Neurophysiological and behavioral correlates of cognitive control during low and moderate intensity exercise

Ryan L. Olson [a,b], Yu-Kai Chang [c], Christopher J. Brush [a], Andrea N. Kwok [a],
Valentina X. Gordon [a], Brandon L. Alderman [a,*]

[a] Department of Exercise Science and Sport Studies, Rutgers University, New Brunswick, NJ, USA
[b] Department of Nutritional Sciences, Rutgers University, New Brunswick, NJ, USA
[c] Graduate Institute of Athletics and Coaching Science, National Taiwan Sport University, Taoyuan County, Taiwan, Republic of China

ABSTRACT

The aim of this study was to examine neurophysiological and behavioral correlates of cognitive control elicited by a modified flanker task while exercising at low and moderate intensities. A secondary aim was to examine cognitive control processes at several time points during an acute bout of exercise to determine whether cognition is selectively influenced by the duration of exercise. Twenty-seven healthy participants completed a modified version of the Eriksen flanker task while exercising on a cycle ergometer at 40% and 60% VO_2 peak and during a no-exercise seated control across three separate days. During task performance, continuous EEG was collected to assess neurocognitive function using the N2 and P3 event-related brain potentials (ERPs). Neurocognitive performance was assessed at 5, 15, and 25 min time points during steady-state exercise. Regardless of intensity, behavioral findings revealed impaired accuracy during both exercise conditions for the flanker task trials that require greater cognitive control. However, faster reaction times were found during moderate-intensity exercise. Neuroelectric measures revealed increased N2 and P3 amplitudes during both exercise conditions relative to rest. Together, these findings suggest divergent effects of exercise on behavioral performance measures accompanied by an upregulation of cognitive control during aerobic exercise. These impairments are discussed in terms of dual-task paradigms and the transient hypofrontality theory.

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It is now well accepted that acute exercise has a positive effect on cognitive functioning when cognition is assessed post-exercise (Brisswalter et al., 2002; Chang et al., 2012; Lambourne and Tomporowski, 2010; McMorris et al., 2011; Tomporowski, 2003). Indeed, meta-analytic reviews have reported small but significant effects of acute exercise on cognitive performance (Chang et al., 2012; Lambourne and Tomporowski, 2010). However, a majority of the studies in this area have assessed cognition following exercise to control for exercise-induced physiological arousal, with relatively fewer studies focusing on cognitive performance during exercise. This is important since a critical methodological factor that might explain the inconsistent findings in the literature relates to the time that cognition is assessed relative to exercise. Additionally, the mechanisms involved and moderators of the relationship are still widely unknown. Understanding important moderators as well as cognitive and brain processes during exercise may help better understand the benefits of exercise participation on cognitive function and brain health.

Previous studies have reported that acute aerobic exercise exerts a small beneficial effect on cognitive performance when assessed during exercise (Chang et al., 2012; McMorris et al., 2011); however, not all studies are in agreement (Dietrich and Sparling, 2004; Pontifex and Hillman, 2007). Several key moderating variables that may impact this relationship have been identified in recent meta-analyses (Chang et al., 2012; Lambourne and Tomporowski, 2010). These moderators (e.g., exercise duration and intensity) may help both explain the discrepant findings and advance our understanding of the complex relationship between acute exercise and cognition. Both meta-analyses suggest that exercise has a selective impact on cognition depending upon when cognition is assessed relative to exercise. Specifically, Lambourne and Tomporowski (2010) reported that cognitive task performance was impaired during exercise; however, these impairments were only observed during the first 20 min. Beyond the initial 20 min of exercise, they observed enhanced performance on cognitive tasks that involved rapid decisions and automatized behaviors. Chang et al. (2012) found no significant differences between effect size measures derived from three different acute exercise paradigms: those that assessed cognitive performance during exercise, immediately following exercise, and after a longer delay (>1 min following exercise). However, based on those studies that assessed cognition during exercise, the

* Corresponding author at: Department of Exercise Science and Sport Studies, Rutgers University, 70 Lipman Drive, New Brunswick, NJ 08901, USA.
E-mail address: alderman@rutgers.edu (B.L. Alderman).

largest effect sizes were observed when cognitive tasks were administered 20 min or longer following exercise onset. These meta-analytic findings are consistent with the conclusions drawn by Brisswalter et al. (2002) who reported consistent positive effects of acute exercise lasting more than 20 min on cognitive performance. Although these reviews are suggestive of the notion that exercise lasting longer than 20 min in duration may facilitate or impair cognition depending on when cognition is assessed, this idea has received very little scientific attention. This research has important theoretical implications and may help elucidate the optimal dose of exercise to prescribe to enhance cognitive performance.

A second key moderator that has been less well studied and may help better characterize the effects of exercise on cognitive performance is exercise intensity. Examining the dose–response relationship between exercise intensity and cognition may help elucidate the psychobiological processes induced by different exercise intensities, and how these processes help explain the effects of exercise on select cognitive processes. Even fewer studies have examined the dose–response effects of exercise on cognitive control (Wang et al., 2013). Cognitive control is a construct from contemporary cognitive neuroscience that refers to top-down, goal directed operations that assist with the selection, scheduling, maintenance, and coordination of processes that underlie perception, memory, and action (Norman and Shallice, 1986; Rogers and Monsell, 1995). Utilizing the Karvonen or heart rate reserve (HRR) method to prescribe exercise intensity, which reflects the difference between maximal and resting heart rate (HR), Wang et al. (2013) randomly assigned 80 typical college-aged adults to low (30% HRR), moderate (50% HRR), and high (80% HRR) intensity exercise conditions or to a no-exercise seated control and administered a cognitive control task (i.e., the Wisconsin Card Sorting Test, WCST) simultaneous with the interventions. They reported impaired WCST performance during high intensity exercise relative to the other three conditions, whereas similar performances were found for the low and moderate intensity exercise conditions. Alternatively, Schmit et al. (2015) examined concurrent changes in cognitive control and cerebral oxygenation (Cox) in the prefrontal region during strenuous exercise performed to exhaustion. Although Cox values were found to decline linearly until exercise exhaustion, there was no systematic impairment of cognitive control during the intense bout of exercise. It remains to be determined whether these findings related to prefrontal activation would persist beyond the first 20 min of exercise and whether there is a dose–response relationship between exercise intensity and cognitive performance. Moreover, it is possible that the intensity of exercise interacts with exercise duration to impact cognition. There is a need to examine the dose–response relationship between exercise intensity and in-task cognitive performance and whether this relationship changes within and beyond the initial 20 min of exercise.

Traditionally, studies in this area have used behavioral performance measures such as response accuracy and reaction time to gauge cognition both during and following exercise. Although these measures have undoubtedly enhanced our understanding of the effects of exercise on cognition, the high temporal sensitivity of event-related brain potentials (ERPs) may allow for greater understanding of covert aspects of cognitive processing, including processes that occur between stimulus presentation and response selection and action. ERPs reflect patterns of voltage fluctuations in the ongoing electroencephalogram (EEG) that are time-locked to a specific event, such as the onset of a stimulus or the execution of a manual response (Kappenman and Luck, 2011). Two components that have been leveraged to better understand the complex nature of cognitive processing during exercise are the N2 and P3 components of the ERP. The N2 component is a negative deflection in the stimulus-locked ERP with a frontocentral scalp distribution that peaks approximately 200–350 ms after stimulus presentation (Botvinick et al., 2004; Clawson et al., 2013; Folstein and Van Petten, 2008), and has been repeatedly associated with the detection of response conflict, the mismatch of a stimulus with a mental template,

and/or increased cognitive control during response inhibition (Folstein and Van Petten, 2008; Larson et al., 2014; Van Veen and Carter, 2002). The P3 component is a positive deflection in the stimulus-locked ERP observed at central and parietal scalp sites approximately 250–500 ms after stimulus onset, and the component amplitude is believed to reflect the allocation of attentional resources during stimulus engagement (Donchin and Coles, 1988; Polich, 2007). The N2 and P3 components have been instrumental in advancing our understanding of cognitive and brain function both during and following acute exercise (Chang et al., 2015; Drollette et al., 2014; Pontifex and Hillman, 2007).

The few studies that have used ERPs to investigate cognition during exercise have reported equivocal results. Pontifex and Hillman (2007) assessed cognition through ERPs while participants cycled at a steady-state corresponding to 60% of maximal HR for approximately 6.5 min. They found global reductions in N2 and increases in P3 amplitude across frontal and lateral electrode sites along with longer N2 and P3 latencies, suggesting cortical inefficiency during stimulus engagement and delays in stimulus evaluation and classification speed. In terms of behavioral performance, exercise resulted in impaired accuracy for the incongruent trials of the flanker task, reflecting the task condition requiring greater amounts of cognitive control. More recently, Vogt et al. (2015) had participants perform mental arithmetic during a moderate intensity bout of self-paced cycling within a virtual environment while EEG was recorded. Although they found an increase in N2 and P3 amplitudes elicited by the virtual environment, these ERPs were not influenced by exercise. Moreover, no significant differences were observed in behavioral performance (response accuracy and reaction time) measures between exercise and control conditions. However, it was conceded that performing a cognitive task while cycling in a virtual environment may have created an increase in cognitive load, which might have obscured any effects of exercise per se on cognition. Taken together, these findings suggest either no changes or perhaps deficits in cognition during exercise, particularly for cognitive control tasks. However, in line with findings from meta-analyses (Chang et al., 2012; Lambourne and Tomporowski, 2010), the influence of exercise lasting longer than 20 min on behavioral and neurophysiological correlates of cognitive control (i.e., N2 and P3 components) warrants investigation.

To date, no study has investigated the dose–response effects of aerobic exercise intensity on cognitive control by recording both behavioral and neuroelectric measures. Moreover, there is a need to investigate the effect of duration on cognitive control processes during the initial 20 min of exercise and thereafter to determine whether there is a delayed benefit of aerobic exercise on cognitive processing. Therefore, the purpose of this study was to assess neurophysiological and behavioral performance measures of cognitive control during a 31 min bout of aerobic exercise performed at 40% and 60% of peak aerobic fitness (VO$_2$ peak) and to examine the time course effects on cognition by assessing neurocognitive performance at 5, 15, and 25 min time points during steady-state exercise. We hypothesized that the ERP measures would exhibit greater sensitivity to the effects of acute exercise on cognitive performance than the behavioral performance measures (see Pontifex and Hillman, 2007, 2008). Based on existing dose–response evidence during exercise, it was hypothesized that both the 40% and 60% exercise conditions would impair response accuracy and N2 and P3 ERP measures compared with rest. Lastly, based on current meta-analytic findings (Chang et al., 2012; Lambourne and Tomporowski, 2010), we expected cognitive benefits for both exercise conditions assessed at 25-min relative to earlier time points following exercise onset.

Methods

Participants

Undergraduate students were recruited from Rutgers University and the surrounding community through the use of flyers and

advertisements. Participants were required to meet the following inclusion criteria: between the ages of 18 and 35, native English speakers, right handed, and reporting normal or corrected-to-normal vision. Participants were excluded if they had a presence or history of cardiovascular, neurological, or musculoskeletal problems that would impact exercise ability, past or present history of psychiatric or neurological disorders (including attention deficit hyperactivity disorder (ADHD), clinical depression or anxiety, or any head injury with loss of consciousness), or were taking medication. Thirty participants who met the inclusion criteria were enrolled in the study. Three participants were eliminated because more than 50% of their trials contained artifacts after artifact detection (Leonard et al., 2012), yielding a final sample of 27 participants. Prior to participation, participants provided written informed consent that was approved by the Institutional Review Board at Rutgers, The State University of New Jersey. Participant demographic and fitness data are provided in Table 1.

Procedures

Participants visited the laboratory on four separate days. Each testing day is referred to as a session. During the first session, participants were given a general description of the study, provided consent, and completed a health history and demographics questionnaire and a physical activity readiness questionnaire (PAR-Q) to ensure safety for the cardiorespiratory fitness assessment and subsequent testing sessions. Participants were asked to avoid exercise for 48 h and caffeine or other stimulants for 3–4 h prior to baseline testing. This was verified upon arrival to the laboratory. Participants were accompanied to an exercise testing room and fitted with a Polar S810 heart rate monitor and had their height and weight measured with a stadiometer and digital scale (Health-O-Meter model 499KL, IL). A maximal cardiorespiratory fitness (VO$_2$ peak) test was then administered while participants cycled on a Lode Corival cycle ergometer. Upon completion of the fitness assessment, participants were scheduled for their remaining three testing sessions, which took place at approximately the same time of day as their initial visit.

For the three experimental sessions, participants completed a no-exercise seated control, a low intensity (40% VO$_2$ peak), and a moderate intensity (60% VO$_2$ peak) exercise bout in counterbalanced order, performed 2–3 days apart to allow adequate recovery from the previous session. The no-exercise seated control involved participants sitting at rest on the cycle ergometer while the exercise conditions consisted of cycling for 31 min at a HR intensity range corresponding to approximately 40% or 60% VO$_2$ peak as determined from the baseline fitness test (i.e., HR achieved at these intensities during maximal VO$_2$). HR ranges were determined prior to participants entering the lab and were monitored throughout each session. In order to standardize additional variables related to work output, data from the maximal fitness test were used to set the initial resistance (Watts) for the exercise sessions. At the start of each experimental session, participants were fitted with a Polar HR monitor and the bike was re-adjusted to the settings established during the baseline fitness test. A 64-channel Geodesic Sensor Net (Electrical Geodesic, Inc, OR) was applied to record continuous

electroencephalographic (EEG) activity. In order to reduce head and upper body movement artifact during neuroelectric recording (Pontifex and Hillman, 2008), participants were asked to maintain a posture where upper body movement was minimized without restricting lower body movement. To further reduce movement artifact and noise, the electrode wire harness was suspended and elevated away from the neck and back region. Participants were verbally read and provided with on-screen instructions for the flanker task. During the last 2 min of a 5 min low intensity warm-up on the bicycle ergometer (women, 70 W; men, 80 W), researchers adjusted the resistance until HR corresponding to 40% or 60% VO$_2$ peak was reached and maintained. Participants also completed a practice block of the flanker task during the 5 min warm-up. HR was continuously recorded and monitored at the beginning and end of each trial block to ensure that participants were maintaining ±5 beats per minute (bpm) of their individually prescribed range of intensity. During the control session, participants were required to maintain the same posture on the cycle ergometer without pedaling for an equivalent amount of time (31 min). Following completion of the final experimental testing session, participants were compensated and briefed on the purpose of the study.

Cardiorespiratory fitness assessment

Cardiorespiratory fitness was assessed by a maximal oxygen consumption (VO$_2$ peak) test performed on a Lode Corival (Lode B.V., Groningen, NLD) cycle ergometer. Prior to testing, participants sat on the ergometer so the seat height and aero bicycle handlebar angle could be adjusted so they were comfortable, yet steady, while maintaining an efficient cycling posture. The seat height was set such that participants' knees were bent by 10 to 20° at full extension on the down stroke. A 2 min warm-up with very light resistance (25 W) was completed prior to the ramped protocol. The protocol involved increasing the resistance of the ergometer by 5 W every 10 s while a steady cadence (RPM) was maintained until volitional exhaustion or VO$_2$ peak criteria were met. Speeds ranged from 50–75 RPM depending on the comfort level and experience of the participant. If the participant was unable to maintain a steady cadence (±5 RPMs of their selected speed) for greater than 10 s, they were given one warning that the test would be terminated unless the RPM was maintained. Following 15 s out of the determined range or on the second warning, the test was terminated and participants were allowed to cool down. VO$_2$ peak (mL∗kg^{-1}∗min^{-1}) was determined from direct expired gas exchange data from a computerized metabolic system (Parvo Medics True Max 2400 Metabolic Cart, ParvoMedics, Inc., Sandy, UT) averaged over 15 s intervals. VO$_2$ peak was determined as the maximal relative rate of oxygen consumption when at least two of the following criteria were met: (1) a plateau in VO$_2$ values despite a progressive increase in workload, (2) maximal heart rate (HR) within 10 beats per minute (bpm) of age-predicted maximal values (220 bpm — age in years), or (3) a respiratory exchange ratio greater than 1.10. A 5 min cool-down was then performed at a self-selected pace with minimal resistance to ensure participants returned to baseline HR values prior to leaving the laboratory.

Eriksen flanker task

Participants completed a modified version of the Eriksen flanker task (Eriksen and Eriksen, 1974) to examine cognitive control. Stimuli consisted of five arrows presented in the center of the computer screen. The central arrow was the target, while the surrounding or flanking arrows on each side of the target served as distractors. Each block of trials consisted of equally weighted congruent and incongruent trials presented in random order. The congruent trials consisted of the central target being flanked by arrows pointing in the same direction (e.g., <<<<<), while incongruent trials involved the target being flanked by arrows pointing in the opposing direction (e.g., <<><<; see Fig. 1). After a practice block of 30 trials, which took place during the 5 min

Table 1
Participant characteristics (M ± SD) overall and by gender.

Measure	Females	Males	Total
n	11	16	27
Age (years)	20.4 ± 1.5	20.5 ± 2.3	20.4 ± 2.0
Height (cm)*	160.1 ± 7.0	176.8 ± 5.8	170.0 ± 10.4
Weight (kg)*	57.6 ± 3.6	74.3 ± 11.4	67.5 ± 13.8
BMI (kg/m^2)	22.4 ± 3.6	23.7 ± 3.0	23.2 ± 3.3
VO$_2$ peak (mL∗kg^{-1}∗min^{-1})*	33.7 ± 7.9	48.2 ± 10.1	42.3 ± 11.7

Note. VO$_2$ peak norms are available in the American College of Sports Medicine (2013) Guidelines for Exercise Testing and Prescription (9th edition).
* Significant difference, unpaired Student's *t* test between females and males, *p* < .05.
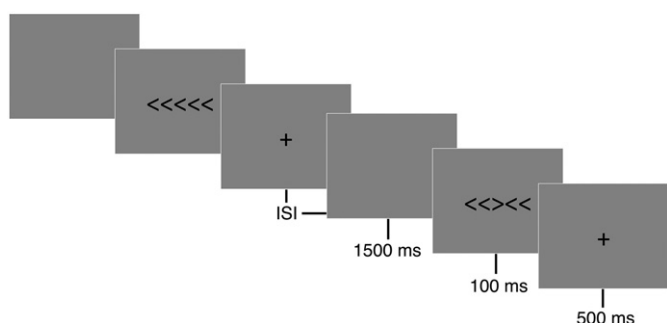
Fig. 1. Modified Eriksen flanker task. Following a 500 ms fixation cross (+), either congruent (<<<<<) or incongruent (<<><<) stimuli were displayed focally for 100 ms on a computer screen. Participants were instructed to respond to the direction of the centrally located target arrow as quickly and accurately as possible. Responses were recorded through a button press corresponding to the direction of the target arrow. A random inter-stimulus interval (ISI) of 1100, 1300, or 1500 ms was used to reduce expectancy effects.

warm-up period, three 6.5 min blocks of trials were presented during each experimental session, separated by 3.5 min of cycling or rest, depending on condition (Fig. 2). During the 3.5 min period between each trial block, participants either maintained steady-state exercise or remained sitting comfortably on the cycle ergometer during the control condition. Regardless of congruency, participants performed a button press with their left thumb when the central target pointed to the left (<) and a button press with their right thumb when the central target pointed to the right (>). Participants' responses were collected via response clickers (left and right) that were attached to custom aero bars affixed to the cycle ergometer. Participants were instructed to respond as quickly and accurately as possible by pressing the left or right response button with the hand that corresponded to the direction in which the target was pointing. The stimuli were presented on a monitor at a distance of 70 cm centered to the nasion. The stimuli were 1.5 cm tall × 8 cm long black arrows centered focally on a white background for 100 ms with a response window of 1500 ms. The vertical and horizontal visual angles were 1.2° and 6.6°, respectively. A random inter-stimulus time interval of 1100, 1300, or 1500 ms was used between

each visual fixation (+) and the stimulus in order to reduce potential anticipatory responses. Performance feedback was provided only during the practice trials.

Electroencephalographic (EEG) data

Continuous EEG activity was recorded from 64 scalp sites using a Geodesic Sensor Net and Electrical Geodesics, Inc. (EGI; Eugene, OR) amplifier system (20 K nominal gain, bandpass = .10–100 Hz). Continuous data were initially referenced to the vertex electrode (Cz) and digitized continuously at 250 Hz with a 24-bit analog-to-digital converter. Impedances were maintained below 50 kΩ. Although lower impedances are typically recommended, previous research has shown acceptable EEG signals when data were collected with higher scalp impedances, and similar values have been used in previous studies of cognitive control (Clayson and Larson, 2013; Millner et al., 2012).

Following collection, data were re-referenced to the average of the left and right mastoids (Bertrand et al., 1985; Tucker et al., 1994) and bandpass filtered with a low-pass frequency of 30 Hz and high-pass frequency of .1 Hz. The continuous EEG data were manually inspected and periods with large movement-related artifacts (eye-blinks and eye movement) were removed using NetStation 4.0 (Electrical Geodesic Inc., EGI). Stimulus-locked epochs were then created from 100 ms pre-stimulus to 1000 ms post-stimulus and baseline adjusted using the 100 ms pre-stimulus period. Prior to artifact detection and removal and to control for potential DC drift often associated with gross movement artifact, a linear detrend was applied to the segmented data where a linear trend line was plotted, the slope was calculated and subtracted from the waveform (Pontifex and Hillman, 2007). NetStation detection software, which allows for the adjustment of settings for detecting and marking artifacts and contaminated segments, was used to detect eye-blinks, vertical and horizontal eye-movements, and bad channels. Marked segments were visually inspected and rejected if they contained 1) eye movements exceeding 55 μV, 2) eye blinks exceeding 140 μV, or 3) greater than or equal to 10 bad channels exceeding 200 μV. In each case, a moving average of 20 samples combined with threshold values was used. Using spherical spline interpolation, bad channels were then replaced from the remaining channels
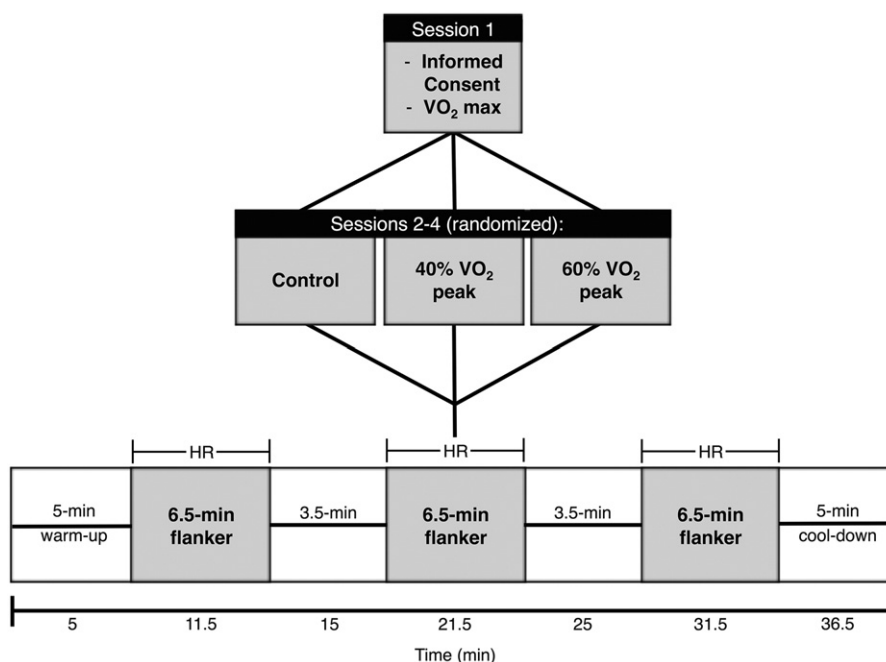

Fig. 2. Study diagram. Following practice trials and a 5-min warm-up period, experimental sessions (2–4) contained three 6.5-min blocks of flanker trials separated by 3.5-min of steady-state exercise or rest (during the control condition). Sessions ended with a 5-min cool-down period.

in "good" segments. Trials were also visually inspected for any remaining artifacts, and data from individual channels containing artifacts were rejected on a trial-by-trial basis. Trials with incorrect behavioral responses were excluded from all analyses.

Consistent with previous ERP research (Folstein and Van Petten, 2008; Polich, 2007) and to reduce selection bias, a priori time windows for the ERP components were established. The N2 component was defined as the mean negative amplitudes within a 200–350 ms window post-stimulus onset, while the P3 component was defined as the mean amplitude within a 250–500 ms window post-stimulus onset. Although peak amplitudes are often used in the literature to define ERP components, Luck (2014) suggests using mean amplitudes to better capture ERP components over an extended period of time, especially when the data collected may be biased by added noise due to muscular or bodily movements during exercise. Moreover, Luck (2014) asserts that it is impossible to estimate the time course or peak latency of an underlying ERP component by looking at a single ERP waveform and this is especially true when two or more ERP components are being compared. Therefore, in the current study we limited our analysis to ERP component amplitudes.

Data analysis

Descriptive statistics were first performed on participant demographic and fitness data. Repeated measures analyses of variance (rANOVA) were used for ERP and behavioral analyses with a 2-tailed alpha level of .05 for all statistical tests, and probability values were adjusted when appropriate with the Greenhouse–Geisser epsilon correction for non-sphericity (Jennings and Wood, 1976). To reduce the potential effect of outliers, trials with RTs beyond the individual mean $\pm$ 3 SD for each trial type were excluded. As a manipulation check of exercise intensity, a 3 (Condition: control, 40%, 60% VO$_2$ peak) $\times$ 3 (Time: Blocks 1–3) rANOVA was conducted to compare HR across conditions. This analysis was expected to reveal significant linear increases in HR from rest to 40% to 60% exercise conditions. Behavioral performance data (i.e., response time and accuracy) were submitted to a 3 (Condition: control, 40%, 60% VO$_2$ peak) $\times$ 3 (Time: Blocks 1–3) $\times$ 2 (Task congruency: Congruent, Incongruent) rANOVA. Additionally, the total number of trials performed during each 6.5 min block was submitted to a 3 (Condition: control, 40%, 60% VO$_2$ peak) $\times$ 3 (Time: Blocks 1–3) rANOVA to determine potential differences in total trials attempted per block. The time blocks refer to when the cognitive task was administered during each condition, with each block representing 6.5 min of cognitive testing. Block 1 began at 5 min , block 2 at 15 min, and block 3 at 25 min following the start of each condition.

For the ERP data, statistical analyses for the N2 and P3 components were performed using 5 electrode sites across the midline (N2: Fz, FCz, and Cz; P3: Cz, CPz, and Pz). The anterior N2 is most robust and frequently examined at frontocentral midline electrode sites (Folstein and Van Petten, 2008; Gehring et al., 1992). Thus, Fz, FCz, and Cz electrodes were used for N2 analyses. N2 data were submitted to a 3 (Condition: control, 40%, 60% VO$_2$ peak) $\times$ 3 (Time: Blocks 1–3) $\times$ 2 (Task congruency: Congruent, Incongruent) $\times$ 3 (Site: Fz, FCz, Cz) rANOVA. To replicate the Pontifex and Hillman (2007) study and because the posterior P3 component is most prominent and commonly studied at centroparietal midline electrode sites (Donchin, 1981; Johnson, 1993), analyses for P3 included the Cz, CPz, and Pz electrode sites. P3 data were submitted to a 3 (Condition: control, 40%, 60% VO$_2$ peak) $\times$ 3 (Time: Blocks 1–3) $\times$ 2 (Task congruency: Congruent, Incongruent) $\times$ 3 (Site: Cz, CPz, Pz) rANOVA.

Results

Mean reaction time (RT), response accuracy, N2 and P3 amplitudes by condition are shown in Table 2. Preliminary analyses revealed no gender differences on behavioral performance variables or amplitude

Table 2
Behavioral and ERP results by condition and time.

	5-min	15-min	25-min
Response accuracy (%)			
Congruent			
Control	99.3 ± 0.2	99.5 ± 0.2	98.5 ± 0.6
40%	98.9 ± 0.3	99.2 ± 0.3	98.6 ± 0.6
60%	98.5 ± 0.6	98.7 ± 0.4	98.8 ± 0.3
Incongruent			
Control	95.6 ± 1.0	95.9 ± 0.6	94.9 ± 1.0
40%	92.7 ± 1.3	92.8 ± 1.3	93.2 ± 1.2
60%	90.9 ± 1.7	92.5 ± 1.6	92.7 ± 1.2
Reaction time (ms)			
Congruent			
Control	311.0 ± 11.9	308.3 ± 10.9	300.6 ± 11.1
40%	313.2 ± 11.7	296.9 ± 13.1	285.1 ± 10.9
60%	294.4 ± 12.0	284.2 ± 10.7	278.9 ± 11.1
Incongruent			
Control	378.9 ± 13.1	373.4 ± 12.2	361.8 ± 12.4
40%	373.3 ± 13.3	362.0 ± 14.6	340.2 ± 12.4
60%	353.0 ± 13.5	342.5 ± 12.9	333.3 ± 12.5
N2 amplitude (μV)			
Congruent			
Control	− 0.9 ± 0.3	− 1.1 ± 0.3	− 1.2 ± 0.4
40%	− 0.8 ± 0.7	− 1.9 ± 0.7	− 2.6 ± 0.6
60%	− 0.7 ± 0.5	− 1.6 ± 0.8	− 1.7 ± 0.7
Incongruent			
Control	− 2.2 ± 0.2	− 1.6 ± 0.2	− 1.5 ± 0.3
40%	− 3.5 ± 0.6	− 3.3 ± 0.7	− 3.1 ± 0.5
60%	− 4.3 ± 0.5	− 2.2 ± 1.2	− 1.8 ± 0.8
P3 amplitude (μV)			
Congruent			
Control	5.6 ± 0.6	5.4 ± 0.6	5.2 ± 0.5
40%	9.8 ± 1.4	9.7 ± 1.6	8.9 ± 1.4
60%	10.2 ± 1.7	9.3 ± 1.2	7.8 ± 0.8
Incongruent			
Control	6.3 ± 0.5	5.8 ± 0.6	5.6 ± 0.6
40%	11.4 ± 1.0	10.5 ± 1.1	10.0 ± 1.5
60%	11.8 ± 1.3	10.4 ± 1.3	9.1 ± 1.0

of the N2 and P3 components. As expected, males had higher VO$_2$ peak (48.2 $\pm$ 10.1 mL$*$kg$^{-1}*$min^{-1} vs. 33.7 $\pm$ 7.9 mL$*$kg$^{-1}*$min^{-1}) values than females. Given no gender differences in cognitive performance, data were collapsed across gender for all subsequent analyses. As a manipulation check of exercise intensity, the 2-way rANOVA revealed a significant main effect of Condition, $F(2,25) = 147.9$, $p < .001$, $\eta^2_p = .91$, with higher HR values elicited by the 40% and 60% VO$_2$ peak conditions compared with rest (see Fig. 3). The two exercise
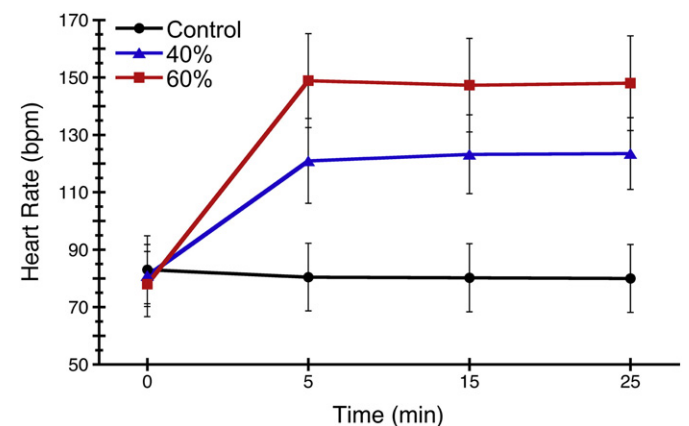

Fig. 3. Average heart rate responses between experimental conditions. Heart rate values are averaged across 6.5 min trial blocks presented at 5, 15, and 25 min. As expected, participants displayed higher heart rates during 40% and 60% VO$_2$ peak conditions compared with rest, with the 60% condition displaying the highest values.

conditions also significantly differed from one another, $p < .001$. The 2-way rANOVA on total trials revealed no significant main effect of Condition, $F(2,25) = .37$, $p > .05$, $\eta^2_p = .03$, or Time, $F(2,25) = .21$, $p > .05$, $\eta^2_p = .02$. There was also no significant Condition × Time interaction, $F(4,23) = 1.4$, $p > .05$, $\eta^2_p = 0.2$. There were approximately 138 trials completed per 6.5 min block.

Behavioral performance

The 3-way rANOVA for response accuracy revealed a main effect of Condition, $F(2,25) = 6.8$, $p < .01$, $\eta^2_p = .31$, and Task congruency, $F(1,26) = 34.4$, $p < .001$, $\eta^2_p = .53$. However, these were superseded by a 2-way interaction of Condition × Task congruency, $F(2,25) = 8.2$, $p < .001$, $\eta^2_p = .35$. Post hoc Bonferroni corrected t tests of Task congruency by Condition revealed a significant decrease in response accuracy for incongruent trials in 40%, $t(26) = 2.7$, $p < .05$, and 60% VO₂ peak conditions, $t(26) = 3.2$, $p < .01$, compared with rest. No significant differences were found between the two exercise conditions for the incongruent trials, $t(26) = .02$, $p > .05$ (see Fig. 4). In addition, no significant differences were found between conditions for congruent trials, $p > .05$. The 3-way rANOVA for RT similarly revealed a main effect of Condition, $F(2,25) = 9.1$, $p < .001$, $\eta^2_p = .38$, and Task congruency, $F(1,26) = 282.7$, $p < .001$, $\eta^2_p = .90$. As anticipated, shorter RT was found for congruent relative to incongruent trials. In terms of Condition, the 60% VO₂ peak condition resulted in faster RT than rest or the 40% VO₂ peak condition. No significant difference was observed between rest and 40% VO₂ peak conditions. In addition, a significant Time main effect was also observed, $F(2,25) = 13.3$, $p < .001$, $\eta^2_p = .47$. Post hoc Bonferroni t tests revealed that participants responded significantly faster across successive time blocks (Block 1: $M = 337.3$ ms, SE = 11.3; Block 2: $M = 327.9$ ms, SE = 11.6; Block 3: $M = 316.7$ ms, SE = 10.8), $p < .05$.

N2 amplitude

Analyses revealed a significant main effect of Task congruency, $F(1,26) = 23.2$, $p < .001$, $\eta^2_p = .47$, which was superseded by Condition × Congruency, $F(2,25) = 3.6$, $p < .05$, $\eta^2_p = .22$, and Congruency × Time, $F(2,25) = 13.4$, $p < .001$, $\eta^2_p = .52$, interactions. Post hoc Bonferroni corrected t tests of Congruency within each Condition revealed greater congruency effects in the exercise conditions (40%: 1.7 μV and 60%: 1.4 μV) compared with the rest condition (0.7 μV), $p < .05$. For the Congruency × Time interaction, t-tests

indicated more negative amplitudes over time for congruent conditions while amplitudes for incongruent conditions become more positive over time, $p < .05$. A Condition main effect approached significance at $p = .07$, with both exercise conditions displaying more negative amplitudes compared with the rest condition (Fig. 5).

P3 amplitude

Analyses revealed a significant main effect of Condition, $F(2,25) = 10.5$, $p < .001$, $\eta^2_p = .46$, with both exercise conditions resulting in larger amplitudes compared with rest (see Fig. 6). A Congruency main effect, $F(1,26) = 9.8$, $p < .01$, $\eta^2_p = .27$, revealed smaller amplitudes for congruent trials compared with incongruent trials. A significant Time main effect, $F(2,25) = 6.5$, $p < .01$, $\eta^2_p = .34$, showed reduced amplitudes over each time block (Fig. 7), $p < .01$. Lastly, a Site main effect, $F(2,25) = 123.7$, $p < .001$, $\eta^2_p = .31$, revealed larger amplitudes displayed at Pz (8.68 μV) and CPz (8.50 μV) electrode sites compared with Cz (8.25 μV). No significant interactions were observed for P3 amplitude (Fig. 8).

Discussion

The aim of this study was to examine neurophysiological and behavioral correlates of cognitive control elicited by a modified flanker task while exercising at low (40% VO₂ peak) and moderate intensity (60% VO₂ peak) relative to a no-exercise seated control condition. A secondary aim was to examine cognitive control processes at several time points during a 31 min bout of acute exercise to determine whether cognition is selectively influenced by the duration of exercise. Behavioral findings revealed impaired response accuracy for the flanker task during exercise, regardless of intensity. However, this decrease in accuracy during exercise only occurred for the more challenging incongruent flanker trials. In terms of RT, participants responded faster during the 60% VO₂ peak condition relative to the 40% VO₂ peak and resting conditions, which did not differ from one another. There was a trend, however, supporting a beneficial dose–response effect of exercise intensity on RT. Neurophysiological findings revealed significantly increased N2 amplitudes (i.e., more negative) during both exercise conditions, which were particularly observed in response to the incongruent flanker task condition (i.e., the task condition requiring greater amounts of cognitive control). Increased P3 amplitude was also found during both exercise conditions, particularly at centroparietal electrode sites, although notably the amplitude of the P3 decreased across time for both exercise and
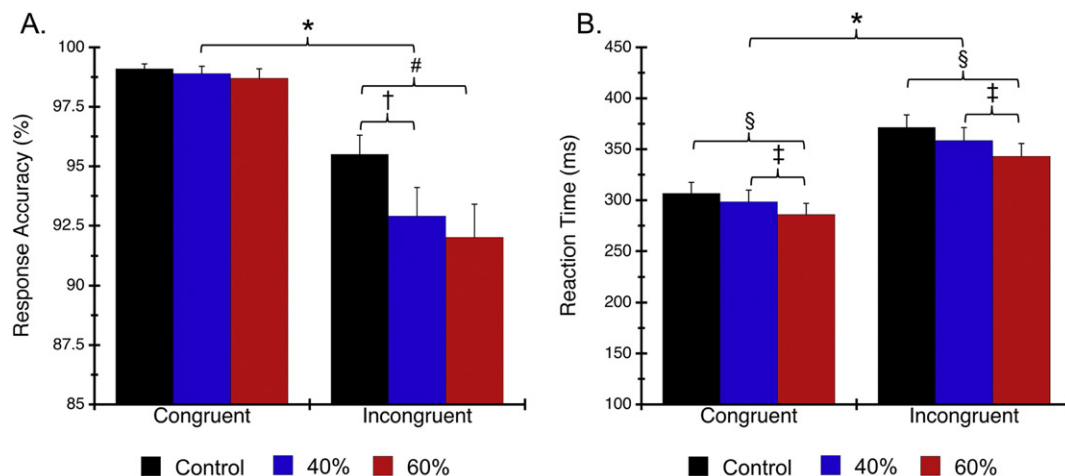

Fig. 4. Mean (±) SE behavioral task performance for: A) response accuracy (%) and B) reaction time (ms) on the flanker task. *Congruency main effect: congruent trials significantly different from incongruent trials; #Condition × Task interaction: control condition significantly different from 60% for incongruent trials only; †Condition × Task interaction: control condition significantly different from 40% on incongruent trials only; §Condition main effect: 60% significantly different from control condition; ‡Condition main effect: 60% significantly different from 40% condition.
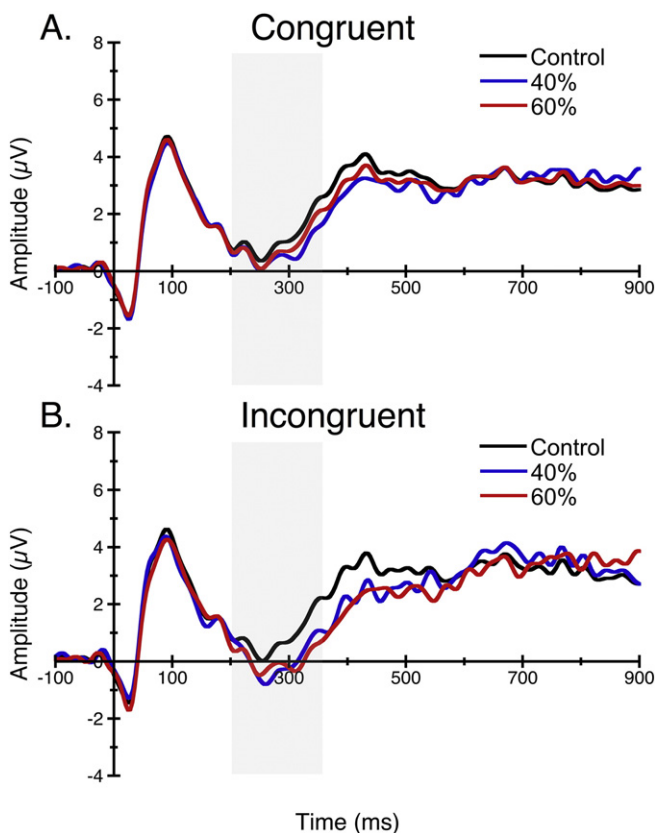
Fig. 5. Stimulus-locked grand average ERP waveforms for N2 by condition for congruent (A) and incongruent (B) flanker task conditions averaged across frontocentral midline electrode sites (Fz, FCz, and Cz). Shading highlights the N2 time window of 200–350 ms post-stimulus onset.
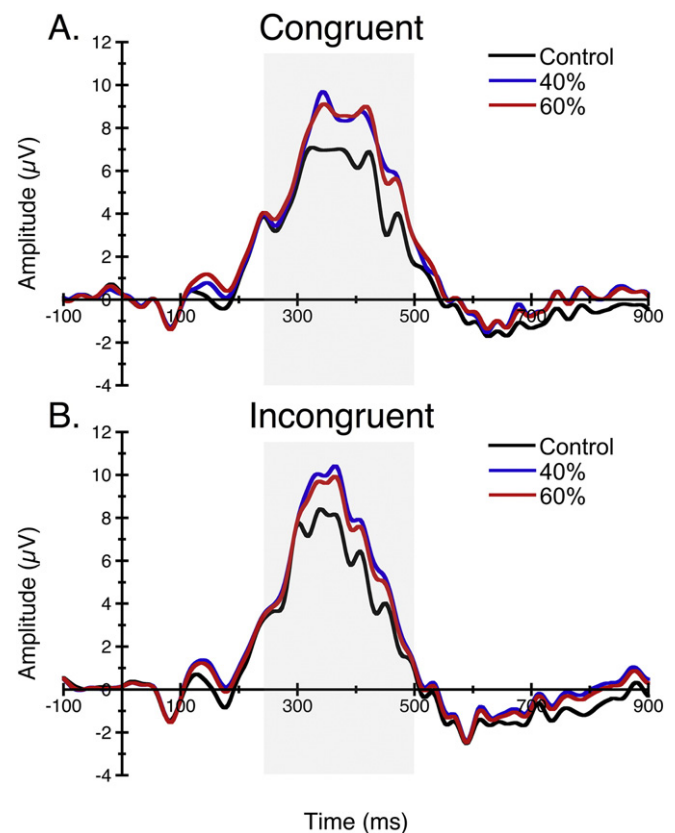

Fig. 6. Stimulus-locked grand average ERP waveforms for P3 by condition for congruent (A) and incongruent (B) flanker conditions averaged across centroparietal midline electrode sites Cz, CPz, and Pz. Shading highlights the P3 time window of 250–500 ms post-stimulus onset.

rest conditions. Together, these findings suggest divergent effects of exercise on behavioral task responses accompanied by an upregulation of cognitive control during a 31 min bout of aerobic exercise.

As expected and replicating a large body of evidence (see Folstein and Van Petten, 2008 for a review), findings indicated impaired accuracy and longer reaction times for trials with high levels of conflict (incongruent trials) relative to trials with low levels of conflict (congruent trials). Further, impaired response accuracy was observed for the flanker task during both exercise conditions, but this decrease in accuracy only occurred for the more challenging incongruent flanker trials. No such effect was observed for congruent trials, suggesting that task conditions that elicit a higher level of conflict and require greater amounts of cognitive control are more selectively influenced by acute exercise. Using a shorter bout of exercise performed at an intensity approximating the 40% VO_2 peak condition in the current study, Pontifex and Hillman (2007) similarly found disruptions in response accuracy only for the incongruent flanker task trials. Schmit et al. (2015) had participants complete the flanker task while cycling at strenuous intensity until exhaustion and found a lower frequency of errors during rest than when exercising for the incongruent flanker trials but not for congruent trials. Yagi et al. (1999) used moderate-to-vigorous intensity aerobic exercise (~65–75% HRmax) on a cycle ergometer to assess exercise-induced activation while performing a visual and auditory oddball task. Participants performed the oddball task during a 10 min rest period, a 10 min exercise bout, and a 10 min recovery period. Behavioral findings for the visual oddball task (auditory excluded) indicated similar reductions in response accuracy during exercise compared with rest or recovery, with non-significant increases in reaction time. Interestingly, others have shown no effect of moderate-to-vigorous intensity aerobic exercise on accuracy (e.g., McMorris and Hale, 2012). For instance, Davranche and McMorris (2009) assessed behavioral

performance measures during a 20 min steady-state cycling exercise at ventilatory threshold, i.e., the point at which ventilation begins to increase non-linearly with increases in work rate (Brooks et al., 2005). During exercise, participants completed a Simon task, which required participants to respond to task-relevant features of a stimulus (color) while inhibiting the task-irrelevant features (spatial location). Although accuracy was unaffected by exercise, the congruency effect in the Simon task (i.e., Simon effect) appeared more pronounced during exercise compared with rest, suggesting that response inhibition is deteriorated during exercise. Collectively, these findings suggest a differential effect of acute exercise on select aspects of cognitive functioning. In 2007, Pontifex and Hillman called for increased research aimed at examining the effects of acute exercise on a variety of tasks that engage different cognitive control and executive functions. This suggestion remains understudied and warrants investigation.

In contrast to the findings on response accuracy, we observed a beneficial dose–response effect of exercise intensity on RT. Specifically, the 60% VO_2 peak condition resulted in faster response times relative to the 40% VO_2 peak and control conditions, although a non-significant trend supported a dose-dependent effect of exercise intensity on RT. Moreover, although there was no significant influence of exercise duration on RT, there was a non-significant trend for faster RT across time during exercise. These observed improvements in RT were not accompanied by a reduction in accuracy (i.e., no speed-accuracy tradeoff). Others have reported that increased physiological arousal during exercise results in faster speed of processing (McMorris and Hale, 2012) and the limited effect of exercise intensity on accuracy may be due to the failure to select cognitive tasks that are sensitive enough to detect exercise-induced changes in performance accuracy. For instance, several authors (Dietrich, 2003; Luft et al., 2009; McMorris and Graydon, 2000) have argued that complex tasks are more likely to be affected by exercise than
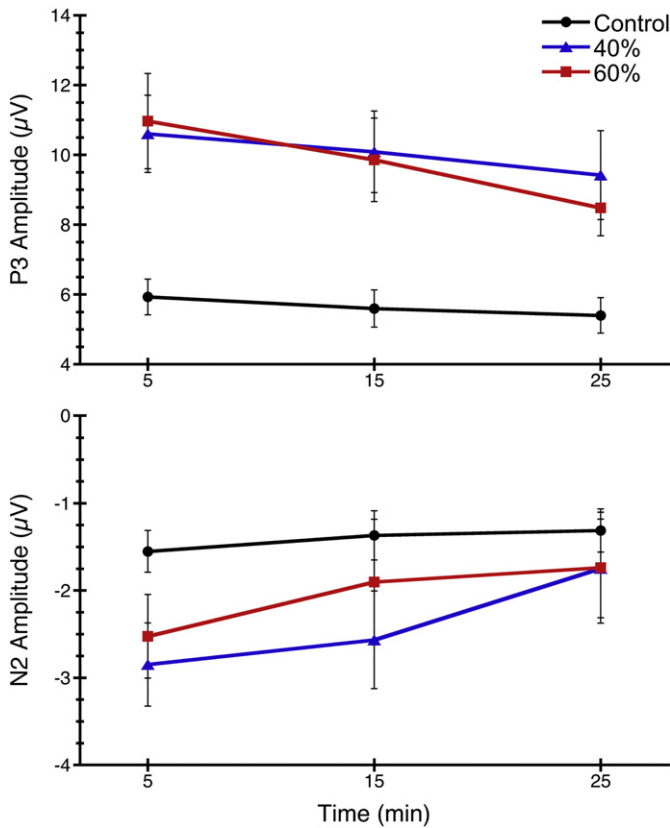
Fig. 7. Amplitudes for P3 and N2 ERP components averaged across 6.5 min trial blocks presented at 5, 15, and 25 min during exercise.

Fig. 8. Stimulus-locked grand average ERP waveforms at Fz, Cz, and Pz electrode sites by condition.

more simple tasks, particularly when cognition is assessed during exercise. The argument that complex tasks are more susceptible to acute exercise of varying intensities is based on the interaction between central executive tasks, brain structure and function, and the physiological stress of exercise. Central executive tasks require greater prefrontal activation relative to other cognitive tasks (Leh et al., 2010) and the prefrontal cortex is particularly sensitive to stress (Arnsten, 2009; McEwen et al., in press; Ramos and Arnsten, 2007). According to the transient hypofrontality theory proposed by Dietrich (2003, 2009; Dietrich and Audiffren, 2011), the initiation and maintenance of exercise results in the signaling and activation of a number of peripheral and central physiological systems in order to meet the neuromuscular, autonomic, and metabolic demands of exercise (Secher et al., 2009). Given a limited attentional resource capacity, the activation of these pathways is predicted to result in a downregulation of metabolic resources to brain regions and circuits that are not essential for exercise (e.g., prefrontal activity). In this study we used a modified Eriksen flanker task, a commonly used measure of frontally-mediated cognitive control that incorporates both simple (congruent) and complex (incongruent) task types, to detect the influence of exercise intensity and duration on neurocognitive function. Our data support the notion that more complex cognitive tasks are sensitive to the subtle influences of acute exercise on RT. The effects of exercise on behavioral responses assessed post-exercise have been studied extensively (Chang et al., 2012; Lambourne and Tomporowski, 2010); however, research examining the effects of exercise on in-task behavioral measures is further warranted to illuminate these divergent effects of acute exercise on accuracy and RT. The current findings suggest that although response processes are faster during exercise, accuracy may be compromised.

In line with previous research (Folstein and Van Petten, 2008; Van Veen and Carter, 2002; Yeung et al., 2004), we observed a larger N2 amplitude for incongruent flanker trials relative to congruent trials. Given
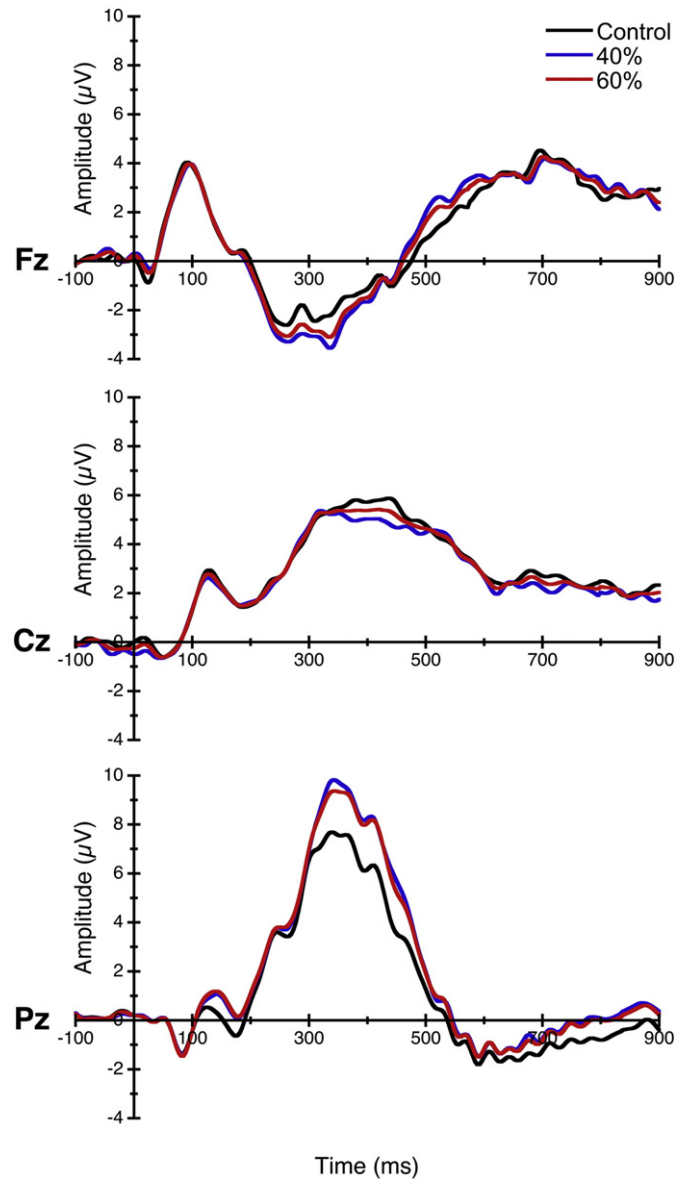
that the N2 is believed to be sensitive to the degree of conflict and the extent to which individuals attend to task-irrelevant information (flanking arrows) compared with task-relevant information (target-stimulus; Larson et al., 2014; Yeung and Cohen, 2006; Yeung et al., 2006), our data adds to the extant literature suggesting a greater amount of cognitive control required to resolve the more difficult task condition. Exercise was also found to modulate N2 amplitude such that the 40% and 60% VO_2 peak conditions resulted in larger N2 amplitudes, particularly for incongruent task trials. Our data conflict with the findings from Pontifex and Hillman (2007), who found decreases in N2 amplitude across frontal, central, and parietal electrode sites during a 6.5 min bout of cycling exercise at 60% of maximal HR. More recently, Vogt et al. (2015) found that a short 5 min bout of cycling exercise did not have a measurable impact on N2 amplitudes. Unfortunately very little information was provided in their study to determine exercise intensity and participants completed the mental arithmetic problems while cycling in a virtual reality environment. Thus, important study design features may account for the discrepant findings. In the current study, we assessed cognitive control processes during a 31 min bout of steady-state exercise performed at 40% or 60% VO_2

peak. Although exercise was found to increase N2 amplitude overall, there was no influence of exercise duration on this component amplitude. Our data suggests that relative to the behavioral findings of impaired accuracy and faster RT, participants recruited greater cognitive control during task performance while exercising compared with rest. Functional magnetic resonance imaging (fMRI) and ERP studies suggest a critical role of the anterior cingulate cortex (ACC) in the N2 component, such that the ACC signals for increased recruitment of cognitive control from lateral prefrontal cortex (PFC) regions during the detection and evaluation of conflicts (Botvinick et al., 1999, 2001; Van Veen and Carter, 2002; Yeung et al., 2004). When viewed in light of the behavioral findings, these results suggest that greater ACC-mediated conflict monitoring is required during exercise, particularly during the more demanding task condition.

Increased P3 amplitude was also observed across centroparietal electrode sites during exercise, suggesting an increase in the amount of attentional resources engaged during the dual-task performance (Polich, 2012). The increase in P3 amplitude during exercise supports the increase in N2, and suggests a greater upregulation of cognitive control and attentional resources necessary for successful task completion. Similar to our findings, Pontifex and Hillman (2007) observed an increase in P3 amplitude over frontal and lateral electrode sites and interpreted this finding as a relative inefficiency of neuroelectric resources during exercise. Interestingly, and opposed to the current findings, Yagi et al. (1999) showed reductions in P3 amplitude during exercise compared with rest and recovery periods. The authors suggest that their subjects treated exercise as a secondary task requiring the allocation of a limited resource (e.g., dual-task interference/distraction). However, it is important to note that half of the participants performed the rest, exercise, and recovery periods to the auditory oddball task first, immediately followed by the rest, exercise, and recovery periods to the visual oddball task. The other half completed the visual oddball task first. Potential residual effects of exercise may have influenced the second block of the procedure, thus washing out the initial period. Furthermore, data and results for standards (80% — Xs) and targets (20% — Os) were not discussed and exercise intensity was higher than the intensities used in the current study. Grego et al. (2004) used a longer duration of moderate-intensity exercise (~66% VO_2 max for 180 min) to study the effects of fatigue on cognitive function (P3) in trained cyclists during an auditory oddball task. During the 1st and 2nd time points (3 and 36 min) there was no difference in P3 amplitude between rest and exercise; however, an increase in P3 amplitude emerged during the 3rd time point (72 min), peaked at the 4th time point (108 min), and was attenuated at the 5th and 6th time points (144 and 180 min). The later changes (5th and 6th time points) occurred concomitantly with changes in insulin, cortisol, epinephrine, and norepinephrine. There were also significant increases in perceived exertion near the end of the exercise bout. The authors suggested that the improvement in cognitive function during exercise, as indexed by the increase in P3 amplitude between 60 and 120 min, may be affected (i.e., reduced) through the combined effects of arousal and central fatigue mechanisms during prolonged exercise. Results from previous studies focusing on acute physical fatigue and cognitive performance have been inconsistent (McEwen, 2012; Moore et al., 2012). Although we did not assess fatigue or exertion levels in this study, it is possible that cognitive performance may be altered by the duration of exercise due to activation of physiological processes during the progression to steady-state exercise. It is also possible that cardiorespiratory fitness may moderate the influence of fatigue on cognition such that higher fit individuals are less impacted by physical fatigue. We did not find a moderating influence of fitness in the current study, but we did not select participants with a wide range of fitness levels (i.e., individuals with very low vs. high levels of fitness). Future research aimed at examining concurrent cognitive, affective, and exertional responses during exercise among individuals varying widely in levels of aerobic fitness is needed.

In terms of theoretical support, the selective effect of exercise on cognitive task performance has been explained in terms of dual-task paradigms and the transient hypofrontality theory (Audiffren et al., 2009; Dietrich, 2009; Pesce, 2009). Performing cognitive tasks while exercising may create a dual-task scenario whereby individuals' attention may be divided in an attempt to successfully accomplish the cognitive task while maintaining appropriate metabolic, cardiovascular, and neuromuscular responses for exercise. In this study, participants completed the cognitive tasks while engaging in steady-state exercise. Our results for response accuracy and increased neurophysiological responses during exercise corroborate previous findings suggesting an inefficiency in the ability to inhibit conflicting responses during exercise (Pontifex and Hillman, 2007). Similar flanker paradigms used in previous studies with healthy young adults have resulted in high levels of performance for both congruent and incongruent flanker trials (Alderman and Olson, 2014; Alderman et al., 2014), thus a finding of impaired accuracy during exercise is meaningful. In line with the transient hypofrontality theory (Dietrich, 2003, 2009; Dietrich and Audiffren, 2011), it was initially hypothesized that response accuracy would be impaired during the exercise conditions due to reduced cortical resources for successful task completion. Although this theory has received some support in acute exercise contexts (Dietrich and Sparling, 2004; Pontifex and Hillman, 2007), not all studies have found impaired executive functioning or cognitive control processing during exercise (Davranche et al., 2015; Schmit et al., 2015). Although the accuracy and ERP data in our study provide support for this theory, the RT data do not. Clearly more work using both behavioral and neuroimaging techniques are warranted to test the tenets of this theory as it relates to acute exercise effects on prefrontally-mediated cognitive performance.

Limitations

There were several limitations in the current study. First, the design of our study may have led to adaptive and learning effects. Our behavioral and neuroelectric findings could, at least partially, be attributed to conflict adaptation over time or learning effects due to prolonged exposure to the flanker task. However, participants were counterbalanced into each condition and were afforded a practice period prior to the initiation of each session. A second limitation relates to the impaired accuracy and ERP measures during exercise combined with the improved reaction time for the 60% VO_2 peak condition. Moreover, there was a non-significant trend for RT such that the 40% condition resulted in faster performance than the no-exercise control. These findings indicate the potential for a speed-accuracy tradeoff during moderate-intensity exercise, where accuracy is impaired (for incongruent trials only) yet reaction time is enhanced. Exercise increased response time efficiency during exercise but resulted in a more inefficient resolution of conflict, possibly due to increased physiological arousal. The speed-accuracy tradeoff in the present study conflicts with findings from McMorris and Hale (2012) who concluded that speed of cognition is modified during exercise, while response accuracy remains relatively unaffected. More research is required to replicate our findings and further understand the nature of acute exercise and speed-accuracy tradeoffs at varying intensities. A third limitation is the restriction to low and moderate intensities of exercise only. Exercise intensities of 40% and 60% of VO_2 peak, which were characterized as low and moderate respectively, were compared with a no-exercise seated control to address dose–response effects on neurocognitive performance during exercise. Wang et al. (2013) used a control and three exercise intensities at 30% HRR, 50% HRR, and 80% HRR, which represented low, moderate, and high intensities, respectively. They found impaired executive function performance on the WCST only for the high intensity condition. Due to the need for restricted movement for the EEG data collection in this study, the full range of exercise intensities were not studied. Future investigation with enhanced methodologies should include both light and vigorous exercise intensities in addition to moderate intensities to more fully characterize the moderating influence of exercise intensity on cognition.

Conclusions

This study adds to the small body of literature that has examined changes in cognitive performance during steady-state exercise. The results further reinforce the complex relationship between acute exercise and neurocognitive performance. We observed impaired accuracy but faster response times during exercise, regardless of intensity. Neuroelectric measures indicated increased neurophysiological responses during exercise which were modulated by exercise intensity. There were no significant effects of exercise duration on behavioral or neurophysiological measures. In summary, these findings suggest divergent effects of exercise on behavioral performance measures accompanied by an up-regulation of cognitive control during aerobic exercise.

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