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Acute exercise has a general facilitative effect on cognitive function: A combined ERP temporal dynamics and BDNF study

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Abstract

This study examined whether acute moderate intensity exercise results in a general or selective improvement in cognitive function. In addition, multiple stimulus-locked ERP components and serum BDNF levels were assessed to investigate potential neurobiological mechanisms underlying acute exercise effects on select aspects of cognitive performance. Thirty young adults were recruited and participated in exercise and reading control sessions in a counterbalanced order. Following treatments, the Stroop task was administrated, and N1, N2, P3, and N450 components of the ERP waveform were recorded and analyzed. Additionally, blood samples were withdrawn immediately following exercise or rest conditions prior to administration of the Stroop task. Acute exercise facilitated response times for both Stroop congruent and incongruent task conditions, with a similar magnitude of improvement. Larger P3 and reduced N450 amplitudes as well as decreased N450 latency were observed following exercise, but no effects on N1 and N2 components were found. This dose of exercise also did not influence serum BDNF levels. These findings suggest that moderate intensity acute exercise results in a generalized rather than selective improvement in cognition. The facilitation may be related to an increase in attentional or neural resource allocation and conflict detection processes reflected by longer latency endogenous components (P3, N450), but is not influenced by earlier sensory and monitoring processes revealed by earlier ERP components or by serum levels of BDNF.

Descriptors: Acute exercise, Executive function, BDNF, ERP, P3, N450

A number of studies have explored the possibility of facilitating cognitive function through acute exercise. It has been concluded that acute exercise, particularly moderate intensity bouts for 20 to 30 min, positively influences cognitive function (Chang, Labban, Gapin, & Etnier, 2012; Kramer et al., 1999; Lambourne & Tomporowski, 2010; Verburgh, Königs, Scherder, & Oosterlaan, 2013). In spite of the consistent evidence from previous studies and meta-analytic reviews, whether specific types or domains of cognitive function are preferentially influenced by acute exercise remains unknown and the underlying mechanisms through which acute exercise impacts brain function has been insufficiently explored.

Derived from the chronic exercise literature (Kramer et al., 1999), a "selective improvement hypothesis" has been proposed to address the differential impact of acute exercise on multiple aspects of cognitive function. Specifically, the hypothesis suggests that acute exercise leads to disproportionately larger effects for executive function tasks that require more extensive amounts of cognitive demand (Hillman, Snook, & Jerome, 2003; McMorris & Hale, 2012). Executive function refers to higher and metalevel cognitive processes that are necessary for achieving purposeful and goal-directed behaviors, especially in nonroutine circumstances (Alvarez & Emory, 2006; Etnier & Chang, 2009). These processes include inhibitory control of attention and prepotent responses (inhibition), updating of working memory (updating), and shifting between changing task demands or sets of rules (shifting; Miyake et al., 2000), as well as more complex processes such as planning and problem solving (Romine & Reynolds, 2005). Executive functions rely on the complex functional network of frontal lobes, including the prefrontal cortex, and are generally assessed through neuropsychological assessments (e.g., Stroop task; Alvarez & Emory, 2006; Etnier & Chang, 2009; Miyake et al., 2000). Chang, Tsai, Huang, Wang, and Chu (2014) found that acute exercise facilitates all Stroop task conditions; however, larger beneficial effects were observed in the task condition that involves executive function (i.e., Stroop color-word) relative to other conditions that reflect basic information processing (i.e., Stroop congruent, Stroop word, Stroop color, and Stroop neutral conditions). The selective improvement on the executive function task condition of the Stroop task may be regulated by heightened activation of dorsolateral prefrontal cortex following acute exercise (Yanagisawa et al., 2010).

In contrast to the selective improvement hypothesis, a general improvement hypothesis emphasizes that acute exercise results in a

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general facilitative effect on cognitive tasks that involve executive function and basic information processing. For instance, Lichtman and Poser (1983) observed a general improvement on both Stroop color and Stroop color-word conditions after a 45-min exercise session that involved an aerobic run and other physical activities. In more recent studies, acute moderate intensity exercise for approximately 20 min has been shown to positively affect multiple Stroop task conditions (Chang, Chi et al., 2014; Chang, Chu, Wang, Song, & Wei, 2015), suggesting a general facilitative effect of acute exercise on multiple cognitive functions. The conflicting support for these two hypotheses plausibly results from methodologies employed in previous studies such as the exercise modality (e.g., aerobic exercise, resistance exercise, or lifestyle physical activity), exercise duration (e.g., from 20 to 45 min), and the selected populations (e.g., younger vs. middle-aged adults; Chang, Chi et al., 2014; Chang, Chu, Wang, Wang et al., 2015; Chang, Tsai et al., 2014; Yanagisawa et al., 2010). These inconsistent findings limit our theoretical and mechanistic understanding of the influence of aerobic exercise on cognition.

ERPs have been utilized to explore potential mechanisms underlying acute exercise and cognition. ERPs refer to patterns of voltage changes in the ongoing EEG that occur in response to a stimulus or an event. Given their high temporal resolution, ERPs allow for the examination of discrete aspects or stages of the information-processing stream, and may help to elucidate the influence of acute exercise on select aspects of cognition. The P3 is a widely examined stimulus-locked component with a maximum and positive deflection between 300 to 600 ms following a stimulus. Although the precise meaning and source localization of the P3 remains unknown, the amplitude is sensitive to the amount of neural or attentional resources allocated to a given task (Polich, 2007), while P3 latency relates to speed of stimulus classification and evaluation (Polich & Kok, 1995), which occurs regardless of behavioral action (Verleger, 1997). Previous acute exercise research has examined P3 measures and observed that during Eriksen flanker and go/no-go tasks, acute aerobic exercise enhances P3 amplitude (Drollette et al., 2014; Hillman et al., 2003, 2009; Kamijo et al., 2009) and decreases P3 latency (Drollette et al., 2014; Hillman et al., 2003; Kamijo et al., 2009), particularly for task conditions that involve the inhibition aspect of executive function. From a neurophysiological perspective, these findings suggest that acute exercise enhances cognition by increasing attentional resource allocation and cognitive processing speed.

Despite these promising findings, studies of acute exercise have predominantly focused on the P3 component of the stimulus-locked waveform, while relatively few studies have focused on other ERP components (e.g., N1). A few acute exercise studies to date have examined N2 elicited by tasks of executive function, and the results are ambiguous. For example, while acute aerobic exercise has been associated with shorter P3 latency and reduced N2 amplitude (Drollette et al., 2014), another acute exercise study failed to observe alterations in N2 following acute exercise (Themanson & Hillman, 2006). Interestingly, Stroth et al. (2009) indicated that only cardiorespiratory fitness, but not acute exercise, influenced P3 and N2 components. It is also noteworthy that the effect of acute exercise on other ERP components such as N1 has yet to be examined. Therefore, the aim of this study was to examine the effects of acute exercise on stimulus-locked ERP components occurring from 50 to 550 ms after stimulus onset, including N1, N2, P3, and N450 components. These ERP components were specifically selected because previous studies have demonstrated that they are reliably elicited by the Stroop task (Lorist & Jolij, 2012; Szucs & Soltesz, 2010), an executive function task that has received increasing research attention in the acute exercise and cognition literature, in part due to the task conditions that allow for the examination of the selective versus general improvement hypotheses of acute exercise (Chang, Chi et al., 2014; Chang, Chu, Wang, Wang et al., 2015; Chang, Tsai et al., 2014; Yanagisawa et al., 2010).

While the temporal sensitivity of ERPs may help to shed light on the effects of acute exercise on cognition, other neurobiological mechanisms such as brain-derived neurotrophic factor (BDNF) represent plausible candidates ripe for investigation. BDNF is a protein and member of the neurotrophin family of growth factors that is in abundance in the hippocampus and cortex, and is associated with learning and memory formation (Tyler, Alonso, Bramham, & Pozzo-Miller, 2002). BDNF has been posited to have an essential role in mediating hippocampal synaptic plasticity (Hennigan, O'Callaghan, & Kelly, 2007) and in the processes of neuroplasticity, including neuronal survival, differentiation, and proliferation (Zagrebelsky & Korte, 2014; Zhao, Deng, & Gage, 2008). Since the original study by Neeper, Gomez-Pinilla, Choi, and Cotman (1995), rodent studies have consistently evidenced an exercise-related upregulation of BDNF gene, mRNA, and/or protein expression in the hippocampus, suggesting an important mediating influence of BDNF in exercise-associated neuroplasticity (see reviews in Cotman, Berchtold, & Christie, 2007; van Praag, 2009; Voss, Vivar, Kramer, & van Praag, 2013). Although acute exercise has been shown to transiently increase circulating levels of BDNF, the nature of the acute exercise stimulus that optimizes BDNF levels in humans remains to be determined. For instance, only acute exercise of vigorous intensity, but not lower intensity, was observed to elevate BDNF levels (Rojas Vega et al., 2006), and elevated serum BDNF levels following high-intensity cycling were associated with enhanced cognitive performance (Griffin et al., 2011). Conversely, acute elevations in BDNF were not found to correlate with either behavioral (Ferris, Williams, & Shen, 2007; Tsai et al., 2014) or ERP indices (Tsai et al., 2014) following acute exercise performed at moderate and vigorous intensity, failing to support a mediational role of BDNF in the acute exercise-related enhancements in cognition. However, it currently remains speculative whether acute moderate intensity exercise affects BDNF responses. Examination of this issue will extend previous research because very few studies are available that have examined both ERP and BDNF responses following a single bout of moderate intensity aerobic exercise (e.g., Tsai et al., 2014). Addressing this limitation may advance our understanding of the mechanisms governing the cognitive-enhancing benefits of exercise.

Using the Stroop task, this study examined the "selective" or "general" improvement hypotheses of acute exercise effects on cognitive function. We also aimed to extend previous research by investigating the temporal dynamics of cognitive processing and potential neurobiological mechanisms by assessing a comprehensive temporal sequence of stimulus-locked ERP components and serum BDNF levels following acute moderate intensity exercise.

Method

Participants

College students were recruited via flyers and advertisements from National Taiwan Sport University. Participants were required to meet the following inclusion criteria: between the ages of 18 and 30 years, right-handed dominance, and reporting normal or corrected-to-normal vision and color perception. Participants were

Table 1. *Demographic and Fitness Characteristics (M ± SD)*

	Male	Female	Total
n	17	13	30
Age (yrs)	22.59 ± 1.50	22.77 ± 1.59	22.67 ± 1.52
Height (cm)	173.12 ± 9.05	158.15 ± 5.55	166.63 ± 10.71
Weight (kg)	70.53 ± 9.51	51.00 ± 4.58	62.07 ± 12.47
Education (yrs)	16.35 ± 0.79	16.46 ± 0.88	16.40 ± 0.81
BMI (kg/m^2)	23.54 ± 2.68	20.39 ± 1.49	22.17 ± 2.72
Digit span forward	14.56 ± 1.50	14.46 ± 1.39	14.52 ± 1.43
Digit span backward	10.69 ± 2.63	11.38 ± 1.81	11.00 ± 2.28
VO_{2peak} ($ml \cdot kg^{-1} \cdot min^{-1}$)	48.08 ± 6.96	39.86 ± 8.33	44.52 ± 8.52
IPAQ (MET)	2704.53 ± 2098.23	2154.08 ± 2414.17	2466.00 ± 2217.58

Note. BMI = body mass index; IPAQ = International Physical Activity Questionnaire; MET = metabolic equivalent.

excluded if they had a presence or history of psychiatric or neurological disorders, cardiovascular disease, and physical disability, or a body mass index (BMI) less than 28. A total of 30 participants met the inclusion criteria and were enrolled in the study.

All participants completed written informed consent approved by the Institutional Review Board of National Taiwan University. Table 1 presents the demographic characteristics for all participants.

Cardiorespiratory Fitness Assessment

Cardiorespiratory fitness was assessed using the YMCA cycle ergometry protocol, a standard submaximal exercise test recommended by the American College of Sports Medicine (2013). The YMCA protocol involved cycling on an electronically braked cycle ergometer (Ergoselect 100/200, Ergoline GmbH, Germany) to obtain the estimated maximal oxygen consumption (VO_{2peak}). Participants were required to complete two to four 3-min stages with a pedal speed setting of 50 rpm during the entire testing session. In the first stage, participants were instructed to cycle at a workload of 150 kgm/min, and heart rate was recorded during the last 15 to 30 s. The initial heart rate assessment was used to determine the subsequent two to three workloads (e.g., heart rate >80 bpm, the 2nd and 3rd workload are 600 kgm and 750 kgm, respectively; heart rate >100, the 2nd and 3rd workload are 300 kgm and 450 kgm, respectively). Once the subsequent two workloads were completed with heart rates maintained between a target zone of 110 and 150 bpm, the protocol was terminated. VO_{2peak} was calculated based upon average heart rate, workload, age, and gender via the graphical method prediction equation (Heyward & Gibson, 2014).

Stroop Task

A computerized version of the Stroop task (Chang, Chu, Wang, Wang et al., 2015) was administered using $Stim^2$ software (Neurosoft Labs, Inc., Sterling VA). The Stroop task consisted of two types of stimuli/task conditions: congruent and incongruent. Congruent trials consisted of one of three color words printed in the Chinese language and in the same ink color [i.e., 藍 (BLUE), 綠 (GREEN), or 紅 (RED) of blue, green, and red ink, respectively). Incongruent trials consisted of the same three word colors but printed in an opposing color [e.g., 藍 (BLUE) presented in red ink color].

The stimuli were 2 × 2 cm displayed focally on a black background on a 17" computer monitor with a visual angle of 2°. Following the presentation of a fixation cross, stimuli were presented for 506 ms with a variable intertrial interval of 383, 583, or 783 ms. Each block consisted of 60 trials consisting of 38 congruent and 22 incongruent trials presented randomly. Six blocks of trials were completed for a total of 360 trials. Participants were instructed to respond as quickly and accurately as possible by pressing either a blue, green, or red button on a response pane (10 cm × 8 cm × 2 cm) that corresponds to the color word name regardless of the ink color the word was presented in. Correct trials included responses that matched the color word of the stimulus and occurred within an interval of 200 ms and 1,000 ms following stimulus onset. Response time and accuracy for congruent and incongruent trials were analyzed offline as two primary behavioral indices of Stroop task performance.

Event-Related Potential Recording and Analysis

Continuous EEG was recorded during Stroop task performance in a sound-attenuated chamber using an elastic cap with 32 Ag/AgCl electrodes (Neuroscan Quick-Cap, Neuroscan Inc., VA) placed according to the International 10/20 system. Horizontal and vertical electrooculograms (EOGs) were monitored by electrodes placed above and below the left eye as well as the outer canthi of both eyes, respectively. The montage was referenced to the average of the right and left mastoids, with the ground electrode placed on prefrontal electrode located on Fpz. Impedance of all electrodes was maintained below 5 kΩ. The EEG was amplified using Neuroscan Synamps2 amplifier (Scan 4.5, Neurosoft Labs, Inc.), with digitizing at a sample rate of 500 Hz, filtering between 0.1 to 100 Hz, and a notch filter at 60 Hz.

EEG data were segmented offline in epochs of 1,200 ms, with the 200-ms prestimulus period used for baseline correction. Only activities within ± 80 μV in correct trials were included for grand averaging. Amplitude and latency measures for ERP components in four a priori defined windows were identified: N1 (50 to 150 ms), N2 (200 to 300 ms), P3 (300 to 550 ms), and N450 (400 to 500 ms). While these ERP components were statistically analyzed based upon three specific electrode sites (i.e., Fz, Cz, Pz), additional topographic scalp distributions are illustrated based upon all 32 electrode sites with interpolation.

Experimental Procedures

Participants visited the laboratory on 3 separate days with at least 3 days' interval. On the first visit, each participant was given a brief introduction of the study, provided consent, and completed a series of questionnaires assessing demographics, safety to participate in exercise, and a fitness assessment through a health history survey and physical activity readiness questionnaire (PAR-Q), amount of daily physical activity measured by the International Physical Activity Questionnaire (IPAQ; Bauman et al., 2009; Liou, Jwo, Yao, Chiang, & Huang, 2008), and intelligence quotient (IQ) score assessed by Digit Span test of the Wechsler Adult Intelligence Scale–Third Edition (WAIS-III; Wechsler & Corporation, 1997). Eligible participants were equipped with a heart rate monitor (Polar RS400; Polar Electro, Finland) and asked to sit and relax quietly in a comfortable chair in a dimly lit room for 20 min to assess resting heart rate. One or two practice blocks of 20 Stroop trials were provided to participants until an accuracy rate of 90% was reached. Lastly, the YMCA cycle ergometry protocol was used to assess cardiorespiratory fitness.

The second and third visits included the experimental treatments (i.e., acute exercise and a sedentary reading control) and were performed at approximately the same time of day, in a

randomized and counterbalanced order. For the acute exercise bout, participants pedaled on the cycle ergometer for a 30-min session that consisted of a 5-min warm up, a 20-min steady-state exercise performed at 60–70% of heart rate reserve, and a 5-min cool down. The pedal cadence was maintained at a constant rate at 70 rpm, and the resistance began at 30 watts and gradually increased until a target heart rate zone was reached. For the reading control session, participants were asked to read physical activity-related books for approximately 30 min. Heart rate and ratings of perceived exertion (RPE; Borg, 1982) were recorded every 2 min throughout the experimental treatment sessions. After an approximately 15-min period to affix the electrode cap for EEG recording, blood samples were drawn and subsequently participants completed the Stroop task while continuous EEG was recorded for the assessment of ERPs. Following completion of the second treatment session, participants were compensated $15 and briefed on the purpose of the study.

Blood Serum Collection and BDNF Analysis

Blood samples were taken from an antecubital vein immediately prior to the Stroop task using blood collection tubes (CAT, BD Vacutainer). Blood samples were centrifuged at 3,000 rpm at 4°C for 15 min after the blood was clot at room temperature (Universal 320R centrifuge; Hettich, Tuttlingen, Germany). The serum was stored at −80°C until marker assays. The concentrations of serum BDNF were quantified using the enzyme-linked immunosorbent assay (ELISA) according to manufacturer's instruction (Chemi-Kine BDNF Sandwich ELISA Kit, Millipore, Billerica, MA). Briefly, the samples—eight serial dilutions of the BDNF standard—were added to the separate wells of the 96-well plate (Chemi-Kine BDNF ELISA plate). Following several incubations and washes, the streptavidin-enzyme conjugate was added to each plate. The reaction was stopped by adding 100 μL stop solution to each well. The absorbances were read using a microplate reader with 450 nm. The standard curve was established using dilution of BDNF samples with known concentrations. Finally, the concentration of the serum BDNF was determined from the regression equation calculated from the BDNF standard curve (range of detection from 7.8 to 1,000 pg/ml). The intra- and interassay coefficients of variation were within the ranges recommended for BDNF, at 5% and 10%, respectively.

Statistical Analysis

All analyses were conducted utilizing SPSS v. 18 (SPSS Inc., Chicago, IL). A 2 (Treatment: exercise vs. reading control) × 3 (Time: resting heart rate [HR], exercise HR, post-HR) repeated measures analysis of variance (ANOVA) was conducted to test the effectiveness of the exercise manipulation. A 2 (Treatment) × 2 (Stroop Task Condition: congruent vs. incongruent) repeated measures ANOVA was computed separately for response time and accuracy to determine the effect of acute exercise on Stroop task performance.

For the ERP measures, a 2 (Treatment) × 2 (Stroop Task Condition) × 3 (Site: Fz, Cz, Pz) repeated measures ANOVA was computed separately for amplitude and latency measures for each component (i.e., N1, N2, P3, N450). A paired samples t test was conducted to determine differences in posttreatment BDNF values between exercise and control sessions. Bivariate Pearson's correlation coeffcients were used to examine associations between BDNF and Stroop task performance following the exercise session.

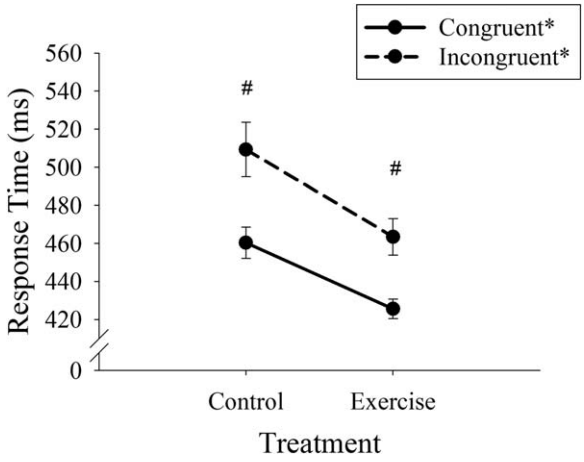

Figure 1. Response time as a function of treatment and Stroop task condition. *Significant difference between treatment. #Significant difference within Stroop task.

Greenhouse-Geisser epsilon corrections were used when necessary to meet the assumption of sphericity. Post hoc comparisons were conducted with familywise alpha levels set at 0.05 prior to Bonferroni correction.

Results

Exercise Treatment Manipulation

Two-way ANOVA revealed a significant main effect for condition, $F(1,29) = 290.39$, $p = .001$, partial $\eta^2 = .91$; time, $F(1,29) = 1263.47$, $p = .001$, partial $\eta^2 = .98$, and a significant interaction of Treatment × Time, $F(1,29) = 2117.84$, $p = .001$, partial $\eta^2 = .99$. Follow-up comparisons revealed that HR assessed during exercise was significantly highest (149.40 ± 6.39 bpm), followed by posttreatment HR (101.37 ± 6.64 bpm) and resting HR (65.93 ± 6.64 bpm), whereas no significant differences were observed in the control condition (treatment HR: 66.00 ± .6.41, posttreatment HR: 64.93 ± 5.22, and resting HR: 64.73 ± 7.04 bpm). In addition, within-treatment and posttreatment HR values were higher for the exercise than control condition. Average HR and RPE values assessed during exercise confirmed that it was performed at moderate intensity (63.54% HRR and RPE of 14.63).

Behavioral Data

Response time. Two-way ANOVAs revealed a significant main effect for treatment, $F(1,29) = 36.01$, $p = .001$, partial $\eta^2 = .55$, with exercise yielding shorter response time than control (444.49 ± 7.05 vs. 484.83 ± 11.04 ms) and for condition, $F(1,29) = 43.87$, $p = .001$, partial $\eta^2 = .60$, with incongruent trials yielding longer response time than congruent task condition (442.96 ± 6.16 vs. 486.36 ± 486.34 ms).

There was also a significant interaction of Treatment × Condition, $F(1,29) = 8.11$, $p = .008$, partial $\eta^2 = .22$. Follow-up analyses revealed that exercise yielded shorter response time for both congruent and incongruent trials (425.56 ± 27.75 and 463.42 ± 52.31 ms) than control (460.36 ± 45.21 and 509.30 ± 78.38 ms), while incongruent trial conditions yielded longer response time in both exercise and control than congruent trials (Figure 1).

Table 2. *ERP Amplitude and Latency Data (M ± SD) Across Treatment and Stroop Task Conditions*

	Control		Exercise	
Component	Congruent	Incongruent	Congruent	Incongruent
		Amplitude (μV)		
N1	−4.03 ± 0.41	−4.34 ± 0.42	−3.54 ± 0.33	−3.53 ± 0.37
N2	1.10 ± 0.78	1.28 ± 0.76	1.08 ± 0.69	1.70 ± 0.82
P3	13.61 ± 1.07	12.06 ± 1.03	14.60 ± 1.01	13.30 ± 1.14
N450	8.96 ± 1.01	7.93 ± 1.07	9.96 ± 0.87	8.68 ± 1.08
		Latency (ms)		
N1	116.12 ± 4.67	117.16 ± 4.84	117.04 ± 9.81	109.56 ± 4.38
N2	246.13 ± 5.39	250.66 ± 5.94	242.53 ± 4.69	242.52 ± 4.50
P3	427.44 ± 12.33	435.33 ± 11.80	457.72 ± 12.09	453.16 ± 13.15
N450	444.31 ± 6.59	452.30 ± 6.00	432.30 ± 5.31	438.16 ± 4.43

Accuracy. Two-way ANOVA revealed a significant main effect for condition, $F(1,29) = 84.89$, $p = .001$, partial $\eta^2 = .75$, with greater accuracy for congruent than incongruent trials (99.24 ± 0.11 vs. 98.59 ± 0.14%). No other significant main effects or interactions were revealed.

ERP Data

Table 2 presents ERP values for each treatment and Stroop task condition, and Table 3 provides a detailed statistical summary table for significant effects.

N1 component. For amplitude, the three-way ANOVA revealed a significant main effect for site, with Cz yielding larger amplitude (−4.57 ± 0.41 μV) than Fz and Pz (−3.38 ± 0.39 and −3.62 ± 0.36 μV). No significant main effects were observed for treatment or condition, $F(1,29) < 4.10$, $p > .05$. No significant two-way, $F(1,29) = 1.15$, $p = .29$; $F(2,58) < .81$, $p > .43$, or three-way interactions, $F(2,58) = .05$, $p = .81$, were observed.

In terms of N1 latency, no significant main effects, $F(1,29) < .57$, $p > .46$; $F(2,58) = 2.07$, $p = .14$, two-way interactions, $F(1,29) = .97$, $p = .33$; $F(2,58) < 1.17$, $p > .29$, or the three-way interaction, $F(2,58) = .23$, $p = .67$, were observed.

N2 component. For amplitude, the three-way ANOVA revealed significant main effects for condition, with the incongruent task condition yielding less negative amplitude than for congruent trials (1.49 ± 0.75 vs. 1.09 ± 0.70 μV), and for site, with lower N2 amplitude for Cz and Pz (1.65 ± 0.80 and 1.78 ± 0.79 μV) than Fz (0.45 ± 0.69 μV). No significant treatment main effects were found, $F(1,29) = .22$, $p > .64$. Further, no significant two-way, $F(1,29) = 1.65$, $p = .21$; $F(2,58) < 2.02$, $p > .24$, or three-way interaction, $F(2,58) = .02$, $p = .05$, were observed.

In terms of N2 latency, the three-way ANOVA revealed a significant main effect for site, with Fz yielding the longest latency (261.37 ± 4.47 ms), followed by Cz (248.19 ± 3.92 ms), which was significantly longer than Pz (226.83 ± 4.53 ms). No significant main effects were observed for treatment or condition, $F(1,29) < 1.66$, $p > .21$. No significant two-way, $F(1,29) = 1.34$, $p = .26$; $F(2,58) < 1.53$, $p > .23$, or three-way interactions, $F(2,58) = 2.75$, $p = .08$, were observed.

P3 component. For P3 amplitude, the three-way ANOVA revealed significant main effects for treatment, with larger amplitude following exercise relative to control (13.95 ± 1.06 vs. 12.84 ± 1.04 μV), and for condition, with congruent trials yielding larger amplitude than the incongruent task condition (14.11 ± 1.01 vs. 12.68 ± 1.06 μV). There was also a significant main effect for site, with larger amplitude at Cz and Pz (15.57 ± 1.30 and 14.89 ± 1.02 μV) than Fz (9.72 ± 0.91 μV).

Table 3. *Statistical Summary Table for Three-Way ANOVA of Treatment, Stroop Task Condition, and Site on ERP Amplitude and Latency*

Measure	Effect	*df*	*F*	*p*	partial η^2
N1 amplitude	Site (Cz > Fz and Pz)	2, 58	6.43	.014	.21
N2 amplitude	Condition (Incongruent > Congruent)	1, 29	4.24	.050	.15
	Site (Cz and Pz > Fz)	2, 58	5.74	.011	.19
N2 latency	Site (Fz > Cz > Pz)	2, 58	52.85	.001	.65
P3 amplitude	Treatment (Exercise > Control)	1, 29	6.93	.015	.22
	Condition (Congruent > Incongruent)	1, 29	34.25	.001	.59
	Site (Cz and Pz > Fz)	2, 58	55.15	.001	.70
	Treatment × Site	2, 58	12.75	.001	.35
	Condition × Site	2, 58	4.13	.039	.15
P3 latency	Site (Fz and Cz > Pz)	2, 58	45.24	.001	.61
N450 amplitude	Condition (Incongruent > Congruent)	1, 29	14.00	.001	.37
	Site (Fz > Cz and Pz)	2, 58	53.71	.001	.69
	Treatment × Site	2, 58	10.18	.001	.30
	Condition × Site	2, 58	4.13	.036	.15
N450 latency	Treatment (Control > Exercise)	1, 29	4.92	.035	.15
	Condition (Incongruent > Congruent)	1, 29	4.19	.050	.13
	Site (Pz > Fz and Cz)	2, 58	8.54	.001	.23

Note. Only significant effects at $p < .05$ are presented.

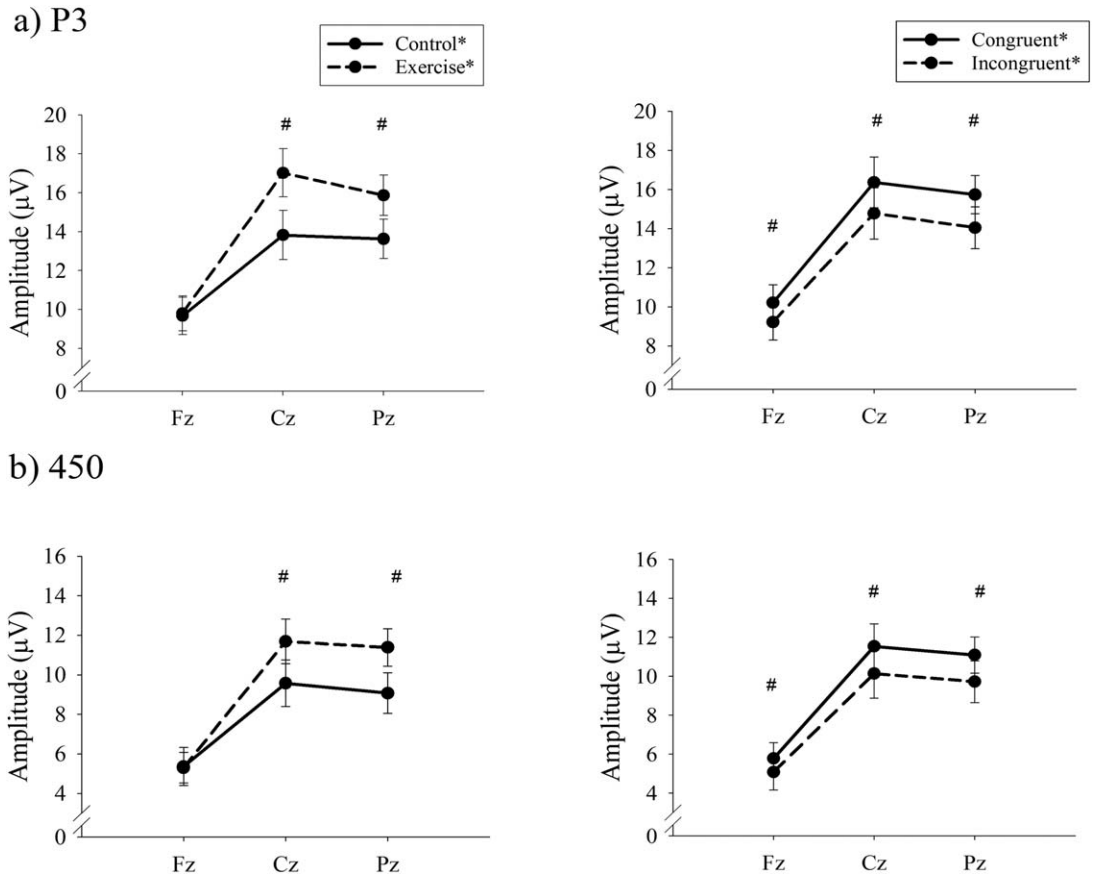

Figure 2. Depiction of the two-way interaction between treatment and electrode site as well as between Stroop task condition and electrode site for (a) P3 amplitude, and (b) N450 amplitude.

There was also significant interaction between Treatment × Site as well as Condition × Site. Follow-up analyses revealed that exercise yielded a larger P3 amplitude at Cz and Pz (16.81 ± 1.37 and 15.65 ± 1.09, $p < .001$) than control (14.34 ± 1.29 and 14.14 ± 0.99, $p < .001$), but this difference was not significant at Fz (9.40 ± 0.94 vs. 10.04 ± 1.00). Greater P3 amplitude was observed at Cz and Pz than Fz in both exercise and control (Figure 2a). Additionally, follow-up analysis revealed that larger P3 amplitude was observed for congruent task trials at Fz, Cz, and Pz (10.21 ± 0.92, 16.36 ± 1.30, and 15.74 ± 0.97, $p < .001$) relative to the incongruent task condition (9.23 ± 0.93, 14.78 ± 1.32, 14.05 ± 1.07, $p < .001$), although larger P3 amplitude was found for Cz and Pz than Fz in both congruent and incongruent conditions (Figure 2a). No significant two-way interaction between Treatment × Condition, $F(1,29) = .48$, $p = .50$, or a significant three-way interaction, $F(2,58) = .73$, $p = .47$, was observed.

In terms of P3 latency, the three-way ANOVA revealed a significant main effect for site, with Fz and Cz yielding longer latency (464.84 ± 10.70 and 462.26 ± 10.60 ms) than Pz (403.14 ± 9.44 ms). No significant main effects were observed for treatment or condition, $F(1,29) < 2.92$, $p > .10$. Moreover, no significant two-way, $F(1,29) = 1.48$, $p = .23$; $F(2,58) < 2.20$, $p > .03$, or three-way interactions, $F(2,58) = 1.52$, $p = .23$, were observed.

N450 component. For amplitude, the three-way ANOVA revealed significant main effects for condition, with more negative amplitude for incongruent than congruent task conditions (8.31 ± 1.04 vs. 9.46 ± 0.90 μV), and for site, with more negative amplitude for Fz (5.42 ± 0.85 μV) than Cz and Pz (10.83 ± 1.19 and 10.40 ± 0.98 μV). No significant treatment main effect was found, $F(1,29) = 3.45$, $p = .08$.

Follow-up analysis for significant interaction between Treatment × Site revealed that exercise resulted in less negative N450 amplitude at Cz and Pz (11.66 ± 1.23 and 11.18 ± 1.01, $p < .001$) than for these sites following control (10.01 ± 1.22 and 9.62 ± 1.01, $p < .001$), but no significant differences were found at Fz (5.13 ± 0.82 vs. 5.72 ± 1.01). However, more negative N450 amplitude was found at Fz than at Cz and Pz in both exercise and control treatment conditions (Figure 2b). Follow-up analysis for the significant interaction between Condition × Site revealed that incongruent trials resulted in more negative N450 amplitude at all sites (5.07 ± 0.92, 10.13 ± 1.26, and 9.71 ± 1.08 for Fz, Cz, and Pz, $p < .001$) than amplitudes at these sites for congruent trials (5.78 ± 0.91, 11.53 ± 1.15, 11.08 ± 0.92, $p < .001$). More negative N450 amplitude was found at Fz than Cz and Pz in both congruent and incongruent task conditions (Figure 2b). No significant two-way interaction between Treatment × Condition, $F(1,29) = .33$, $p = .57$, or a significant three-way interaction, $F(2,58) = 1.77$, $p = .19$, was observed.

For N450 latency, the three-way ANOVA revealed a significant main effect for treatment, with shorter latency following exercise compared with control (435.23 ± 4.50 vs. 448.31 ± 5.91 ms). There was also a significant main effect for condition, with incongruent trials yielding longer latency than congruent task trials (445.23 ± 4.13 vs. 438.31 ± 5.14 ms), and for site, with longer latency observed at the Pz (455.62 ± 6.17 ms) relative to Fz (436.44 ± 4.92) and Cz (433.24 ± 5.34 ms). No significant two-

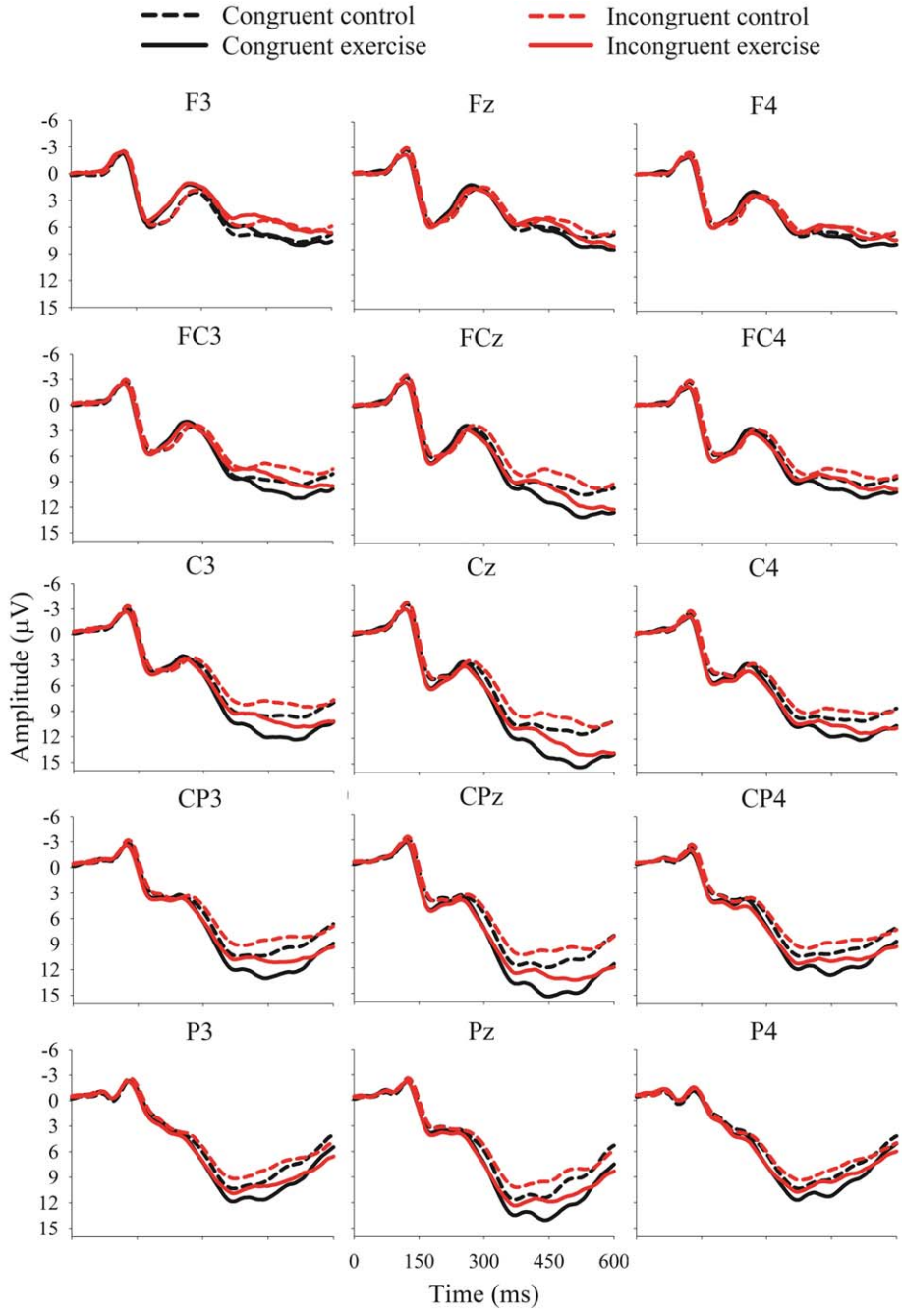

Figure 3. Grand-averaged ERP waveforms as a function of treatment and Stroop task conditions.

way, $F(1,29) = .21$ $p = .65$; $F(2,58) < 2.01$, $p > .15$, or three-way interactions, $F(2,58) = 2.05$, $p = .14$, were observed.

Figure 3 illustrates the grand-averaged ERP waveform for each treatment and Stroop task conditions, and Figure 4 illustrates the topographic scalp distribution separated into 10 different time epochs from 50 to 550 ms following the stimulus onset to depict scalp topographies during the ERP components of interest.

BDNF

A paired samples *t* test revealed that there was no significant difference in serum BDNF levels between control and exercise treatment conditions (366.98 ± 95.98 vs. 315.82 ± 142.03 pg/ml, $t(29) = 1.55$, $p = .13$). Additional statistics for BDNF levels following control and exercise sessions were as follows, respectively: maximum (556.62 pg/ml vs. 554.01 pg/ml), minimum (197.89 pg/ml vs. 81.71 pg/ml), kurtosis (0.12 vs. 0.11), and skewness (−.43 vs. −1.23).

Although serum BDNF level was negatively correlated with response times for both congruent and incongruent Stroop task conditions following exercise, these correlations were nonsignificant ($r = -.31$ to $-.33$, $p > .08$).

Discussion

The purpose of this study was to determine whether acute moderate intensity exercise results in a general or selective improvement in

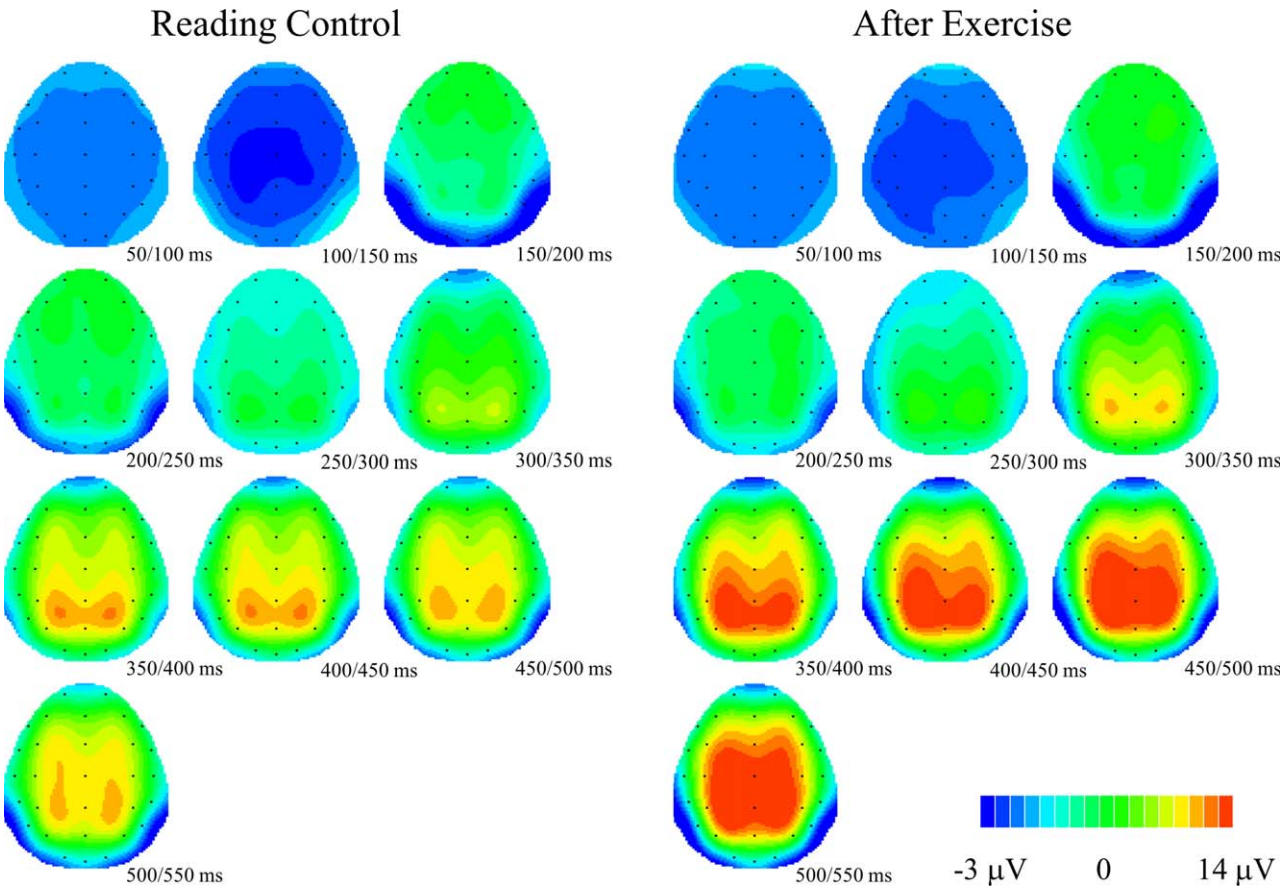

Figure 4. Scalp topographic maps presented in 10 relevant time windows from 50 to 550 ms following Stroop task stimulus onset. Larger P3 and reduced N450 amplitudes elicited by the Stroop task were observed following acute moderate intensity exercise.

cognitive function, and to investigate potential neurobiological mechanisms by examining several stimulus-locked ERP components and serum BDNF levels as potential mediators of the effects of acute exercise on cognition. The primary findings revealed that acute moderate intensity exercise facilitates performance on both congruent and incongruent Stroop task conditions, and the magnitude of effect across task conditions was similar. That is, the general improvement hypothesis was supported with acute exercise having a positive effect on the different task conditions of the Stroop task rather than selective effects for task conditions requiring executive function (i.e., only incongruent trials). Additionally, the ERP findings demonstrated that acute exercise influences P3 and N450 components, but does not influence earlier N1 and N2 components. Specifically, acute exercise increased P3 amplitude, decreased N450 amplitude, and resulted in shorter N450 latency compared to the sedentary reading control, regardless of Stroop task conditions. Lastly, acute exercise did not have a meaningful influence on serum BDNF levels, and correlations between BDNF and Stroop task performance were nonsignificant.

Task Performance

The present finding of shorter response time and increased accuracy for the Stroop congruent task condition compared to incongruent trials reflects the typical "Stroop effect" and suggests a greater amount of inhibitory cognitive control needed to resolve prepotent but incorrect responses (Chang, Tsai et al., 2014). This finding also supports the Stroop task design we employed in this study. Consistent with previous studies (Chang, Chi et al., 2014; Chang, Chu, Wang, Wang et al., 2015; Lichtman & Poser, 1983), acute moderate intensity exercise resulted in shorter response times for both Stroop task conditions, providing additional support for the previously observed general improvement in both basic information processing and the more demanding inhibition aspect of executive function. The lack of significant differences in accuracy also demonstrates that the facilitation in cognitive performance was not the result of a speed-accuracy trade-off. Interestingly, we found that acute exercise-induced increase in cognitive performance was similar for Stroop congruent and incongruent task conditions, further supporting a general improvement hypothesis of acute exercise. Exercise-induced arousal might be a possible underlying mechanism of the beneficial Stroop effect associated with acute exercise. Indeed, arousal has been long recognized as a potential hypothesis; that is, acute aerobic exercise may induce an optimal state of physiological arousal that is associated with facilitated cognitive functioning (Brisswalter, Collardeau, & Rene, 2002; Cooper, 1973; Hillman et al., 2003; Kamijo et al., 2009). Accordingly, the present findings suggest that acute moderate intensity aerobic exercise for 20 to 30 min that is currently recommended by the American College of Sports Medicine (2013) results in a generalized enhancement in multiple cognitive functions.

P3 Component

The P3 is a longer latency endogenous component that reflects increased neural inhibitory processes that occur when stimulus and

task demands engage fundamental cognitive mechanisms (Fabiani, Gratton, & Federmeier, 2009; Polich, 2012). The P3 elicited by the Stroop task is also thought to represent cognitive processes related to semantic conflict. The smaller P3 amplitude observed for Stroop incongruent compared to congruent trials across midline electrode sites and particularly in the central-parietal region replicates findings from previous studies (Eppinger, Kray, Mecklinger, & John, 2007; Ila & Polich, 1999; Potter, Jory, Bassett, Barrett, & Mychalkiw, 2002) and may reflect the experience of greater semantic conflict and task difficulty during performance of Stroop incongruent trials.

Although acute moderate intensity exercise did not influence P3 latency, an enhanced P3 amplitude in the central-parietal region was observed for Stroop incongruent trials following acute exercise versus control, replicating previous studies that have incorporated inhibition-related cognitive tasks (e.g., Eriksen flanker task; Drollette et al., 2014; Hillman et al., 2003, 2009). These results imply that acute exercise improves behavioral performance on more demanding executive function tasks via the recruitment of more neural or attentional resource allocation. The findings also suggest that the neurophysiological mechanisms related to Eriksen flanker and go/no-go tasks in previous acute exercise studies may also extend to performance on the Stroop task. The novel finding of this study, however, was that a similar enhancement in P3 amplitude was observed for the Stroop congruent trial condition, suggesting that acute exercise may also engage more attentional resource allocation processes in tasks more closely related to basic information processing. Notably, given that P3 is sensitive to physiological arousal and that an inverted-U relation between exercise intensity and P3 amplitude has been demonstrated (Kamijo et al., 2004), the current findings further support a physiological arousal hypothesis of acute exercise effects on generalized cognitive performance. Collectively, the evidence suggests that acute moderate intensity exercise enhances attentional resource allocation, and increased exercise-related physiological arousal is associated with P3 amplitude, regardless of Stroop task types.

Other ERP Components

One novel contribution of this study is the examination of the temporal nature of cognition following acute moderate intensity exercise by examining several stimulus-locked ERP components elicited by the Stroop task, and their patterns of change following acute exercise. For instance, while N450 is similarly recognized as a long latency endogenous component (Greenham, Stelmack, & Campbell, 2000), N450 represents distinct cognitive processes from P3. The N450 is a frontocentral negativity sensitive to conflict monitoring processes, such that larger N450 amplitude for incongruent relative to congruent Stroop trials reflects monitoring processes involved in conflict detection (Badzakova-Trajkov, Barnett, Waldie, & Kirk, 2009; Larson, Clayson, & Clawson, 2014), and our study replicates the finding of larger N450 amplitude for incongruent Stroop trials. The link between N450 and conflict processes, particularly conflict detection, was further supported by studies using source localization analyses, suggesting a neural generator originating in the anterior cingulate cortex (ACC), a region consistently associated with conflict detection processes (Coderre, Conklin, & van Heuven, 2011; Szűcs & Soltész, 2012). Regarding the effects of acute exercise, we observed a reduced (i.e., more positive) N450 amplitude in the centroparietal region and reduced N450 latency across all midline electrode sites. Our N450 and behavioral results postexercise corroborate the findings from Li et al. (2014), who demonstrated using fMRI a deactivation in ACC following cessation of an acute bout of exercise. Taken together, our findings suggest that the facilitation of Stroop task performance following acute moderate intensity exercise may result from enhanced conflict detection and monitoring processes.

While N1 is sensitive to a discrimination process during selective attention (Vogel & Luck, 2000) and stimulus feature detection (Zhu, Zhang, Wu, Luo, & Luo, 2010), they share similar characteristics and in general are related to perceptual and sensory processing. Our findings that acute moderate intensity exercise failed to impact N1 suggests a limited influence on selective attention and stimulus detection in early stages of information processing, at least in young adults. Intriguingly, this finding further extends previous research demonstrating little effects of acute exercise on tasks involving basic/discriminatory information processes (e.g., auditory oddball task), and no association between acute exercise and early ERP components (e.g., N1, P2; Magnie et al., 2000; Nakamura, Nishimoto, Akamatu, Takahashi, & Maruyama, 1999). These findings imply a minimal influence of acute moderate intensity exercise on early ERP components related to a variety of early-stage information processes. Alternatively, the cognitive processes reflected by these early ERP components may be relatively intact and stable in young adults and not influenced by biological responses from acute exercise.

N2, another commonly studied stimulus-locked component, is associated with the detection of response conflict, the mismatch of a stimulus with a mental template, or the upregulation of cognitive control during early stages of response inhibition (Tillman & Wiens, 2011; Van Veen & Carter, 2002). Our findings of smaller amplitude for incongruent task trials conflicts with previous findings (Larson et al., 2014); however, N2 may not be elicited by the Stroop task as much as other tasks that involve inhibitory cognitive control (West, Jakubek, Wymbs, Perry, & Moore, 2005). Whether acute exercise influences N2 elicited by tasks of inhibition remains ambiguous, with some studies demonstrating no effect (Stroth et al., 2009; Themanson & Hillman, 2006) while others have shown a reduced postexercise N2 amplitude (Drollette et al., 2014). Our finding is in line with previous studies showing no effect of acute exercise on N2, and extends N2 findings from a modified flanker (Themanson & Hillman, 2006) and go/no-go (Stroth et al., 2009) tasks to the Stroop task, suggesting a generalized lack of influence of acute exercise on N2 component processes related to inhibition. It should be noted that Drollette et al. (2014) only found a smaller N2 amplitude induced by acute exercise for children with lower inhibitory capacity but not among those with higher capacity, suggesting a modulatory role of age and individual difference factors on the acute exercise and N2 relationship. Collectively, our findings suggest that acute moderate intensity exercise does not influence early information processes through the stages of detecting and resolving conflict in young adults, although given that this is the first study to examine the temporal dynamics of cognition following acute exercise, more studies are warranted to confirm our findings.

Serum BDNF Level

Novel to our findings is that acute moderate intensity exercise did not increase serum BDNF levels and postexercise levels of BDNF did not correlate with Stroop task performance, suggesting a limited mediational role of BDNF on the acute exercise and cognition relationship. Although the finding is inconsistent with rodent studies, it should be noted that the role of BDNF in mediating the acute

exercise effects on cognition remains debatable. For example, a meta-analysis indicated that only 69% of studies with humans demonstrated a meaningful increase in BDNF after acute exercise (Knaepen, Goekint, Heyman, & Meeusen, 2010) and elevated serum BDNF has been shown to increase after vigorous intensity exercise (i.e., exercise to exhaustion or 10% above ventilatory threshold, VT), but not at moderate (e.g., 70% VO_2max; Ströhle et al., 2010) or lower intensities (e.g., 20% below VT; Ferris et al., 2007; Rojas Vega et al., 2006). Thus, postexercise BDNF levels may be exercise intensity dependent. Furthermore, whether BDNF meditates the relationship between acute exercise and cognition has generally only been indirectly examined, rather than tested using mediational analyses. For example, the cognitive-enhancing role of BDNF suggested by Griffin et al. (2011) is based upon elevations following high intensity exercise. Our finding is in accord with another recent study demonstrating nonsignificant correlations between BDNF, cognitive performance, and ERP measures following acute moderate intensity exercise (Tsai et al., 2014). Interestingly, previous studies have suggested that there is a possible inverted U-shaped trend between exercise intensity and cognition, with moderate intensity exercise resulting in optimal cognitive benefits compared to lower and higher intensities of exercise (Arent, Landers, Matt, & Etnier, 2005; Chang & Etnier, 2009; McMorris & Hale, 2012). If that is the case, the transient elevation of BDNF following high intensity, but not moderate intensity, exercise seems questionable as a plausible mediator between acute exercise and cognition. Although the role of BDNF in the acute exercise-cognition relation remains plausible, there is currently little evidence to support serum BDNF levels as a viable neurobiological mechanism of the cognitive enhancements observed following acute moderate intensity exercise.

Limitations and Future Directions

There are several limitations to the present study. First, unlike animal studies that are able to assess central BDNF levels, at present studies with humans are limited to the assessment of peripheral BDNF (e.g., serum) that may only provide an indirect association relative to central expression levels. Moreover, the upregulation of serum BDNF following exercise may be related to BDNF stored in platelets (Lommatzsch et al., 2005) or induced by muscle contraction involved in gross bodily movement (Matthews et al., 2009). However, BDNF can reciprocally cross the blood-brain barrier (Karege, Schwald, & Cisse, 2002), and it has been suggested that up to 70% to 80% of elevated peripheral levels of BDNF following acute exercise may be contributed by the brain (Rasmussen et al., 2009), implying a link between central and peripheral BDNF expression. A second limitation is the relatively small sample size, which is particularly relevant for the BDNF findings and interpretation. Although a nonsignificant correlation between BDNF level and response time was observed, the p value was not far from significance ($p < .1$), implying that a relationship may be observed when employing larger sample sizes. Further study is recommended to test this possibility. Lastly, we used a healthy young adult sample, and several individual difference factors may impact the findings. Future studies may benefit by examining individual differences to determine for whom and under what situations acute exercise benefits cognition. Aerobic fitness and gender are two candidate individual difference variables. Recent studies have demonstrated that individuals with higher cardiorespiratory fitness demonstrate larger P3 amplitudes following acute exercise relative to their lower fit counterparts, suggesting a moderating role of aerobic fitness (Tsai et al., 2014); however, another recent study showed a curvilinear relationship between fitness level and an acute exercise-induced benefit in Stroop task performance, with moderately fit individuals showing the largest acute exercise benefit compared to lower and higher fit groups (Chang, Chi et al., 2014). Collectively, these findings suggest an interesting moderating influence of fitness on the acute cognitive effects of exercise, and this influence and the underlying mechanisms require further investigation. Another proposed consideration is the issue of task difficulty and cognitive processes engaged by the Stroop task. Although the incongruent task condition engages greater cognitive demands than congruent condition, the negative priming condition is more complex than the color-word interference task condition. In the negative priming condition, the ink color of each word is the same as the color word stimulus from the previous trial. For example, if the color word on the previous item was *blue*, the ink color of the current item would be blue. This condition requires the same selective attention as the color-word interference condition but places an extra burden on inhibitory processes, as the correct response to the new stimulus is the color that the person has just inhibited in the previous trial. It is worth examining this additional task condition to advance our understanding of the relationship between acute exercise and level of cognitive executive demands.

Conclusion

Our findings indicate that acute moderate intensity exercise enhances multiple cognitive functions as assessed by the Stroop task, and the results support a generalized versus specific improvement hypothesis of acute exercise. This is the first study to examine the temporal dynamics of cognitive processing and plausible underlying neurobiological mechanisms using both stimulus-locked ERP components as well as circulating serum BDNF levels. Acute exercise was associated with enhanced attentional resource allocation and conflict detection processes as reflected by P3 and N450 components, but did not influence earlier sensory processes reflected by N1 and N2 ERP components. Thus, in young adults, acute moderate intensity exercise influences later stages of the information processing stream. Our findings also suggest that serum levels of BDNF following acute moderate intensity exercise do not influence inhibition as assessed through Stroop task performance. Future research addressing exercise intensity, central versus peripheral levels of BDNF, executive function domain, and important individual difference variables is warranted to further our mechanistic understanding of the acute exercise and cognitive function relationship.

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