Task Congruency × Site interaction examined differences between Task Congruency at each Site, and indicated that congruent trials exhibited faster latency than incongruent trials at midline (z's) and right lateral (8's) sites, t's $(40) \geqslant 2.6$, $p \leqslant .01$. Decomposition of the Region × Site interaction examined differences between electrode sites within each Region, and indicated that electrode sites differed at centro-parietal, $F(4, 37) = 4.7$, $p = .004$, $\eta^2 = .3$, and parietal, $F(4, 37) = 13.5$, $p < .001$, $\eta^2 = .6$, regions. In the centro-parietal region, Bonferroni corrected t tests indicated shorter latency at CPz relative to TP7, CP3, and CP4, t's $(40) \geqslant 3.1$, $p \leqslant .004$; and in the parietal region, shorter latency was found at Pz relative to all other sites, t's $(40) \geqslant 3.4$, $p \leqslant .002$.

3.5.2. P2 latency

No significant main effects or interactions were observed.

3.5.3. N2 latency

Analyses revealed main effects of Task Congruency, $F(1, 40) = 12.4$, $p = .001$, $\eta^2 = .2$; Region, $F(4, 37) = 32.8$, $p < .001$, $\eta^2 = .8$; and Site, $F(4, 37) = 6.6$, $p < .001$, $\eta^2 = .4$; which were superseded by three 2-way interactions of Condition × Region, $F(4, 37) = 3.0$, $p = .03$, $\eta^2 = .2$, Task Congruency × Region, $F(4, 37) = 3.3$, $p = .02$, $\eta^2 = .3$, and Region × Site, $F(16, 25) = 3.1$, $p = .006$, $\eta^2 = .7$. Decomposition of the Condition × Region interaction examined differences in Condition within each Region, and reveled shorter latencies for rest, compared to exercise, at the centro-parietal, $t(40) = 2.7$, $p = .01$, and parietal, $t(40) = 2.9$, $p = .007$, regions. Decomposition of the Task Congruency × Region interaction reveled shorter latency for congruent, relative to incongruent, trials at the frontal, $t\ (40) = 3.1$, $p = .003$; fronto-central, $t(40) = 3.0$, $p = .005$; and centro-parietal regions, $t(40) = 2.8$, $p = .008$. Decomposition of the Region × Site interaction indicated that electrode sites differed at centro-parietal, $F(4, 37) = 5.3$, $p = .002$, $\eta^2 = .37$, and parietal, $F(4, 37) = 9.4$, $p < .001$, $\eta^2 = .5$, regions. Bonferroni corrected t tests for the centro-parietal region indi-

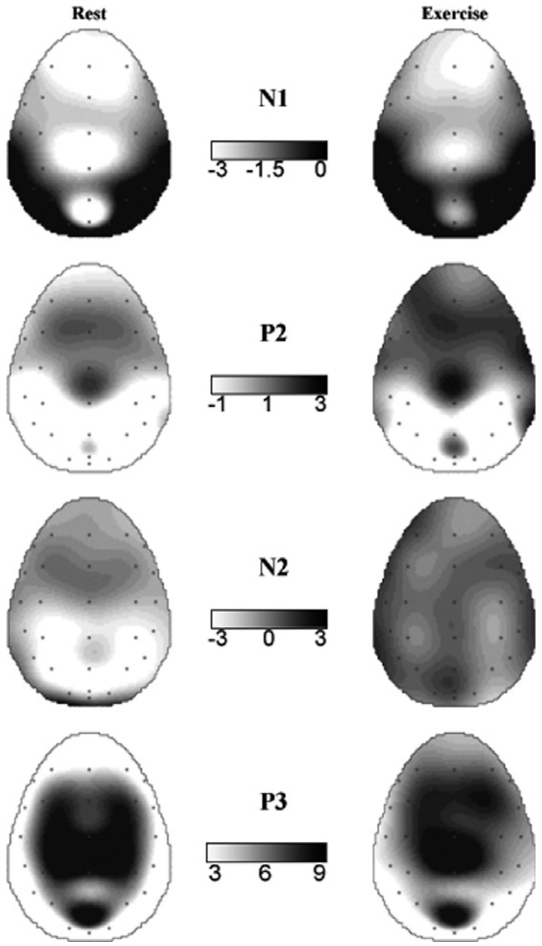

Fig. 3. Topographic maps for exercise and rest for each ERP component.

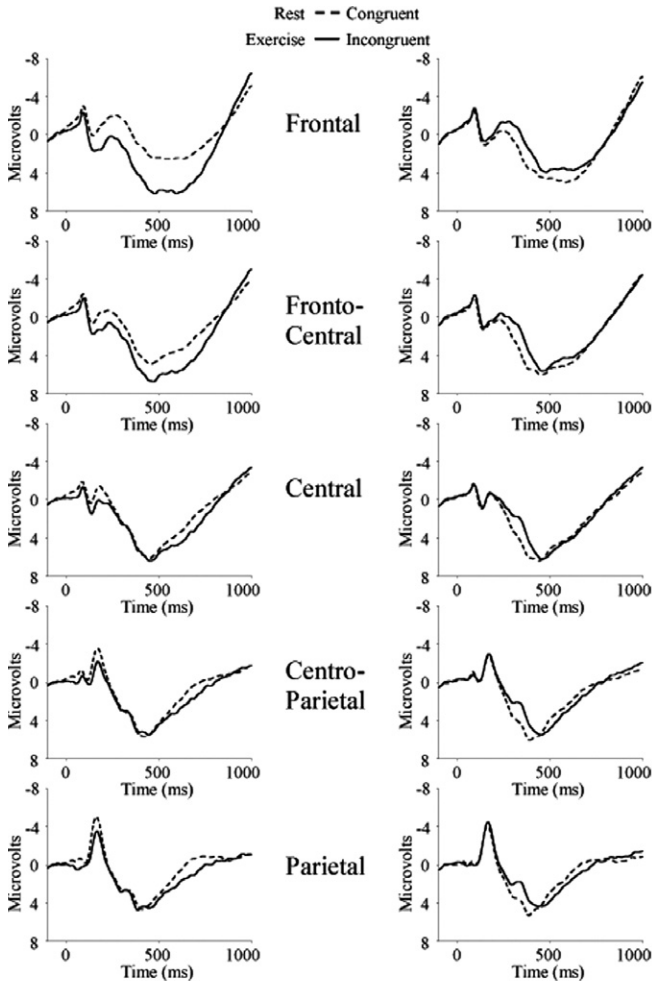

Fig. 4. Regional grand average waveforms for exercise versus rest conditions (left side), and congruent versus incongruent trials of the flanker task (right side).

cated longer latency at CPz relative to TP7, CP3, and CP4, *t*'s (40) ⩾ 3.0, $p \leqslant .005$; and the parietal region exhibited longer latency at P7 and Pz relative to P3, *t*'s (40) ⩾ 3.2, $p \geqslant .003$, and at P8 relative to P7, P4, and Pz, *t*'s (40) ⩾ 3.1, $p \leqslant .005$.

3.5.4. P3 latency

Analyses revealed main effects of Condition, $F(1, 40) = 10.9$, $p = .002$, $\eta^2 = .2$, with rest (444.2 ± 34.0 ms) resulting in shorter latency than exercise (463.7 ± 38.0 ms); Task Congruency, $F(1, 40) = 44.5$, $p < .001$, $\eta^2 = .5$; Region, $F(4, 37) = 8.7$, $p < .001$, $\eta^2 = .5$; and Site, $F(4, 37) = 4.8$, $p = .003$, $\eta^2 = .7$. In addition, a 2-way interactions of Task Congruency × Region, $F(4, 37) = 2.8$, $p = .04$, $\eta^2 = .2$, was observed, with follow up analyses indicating shorter latency for congruent, relative to incongruent, trials across all regions, *t*'s (40) ⩾ 2.8, $p \leqslant .008$. Decomposition of the Site effect revealed that lateral sites (7's, 8's) exhibited longer latencies than medial sites, *t*'s (40) ⩾ 3.3, $p \leqslant .002$.

4. Discussion

The main findings revealed that response accuracy during moderately intense aerobic exercise decreased for incongruent trials relative to the rest condition. No such effect was observed for congruent trials or for RT. With regard to the neuroelectric data, decreased amplitude was observed for the N1 component at parietal scalp sites and globally for the N2 component for exercise compared with rest. The P2 and P3 components revealed larger amplitude during exercise frontally, with increased amplitude also occurring at sites over the lateral regions only for the P3 component. ERP component latency was also affected by in-task exercise, with longer N2 and P3 latencies observed at central–parietal and parietal sites, relative to rest. These findings indicate that in-task exercise may decrease efficiency of the neuroelectric system and relate to deficits in task performance.

4.1. Task performance

Replicating previous research, results indicated shorter RT and increased response accuracy for congruent relative to incongruent trials of the flanker task (Eriksen and Schultz, 1979; Hillman et al., in press; Kramer et al., 1994; Posthuma et al., 2002; Spencer and Coles, 1999).

Further, selective deficits in task performance were observed during exercise compared to rest, with decreased accuracy during incongruent trials. Of interest is the fact that response accuracy decreased during exercise using a task that typically results in a high level of task performance. That is, previous reports (Hillman et al., in press; Kramer et al., 1994; Zeef et al., 1996) have found low error rates using flanker tasks. As such, the observed decrease in accuracy for incongruent trials is particularly noteworthy, and suggests a relative inefficiency in the ability to inhibit competing responses during exercise. This finding, which corroborates Dietrich and Sparling's (2004) observation of selective deficits in performance for executive control tasks, may be a result of the dual task nature of the paradigm, since participants were asked to exercise and perform a cognitive task simultaneously. Accordingly, these data provide support for the transient hypofrontality hypothesis, which suggests reduced performance on executive control tasks subserved by the frontal lobe during exercise.

However, findings reported herein are contrary to those of other in-task exercise research (Collardeau et al., 2001; Davranche and Audiffren, 2004; Pesce et al., 2002), which observed improvements in task performance during moderate-intensity exercise. Especially relevant are the findings of Pesce and colleagues (2002) who reported improvements during exercise on a task requiring cognitive flexibility, one component of executive control. The current behavioral findings add little insight into the underlying basis for the discrepant findings across earlier studies (Dietrich and Sparling, 2004; Pesce et al., 2002). Clearly, the relationship between in-task aerobic exercise and task performance is not straight-forward and may vary based on the particular subset of executive control processes engaged by task demands. Future research will need to examine this relationship across a variety of tasks that engage different executive control functions.

4.2. ERP component amplitude

The current findings replicate several earlier studies examining ERP components of executive control (Ridderinkhof et al., 2002). Specifically, task congruency resulted in smaller N2 amplitude for congruent, relative to incongruent, trials (Ridderinkhof et al., 2002; Yeung et al., 2004), but was unrelated to N1 or P2 amplitude. Further, P3 amplitude was found to be larger for congruent, relative to incongruent, trials at sites over the frontal region.

ERP component amplitude was also modulated during exercise, as smaller N1 amplitude was observed at parietal scalp sites during exercise relative to rest. Given that the N1 component is believed to represent neuroelectric resources underlying a general-purpose visual discrimination mechanism (Luck, 1995; Vogel and Luck, 2000), the reduced N1 amplitude during exercise suggests degradation of visual attention. Increases in P2 amplitude at frontal and central scalp sites were also observed during exercise relative to rest. Prior research has indicated that P2 amplitude may correspond to increased levels of selective attention during information processing (Talsma and Kok, 2001). Using this model, the current findings suggest that selective attention processes may increase during exercise, possibly in an effort to increase top–down cognitive control. That is, given the degradation of visual attention (as reflected by decreased N1 amplitude), increases in selective attention (as reflected by increased P2 amplitude) may be necessary to successfully process task-relevant information.

Global decreases in N2 amplitude across scalp sites were also observed during exercise relative to rest. Previous research has indicated that N2 amplitude is associated with response inhibition during tasks that elicit conflict (Ridderinkhof et al., 2002), with increased amplitude reflecting greater conflict monitoring (Yeung et al., 2004). However, increases in top–down cognitive control might relate to reductions in response conflict (Carter et al., 2000), which Colcombe and colleagues (2004) suggest results in reduced activation of the anterior cingulate cortex (ACC). Since the N2 component is believed to be generated by the ACC (van Veen and Carter, 2002), reduced activation should relate to smaller N2 amplitude (Yeung et al., 2004).

Larger P3 amplitude was also observed at electrode sites over the frontal and bilateral regions indicating more diffuse activation during exercise relative to rest. The P3 is thought to index the allocation of attentional resources during environmental interaction (Polich and Kok, 1995), with the amplitude proportional to the amount of attentional resources devoted to a given stimulus or task. Given the increased amplitude observed during exercise, it would follow that greater attentional resource allocation may be necessary for successful task completion. These P3 findings appear counter to Dietrich and Sparling's (2004) transient hypofrontality hypothesis, which would predict inhibition of information processing resources in the frontal lobe. Rather, the observed increased neuroelectric activation, along with the reduction in response accuracy may related to the increased recruitment of neural resources or a breakdown of inhibition, which have been found to relate to inefficiency of executive control function in younger adults (Rypma and D'Esposito, 2000). As such, greater P3 amplitude may reflect a relative inefficiency of neuroelectric resources during exercise, rather than an insufficient amount of resources.

As mentioned above, the addition of exercise creates a dual task environment in which the participant must successfully negotiate the demands imposed by the cognitive task, and allocate resources toward the maintenance of steady-state exercise. In the baseline condition, only the cognitive task is performed. Accordingly, one might expect that P3 amplitude would be modified by the dual task environment to better accommodate the additional requirements imposed. Given the relatively poor spatial resolution of ERPs, it is unclear whether the more diffuse topographical pattern of activation is reflective of increased activation of the motor and/or cardiovascular centers in the cerebral cortex, compensatory neural resource allocation associated with the dual task environment, or a combination of the two. Research by Williams and colleagues (Williams et al., 2006) has identified the insular cortex and the medial prefrontal cortex (i.e., ACC), as well as the thalamic region, as the functional neuroanatomy involved in central command-induced changes in regional blood flow during exercise. Other research (Colcombe et al., 2004) examining executive control function using a flanker task has also implicated the medial prefrontal cortex (i.e., ACC). As such, it is likely that the dual demands imposed by an environment that requires simultaneous performance of a cognitive task during steady-state exercise would act to decrease efficiency of processes mediated by brain regions that subserve both gross motor movement inherent in exercise and cognitive function due to competition for available resources.

4.3. ERP component latency

The above amplitude findings relating to cognitive inefficiency are intriguing when considered along with the ERP component latency data, which also replicated previous literature. Specifically, shorter N2 (Yeung et al., 2004) and P3 (Hillman et al., 2003, 2004; Zeef et al., 1996) latencies were observed for congruent relative to incongruent trials. Relative to in-task exercise, results indicated longer N2 and P3 latencies across task congruency conditions when compared to rest. These findings suggest that during exercise there is a delay in cognitive processing speed related to response inhibition (i.e., N2) and stimulus discrimination (i.e., P3) processes. Similar to the changes in ERP component amplitudes, the longer N2 and P3 latencies may reflect the additional requirements imposed during exercise, and the competition for available neural resources, while performing a cognitively demanding task.

Taken together, the neuroelectric data suggest decreases in visual discrimination (i.e., smaller N1) may elicit greater online top–down cognitive control, to correct for deficits in stimulus acquisition. One such online process may be increases in selective attention (i.e., larger P2). Additionally, greater recruitment of neural resources and delayed processing speed are reflected in more diffuse P3 amplitude and longer N2 and P3 latencies, respectively, in a further effort to correct for early online deficits. Thus, it appears that early deficits in stimulus acquisition may lead to inefficiency of cognitive processing despite attempts to increase top–down cognitive control. Reduced ability to engage response inhibition processes during a conflicting task (i.e., reflected in smaller N2) as well as poorer task performance during incongruent trials provide further indication of cognitive inefficiency during exercise.

Although it is convenient to discuss exercise effects on various aspects of cognitive function by relating individual ERP components to the processes that they reflect, in-task exercise may exert a global influence on the neuroelectric system that is reflected across the multiple individual components. An alternative explanation for the current findings may relate to changes in general cortical arousal. Polich and Kok (1995) proposed that exercise (both chronic and acute) increases P3 amplitude through an overall increase in general arousal. This arousal hypothesis has also been extended to other ERP components as well (Karlin, 1970). For example, the N1–P2 complex is thought to be modulated by increases in arousal. However, these data are contrary to the current findings, as decreased N1 amplitude was observed during exercise. Moreover, Ritter et al. (1983) and Vogel and Luck (2000) suggest that modulation of N1 amplitude may be independent of arousal. In addition, increases in general arousal should result in global increases in ERP component amplitudes across recording sites. The findings herein did not support this notion, as amplitude modulation during exercise was, in most instances, localized to specific regions that differed across components.

In summary, aerobic exercise of moderate intensity was detrimental to cognition, with selective deficits in task performance on trials requiring greater amounts of executive control, and a more general deficit in the efficiency of the neuroelectric system across conditions requiring variable amounts of executive control. The findings suggest competition for available resources imposed by a dual task environment may lead to the recruitment of additional neuroelectric resources and a reduction in task performance on executive control tasks.

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