

CARDIORESPIRATORY FITNESS AND ACUTE AEROBIC EXERCISE EFFECTS ON NEUROELECTRIC AND BEHAVIORAL MEASURES OF ACTION MONITORING

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Abstract—Cardiorespiratory fitness and acute aerobic exercise effects on cognitive function were assessed for 28 higher- and lower-fit adults during a flanker task by comparing behavioral and neuroelectric indices of action monitoring. The error-related negativity, error positivity, and N2 components, as well as behavioral measures of response speed, accuracy, and post-error slowing were measured following a 30-minute acute bout of treadmill exercise or following 30-minutes of rest. A graded maximal exercise test was used to measure cardiorespiratory fitness by assessing maximal oxygen uptake. Results indicated that higher-fit adults exhibited reduced error-related negativity amplitude, increased error positivity amplitude, and increased post-error response slowing compared with lower-fit adults. However, acute exercise was not related to any of the dependent measures. These findings suggest that cardiorespiratory fitness, but not acute aerobic exercise, may be beneficial to behavioral and neuroelectric indices of action monitoring following errors of commission by increasing top-down attentional control. © 2006 IBRO. Published by Elsevier Ltd. All rights reserved.

Key words: physical activity, executive control, cognitive function, error-related negativity, event-related potentials, interference control.

The study of physical activity and cardiorespiratory fitness influences on cognitive and behavioral functioning has grown in interest over recent decades. The beneficial effects of acute and chronic exercise on cognitive, emotional, and motor processes appear to be robust (Boutcher and Landers, 1988; Bashore, 1989; Bashore and Goddard, 1993), with the extant literature indicating that aerobically fit individuals perform better on a variety of tasks involving attention, cognition, and memory (Colcombe and Kramer, 2003; Etnier et al., 1997). Further, in older adults this relationship appears to be greater for tasks or task components requiring extensive executive control (Kramer et al., 1999, 2000) suggesting that although cardiorespiratory

fitness has exhibited a general relationship with improvements in cognition (e.g. Blumenthal et al., 1991; Hill et al., 1993), the relationship is selectively larger for aspects of cognitive function involving executive control (Colcombe and Kramer, 2003).

The term “executive control” has been used to describe a subset of processes concerned with the selection, scheduling, and coordination of computational processes that are responsible for perception, memory, and action (Norman and Shallice, 1986; Meyer and Kieras, 1997). One paradigm that manipulates executive control requirements is the Eriksen flanker task (Eriksen and Eriksen, 1974). This task requires participants to discriminate between target stimuli that are flanked by an array of other stimuli, which have different responses associated with them. Differences in error rate and response speed are observed between congruent and incongruent conditions with the former condition eliciting faster and more accurate responses compared with the latter condition (Eriksen and Schultz, 1979). Incongruent trials require greater amounts of interference control (one aspect of executive control) and result in response delays due to activation of the incorrect response (elicited by the flanking stimuli), which competes with the correct response elicited by the centrally placed target stimulus (Spencer and Coles, 1999).

Although a variety of cognitive tasks has been used to study the relationship between cardiorespiratory fitness and behavioral indices of cognitive processing, the evaluation of event-related brain potentials (ERPs) has been limited. That is, the majority of cardiorespiratory fitness and ERP research has focused on the P3 component (Bashore, 1989; Dustman et al., 1990; Hillman et al., 2004, 2006), with few exceptions (e.g. stimulus preceding negativity and contingent negative variation; Hillman et al., 2002; N400; Magnié et al., 2000). The inclusion of other ERP components may lead to a deeper understanding of the relationship between fitness and cognitive function. Specifically, multiple ERP components have been associated with action monitoring processes for purposes of improving task performance through error detection and correction. To date, there is a paucity of research examining these components in relation to cardiorespiratory fitness.

Error-related negativity (ERN)

One component associated with action monitoring processes is the ERN (Gehring et al., 1993; or error negativity (N_e); Falkenstein et al., 1991). The ERN, or N_e , is a negative-going component observed in response-locked ERP

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Abbreviations: ACC, anterior cingulate cortex; ACSM, American College of Sports Medicine; bpm, beats per minute; EEG, electroencephalogram/electroencephalographic; ERN, error-related negativity; ERP, event-related potential; GXT, graded exercise test; HR, heart rate; N_e , error negativity; P_e , error positivity; RER, respiratory exchange ratio; RPE, Ratings of Perceived Exertion; RT, reaction time; VO_2 max, maximal oxygen uptake.

averages of incorrect responses committed during task completion. It is maximal over fronto-central recording sites and peaks shortly after incorrect responses in speeded reaction time (RT) tasks (Falkenstein et al., 1991; Gehring et al., 1993). Researchers have localized the source of the ERN to be at or very near the anterior cingulate cortex (ACC) using dipole localization techniques (Dehaene et al., 1994; van Veen and Carter, 2002), and corroborating evidence has been provided by both neuroimaging (Carter et al., 1998) and magneto-encephalography studies (Miltner et al., 2003). Neuroimaging findings have established that the functional significance of ACC activation is related to action monitoring and evaluation during tasks requiring extensive executive control (Carter et al., 2000). Further, Gehring and Knight (2000) have shown that the ACC exhibits a functional interaction with the prefrontal cortex during action monitoring processes and compensatory/corrective actions following error responses. The ERN is generally believed to reflect a cognitive learning mechanism used to correct an individual's incorrect responses during subsequent environmental interaction through either the monitoring and detection of error responses (Holroyd and Coles, 2002) or response conflict (Yeung et al., 2004).

Error positivity (P_e)

A second ERP component related to action monitoring processes following error responses is the P_e (Falkenstein et al., 1990, 2000). The P_e is a positive-going component observed in response-locked ERP averages of incorrect responses. It is maximal over centro-parietal recording sites and peaks after the ERN (about 300 ms following an incorrect response). The P_e has been described as an emotional reaction to the commission of an error (Falkenstein et al., 2000; van Veen and Carter, 2002), a post-response evaluation of an error (Davies et al., 2001; Falkenstein et al., 1990), or the allocation of attentional resources toward an error following error commission (i.e. similar to the allocation of attention reflected in ERP components of stimulus processing; Mathewson et al., 2005). Research using dipole localization techniques has identified generators of the P_e in the rostral ACC (van Veen and Carter, 2002). Although both the ERN and P_e are associated with neural processes in the ACC, the two components have distinct neural generators and are believed to be independent of each other (Herrmann et al., 2004).

N2

A third ERP component associated with action monitoring is the N2, which refers to a negative-going component observed in stimulus-locked averages of correct responses. It is maximal over fronto-central recording sites and peaks between 150 and 350 ms after stimulus presentation. The N2 has been localized to the same area of the ACC as the response-locked ERN using neuroimaging techniques (van Veen and Carter, 2002), leading some researchers to suggest that the N2 and ERN may reflect similar conflict monitoring functions during correct and incorrect responses, respectively. Specifically, ACC activation reflect-

ing conflict monitoring occurs prior to the response during correct trials and is reflected by the N2. During incorrect trials, this activation occurs immediately following the response and is reflected by the ERN (van Veen and Carter, 2002; Yeung et al., 2004).

Physical activity and action monitoring

As mentioned previously, the relationship between cardiorespiratory fitness and ERP components reflecting action monitoring processes has not been examined. However, research examining the relationship between self-reported physical activity behavior and ERN amplitude during a task requiring variable amounts of executive control (i.e. task switching) revealed decreased ERN amplitude and relatively greater response slowing following errors for physically active, compared with sedentary, participants (Themanson et al., in press). Given that post-error response slowing is a behavioral indicator of increased recruitment and implementation of top-down attentional control to improve task performance (Gehring et al., 1993; Kerns et al., 2004), these findings suggest increased top-down attentional control among physically active individuals (Themanson et al., in press). Evidence for increased top-down attentional control may also be observed in the neuroelectric system through a relative reduction in ERN amplitude associated with a decrease in response conflict and the related activation of action monitoring processes for more physically active individuals (Themanson et al., in press). The reduction in ERN amplitude with increased physical activity corroborates earlier research that observed a relationship between aerobic training and a reduction in ACC activation for aerobically trained older adults compared with their sedentary counterparts, which is also suggestive of a decrease in response conflict with increases in aerobic fitness (Colcombe et al., 2004).

Given the findings of reduced ERN amplitude for physically active individuals (Themanson et al., in press) and reduced response conflict for aerobically trained older adults (Colcombe et al., 2004), it follows that ERN amplitude would be reduced for individuals exhibiting greater cardiorespiratory fitness. Similarly, since the N2 component has also been associated with conflict monitoring processes (Yeung et al., 2004), a relative reduction in N2 amplitude for higher-fit individuals would be expected as a result of increases in top-down attentional control associated with increased levels of cardiorespiratory fitness and related reductions in response conflict. Further, assuming that individuals attend to and evaluate errors in an attempt to correct behavior and enhance future performance, a relative increase in P_e amplitude for higher-fit individuals would also be expected, since it would reflect either the evaluation of a commission error (Davies et al., 2001; Falkenstein et al., 1990) or the allocation of attentional resources toward an error (Mathewson et al., 2005).

Acute aerobic exercise and cognitive function

Although the relationship between physical activity behavior and action monitoring processes has been explored, the relationship between acute bouts of exercise and this

aspect of cognition has not been investigated. Hillman et al. (2003) noted a post-exercise increase in the allocation of attentional resources in stimulus-locked ERPs during a flanker task, indicating that upstream processes related to stimulus acquisition may be influenced by acute exercise participation. Further, these data may be predictive of a relative decrease in ERN amplitude. That is, an increase in the allocation of attentional resources during stimulus updating would implicate an increase in top-down attentional control, perhaps leading to a reduction in response conflict associated with task execution (i.e. reduced ERN amplitude). Accordingly, a relative decrease in N2 amplitude following exercise would also be predicted given that the N2 has been related to pre-response conflict monitoring (Yeung et al., 2004). Finally, given that a recent examination of the P_e indicates that the amplitude may reflect the allocation of attention toward an error in a manner similar to the allocation of attention during stimulus processing of correct trials (i.e. P3 amplitude; Mathewson et al., 2005), it follows that acute exercise may also influence P_e amplitude.

Thus, the present study was designed to selectively examine a subset of executive control processes by evaluating the influence of cardiorespiratory fitness and an acute bout of aerobic exercise on neuroelectric (ERN, P_e , N2) and behavioral indices of action monitoring during the completion of a flanker task. With respect to task performance, it was expected that higher-fit participants would display significantly shorter RT compared with lower-fit participants (Kramer et al., 1999), and RT would be shorter following an acute bout of exercise compared with following rest for all participants (Hogervorst et al., 1996). With respect to neuroelectric indices of action monitoring processes, it was predicted that higher-fit participants would exhibit a relative decrease in ERN and N2 amplitudes as well as a relative increase in P_e amplitude, compared with lower-fit participants. Further, an acute bout of exercise was predicted to decrease ERN and N2 amplitudes and increase P_e amplitude compared with rest. Behaviorally, it was predicted that response slowing following response errors would be greater for higher-fit participants, corroborating previous research (Themanson et al., in press) and providing additional support for the notion of increased top-down attentional control among fit individuals. That is, increased top-down attentional control in higher-fit individuals might significantly reduce response conflict and be reflected in a more efficient neuroelectric profile of conflict-related action monitoring processes (i.e. reduced ERN amplitude) as well as heightened neural (i.e. increased P_e amplitude) and behavioral (i.e. increased slowing of responses following errors) adjustments following error commission.

EXPERIMENTAL PROCEDURES

Participants

Twenty-eight participants (14 males, 14 females) who varied in their level of cardiorespiratory fitness were recruited from undergraduate kinesiology courses at the University of Illinois at Urbana-Champaign.

Table 1. Mean values (SD) for VO_2 by group and by sex within each group

Measure	Group	
	Higher-fit	Lower-fit
VO_2 max (ml/kg/min)	56.3 (7.9)	38.7 (7.5)
VO_2 max (ml/kg/min) for females	50.9 (4.7)	33.2 (5.0)
VO_2 max (ml/kg/min) for males	61.6 (6.7)	44.2 (5.1)

Participants were pre-screened in their courses to determine the amount and duration of aerobic activity that they engaged in per week. From this screening, 29 participants were selected to obtain the two age- and sex-matched fitness groups. One participant did not achieve the requirements of a maximal fitness assessment (see below) and was excluded from the analyses. All participants reported being free of adverse health conditions, neurological disorders, any medications that influence CNS function, and had normal (or corrected to normal) vision based on the minimal 20/20 standard. Participants were instructed not to exercise on the days of their laboratory visits, and reported their compliance with this request. Participants were selected into the higher-fit group if their age- and sex-matched maximum oxygen consumption (VO_2 max) achieved during a graded exercise test (GXT) was above the 80th percentile based upon American College of Sports Medicine (ACSM) guidelines (ACSM, 2000). The average VO_2 max for this group was well above the 90th percentile. The remaining participants were selected into the lower-fit group. The average VO_2 max for this group equated to the 50th percentile (see Table 1). The two groups were gender-balanced, with seven males and seven females in each group.

Procedure

After providing informed consent in accordance with the institutional review board at the University of Illinois, participants visited the laboratory at the same time of day on two separate occasions with no more than seven days between experimental sessions. The two sessions (post-rest, post-exercise) were counterbalanced across participants to minimize potential practice effects. During the post-rest session, participants rested quietly for 30 min. During the rest period, participants sat in a chair and were allowed to read from a selection of popular magazines. The experimenter then prepared the participants for neuroelectric measurement and participants' responses (ERPs, RT, response accuracy) were collected during an Eriksen flanker task (Eriksen and Eriksen, 1974). Following completion of the task, participants completed a GXT to assess their VO_2 max, which is considered to be the criterion measure of cardiorespiratory fitness (ACSM, 2000). During the exercise session, participants completed a 30-min bout of treadmill exercise, followed by the completion of the flanker task. The flanker task was not initiated until participants' heart rate (HR) had returned to within $\pm 10\%$ of their pre-exercise level ($M=40.1$ min post-exercise, $S.D.=13.9$). To be consistent with previous acute exercise research (Hillman et al., 2003), participants were instructed to exercise at a level that was "somewhat hard" to "hard" on the 16-point (from 6 to 20) Ratings of Perceived Exertion (RPE) scale (Borg, 1970). This intensity derived a mean HR ($M=161.0$ beats per minute (bpm), $S.D.=13.9$) of 82.8% of their maximal HR achieved on the GXT ($M=194.5$ bpm, $S.D.=9.8$), confirming that participants were exercising at a vigorous, yet submaximal, level. Upon completion of the second session, participants were briefed on the purpose of the experiment.

Task

Participants completed incongruent and neutral conditions of the Eriksen flanker task (Eriksen and Eriksen, 1974), which required

them to respond as quickly as possible to a target letter presented focally on a computer monitor from a distance of 1 m. Target stimuli (the letters “F” and “X”) required participants to respond with their left and right thumbs, respectively. The incongruent condition had the target letter flanked by the opposing target stimuli (i.e. FXF or XFX) and the neutral condition had the target letter flanked by letters with no response assignment (e.g. LFL or LXL). The two conditions were equiprobable and randomly ordered, with the stimuli consisting of black letters presented on a white background. Five task blocks, each consisting of 144 trials, were presented to participants with a two-minute rest between blocks. The stimulus duration for each trial was 500 ms with a 1500 ms inter-stimulus interval. The task blocks were counterbalanced across participants. Stimulus presentation, timing, and measurement of behavioral response time and accuracy were controlled by Neuroscan Stim software (v 2.0; Compumedics USA, El Paso, TX, USA). Participants were given task instructions and allowed 12 practice trials prior to each of the two EEG sessions.

Measures

Cardiorespiratory fitness. The GXT was conducted on a Life Fitness 9100 treadmill (Brunswick Corporation, Schiller Park, IL, USA) using a modified Bruce protocol (Dengel et al., 1994). Respiratory exchange ratio (RER) and 30-s averages for oxygen uptake (VO_2) were collected using a computerized indirect calorimetry system. All participants achieved VO_2 max as defined by meeting two out of the following three criteria: age-predicted maximum HR obtained, $\text{RER} > 1.1$, or an observed plateau in VO_2 despite an increase in workload.

ERPs. Electroencephalographic (EEG) activity was measured using a Quik-cap (Neuro Inc., El Paso, TX, USA) with 11 Ag–AgCl electrodes at Fz, FCz, FC1, FC2, Cz, C1, C2, CPz, Pz, POz, and Oz, referenced to the left mastoid, while AFz served as the ground electrode. Bipolar electrooculographic activity (EOG) was recorded to monitor eye movements using Ag–AgCl electrodes placed above and below the right orbit and on the outer canthus of each eye. All electrodes were positioned according to the international 10–20 system (Jasper, 1958) and electrode impedances were kept below 10 k Ω . Neuroscan Synamps bioamplifiers (Neuro Inc.) were used to continuously digitize (500 Hz sampling rate) and amplify (500 \times) the raw EEG signal with a 70 Hz low-pass filter, which included a 60 Hz notch filter. EEG activity was recorded using Neuroscan Scan software (v 4.3.1).

For the ERN component, offline EEG processing included: eyeblink correction using a spatial filter (Compumedics Neuroscan, 2003), re-referencing to average mastoids, response-locked epoching (–500–1500 ms relative to behavioral response), baseline correction (100 ms time window ranging from –200 ms to –100 ms prior to the response; Nieuwenhuis et al., 2002), low-pass filtering (15 Hz; 24 dB/octave), and artifact rejection (epochs with signal that exceeded $\pm 75 \mu\text{V}$ were rejected). Average ERP waveforms for correct trials were matched to error trial waveforms on response time and number of trials to protect against differential artifacts of the stimulus-related activity overlapping the response-locked ERP activity (Coles et al., 2001). ERN was quantified as the maximum negative deflection between 0 and 200 ms post-response in each of these two average waveforms. Matching involved selecting individual correct trials for each participant, without replacement, that matched the response time for each of the error trials for that individual. Considering error trials tend to be associated with faster RT than correct trials (Falkenstein et al., 2001; Mathewson et al., 2005; Yeung et al., 2004), this procedure removes any artifacts that may exist in the timing of processing due to differences in response latency for correct and error trials and results in an equal number of matched-correct trials and error trials for each individual to compare differences across accuracy

conditions. The average number of error trials following exercise for higher- and lower-fit participants was 37 and 32, respectively. Following rest, the average number of error trials for higher- and lower-fit participants was 34 and 27, respectively.

Offline EEG processing of the P_e component was identical to those described for the ERN. The P_e was quantified as the maximum positive deflection between 200 and 500 ms post-response (Falkenstein et al., 2000) in each of the two average waveforms (error and matched-correct).

Offline processing for the N2 component included: eyeblink correction using a spatial filter (Compumedics Neuroscan, 2003), re-referencing to average mastoids, stimulus-locked epoching (–100–1000 ms relative to stimulus onset), baseline correction (pre-stimulus period), low-pass filtering (30 Hz; 24 dB/octave), and artifact rejection (epochs with signal that exceeded $\pm 75 \mu\text{V}$ were rejected). N2 was quantified as the maximum negative deflection between 150 and 400 ms (Mathalon et al., 2003) post-stimulus onset in the average waveform derived from correct responses.

Response time and accuracy. Behavioral data were collected on response latency (i.e. time in ms from the presentation of the stimulus) and response accuracy (i.e. number of correct and incorrect responses) for all trials across task blocks. Errors of omission (non-responses) were categorized as incorrect responses for calculations of response accuracy, though those trials could not be included in the creation of ERP waveforms due to the lack of a behavioral response. Average response latencies were calculated for each participant for: 1) correct trials, 2) error trials, 3) matched-correct trials (the subset of correct trials matched to specific error trials based on RT), 4) correct trials following an error trial, and 5) correct trials following a matched-correct trial. Each participant's average RT for correct trials following error trials was compared with his or her average RT for correct trials following matched-correct trials in statistical analyses to provide a measure of post-error response slowing, which is a behavioral indicator of increased recruitment and implementation of top-down attentional control (Gehring et al., 1993; Kerns et al., 2004). Due to the consistent finding that average RT on error trials is faster than average RT on correct trials (Mathewson et al., 2005; Yeung et al., 2004), this comparison accounts for any effects of slowing that are present simply because responses on error trials generally tend to be faster than responses on correct trials.

Statistical analysis

For ERN and P_e amplitudes, an omnibus analysis using a 2 (Accuracy: error, correct) \times 4 (Site: Fz, FCz, Cz, Pz) multivariate repeated measures ANOVA (Rodríguez-Fornells et al., 2002) was conducted first to verify that these data conformed to the expected topography and accuracy effects. For N2, the omnibus analysis was a 2 (Session) \times 4 (Site) \times 2 (Congruency) multivariate repeated measures ANOVA. ERN and P_e data were analyzed using 2 (Fitness: higher, lower) \times 2 (Session: post-rest, post-exercise) \times 2 (Accuracy: error, correct) \times 4 (Site: Fz, FCz, Cz, Pz) mixed-model multivariate tests with repeated measures. Analyses were conducted for the four midline sites due to evidence that localizes the ERN at or near the ACC (Carter et al., 1998; Dehaene et al., 1994; Miltner et al., 2003), which would correspond to the FCz electrode site. ERN and P_e analyses did not include a Congruency factor (i.e. incongruent, neutral) due to an insufficient number of errors in the neutral condition (examination of ERN and P_e limited to incongruent error trials resulted in a similar pattern of significant findings.). N2 data were analyzed with a 2 (Fitness) \times 2 (Session) \times 4 (Site) \times 2 (Congruency) mixed-model multivariate test with repeated measures for correct trials only. Behavioral data were tested with a 2 (Fitness) \times 2 (Session) \times 2 (Accuracy) \times 2 (Congruency) repeated measures MANOVA to examine group differences in the speed of responses and a 2 (Fitness) \times 2 (Session) \times 2 (Congruency) repeated measures MANOVA to determine group differences in the accuracy

Table 2. Mean values (SD) for participant demographic and exercise variables by group

Measure	Group	
	Higher-fit	Lower-fit
Age (years)	20.1 (1.7)	20.6 (2.4)
Height (cm)	171.9 (9.6)	172.9 (10.4)
Weight (kg)*	62.6 (10.9)	75.8 (16.1)
Resting HR at post-rest session*	60.8 (10.9)	75.8 (12.5)
Max HR at GXT	191.1 (10.6)	197.9 (7.8)
RPE at GXT	18.9 (1.2)	18.9 (1.1)
Resting HR at exercise session*	62.1 (8.9)	77.4 (10.1)
HR at beginning of first task block after exercise*	65.9 (8.0)	86.2 (12.5)
Max HR at exercise treatment	168.4 (11.9)	171.4 (15.5)
RPE at exercise treatment	13.7 (.5)	14.2 (1.0)

* Denotes $P < .05$.

of responses. The Wilks' lambda statistic was used for analyses with three or more within-subject levels, and post hoc comparisons were conducted using Tukey's honestly significant difference (HSD) tests.

RESULTS

Participant characteristics

Participants' demographic data and exercise measures are provided in Table 2. Between-subject t -tests indicated a Fitness effect for VO_2 max, $t(26)=6.05$, $P < .001$, confirming that higher-fit participants exhibited greater oxygen consumption as compared with lower-fit participants. Similarly, lower resting HR at the exercise and post-rest sessions, $t_s(26) \geq 3.03$, $P < 0.01$, and lower HR at the time of the first task block during the exercise session, $t(26)=5.01$, $P < 0.001$, were observed for higher-fit, compared with lower-fit, participants. Finally, higher-fit participants weighed less than lower-fit participants, $t(26)=2.53$, $P < .02$, while no fitness differences were observed for age ($P=0.53$), height ($P=0.79$), RPE during exercise or GXT (P 's > 0.15), and max HR during exercise or GXT (P 's > 0.07).

ERN amplitude

The omnibus analysis revealed significant effects for Accuracy, $F(1,27)=8.64$, $P=0.007$, $\eta^2=.24$, Site, $F(3,81)=21.39$, $P < 0.001$, $\eta^2=.44$, and Accuracy \times Site, $F(3,81)=18.24$, $P < 0.001$, $\eta^2=.40$. Post hoc Tukey tests revealed the expected significant and largest Accuracy effect at FCz, with larger ERN amplitude for error ($M=-4.43 \mu V$, S.D.=2.77) compared with matched-correct ($M=-.22 \mu V$, S.D.=2.61) trials. A smaller, yet significant, Accuracy effect was evidenced at Cz when comparing error ($M=-1.53 \mu V$, S.D.=3.33) to matched-correct ($M=1.82 \mu V$, S.D.=2.99) ERN amplitude. No significant effect of Accuracy was observed at Fz or Pz. Thus, subsequent ERN analyses used amplitude scores from the waveforms at FCz (Falkenstein et al., 2001). See Fig. 1 for grand-averaged ERN waveforms by site.

ERN analyses revealed a Fitness \times Accuracy interaction, $F(1,26)=4.13$, $P < 0.05$, $\eta^2=.14$, with follow-up Tukey tests indicating that ERN amplitude was significantly

smaller for higher-fit ($M=-3.30 \mu V$, S.D.=2.33), compared with lower-fit ($M=-5.57 \mu V$, S.D.=2.78), individuals during error trials. No significant effect was present between higher- ($M=-.38 \mu V$, S.D.=2.63) and lower- ($M=.06 \mu V$, S.D.=2.67) fit individuals for ERN amplitude on matched-correct trials (see Fig. 2a). Finally, no significant effects including Session (P 's > 0.53) were observed, indicating that the single acute bout of moderately-hard aerobic treadmill exercise did not influence ERN amplitude (see Fig. 2b).

P_e amplitude

The omnibus analysis revealed significant effects for Accuracy, $F(1,27)=10.58$, $P=0.003$, $\eta^2=.28$, Site, $F(3,81)=4.96$, $P=0.008$, $\eta^2=.28$, and Accuracy \times Site, $F(3,81)=13.19$, $P < 0.001$, $\eta^2=.51$. Post hoc Tukey tests revealed the expected significant and largest Accuracy effect at Pz, with larger P_e amplitude for error ($M=10.72 \mu V$, S.D.=5.87) compared with matched-correct ($M=3.38 \mu V$, S.D.=5.16) trials. A smaller, yet significant, Accuracy effect was evidenced at Cz when comparing error ($M=10.31 \mu V$, S.D.=7.33) to matched-correct ($M=5.29 \mu V$, S.D.=4.09) P_e amplitude. No significant effect of Accuracy was observed at Fz or FCz. Thus, subsequent P_e analyses used amplitude scores from the waveforms at Pz (Falkenstein et al., 2000). See Fig. 1 for grand-averaged P_e waveforms by site.

P_e analyses revealed a Fitness \times Accuracy interaction, $F(1,26)=9.38$, $P=0.005$, $\eta^2=.27$, with follow-up Tukey tests indicating that P_e amplitude was significantly larger for higher-fit ($M=12.41 \mu V$, S.D.=5.39), compared with lower-fit ($M=7.92 \mu V$, S.D.=4.15), individuals during error trials. No significant effect was present between higher- ($M=2.82 \mu V$, S.D.=4.21) and lower- ($M=3.53 \mu V$, S.D.=5.27) fit individuals for P_e amplitude on matched-correct trials (see Fig. 2c). Finally, no significant effects involving Session were observed (P 's > 0.20), indicating that the single acute bout of moderately-hard aerobic treadmill exercise did not influence P_e amplitude (see Fig. 2d).

N2 amplitude

The omnibus analysis revealed a significant effect for Site, $F(1,27)=20.76$, $P < 0.001$, $\eta^2=.44$, and Congruency \times Site, $F(3,81)=3.29$, $P=0.037$, $\eta^2=.10$. Post hoc Tukey tests revealed no significant Congruency effects at any site. Subsequent N2 analyses using amplitude scores from the waveforms at FCz (Yeung et al., 2004), exhibited no significant effects for Fitness, Session, or Congruency. These findings suggest that N2 amplitude was not influenced by cardiorespiratory fitness, an acute bout of exercise, or variable amounts of interference control elicited by the task conditions in the flanker paradigm (see Fig. 3).

RT and accuracy

Analyses of error and matched-correct trial RT revealed no significant Fitness or Session effects, indicating that neither fitness level ($P=0.43$) nor an acute bout of exercise ($P=0.09$) was related to RT. Analyses of correct RT re-

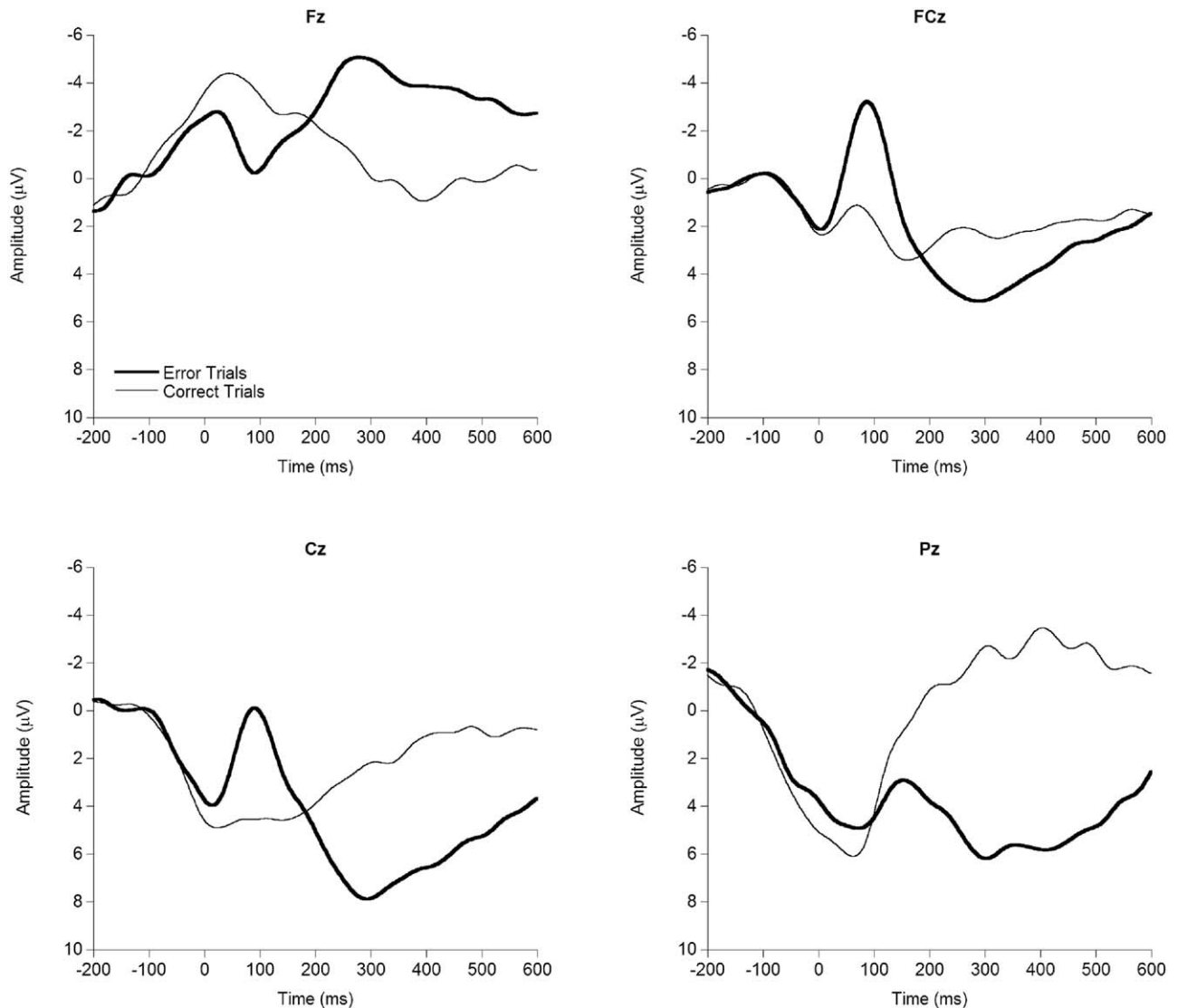


Fig. 1. Grand averaged response-locked waveforms at the four midline electrode sites (Fz, FCz, Cz, Pz) for error and correct trials.

vealed the predicted significant effect for Congruency, $F(1,26)=56.64$, $P<0.001$, $\eta^2=.68$, with longer RT for incongruent, ($M=459$ ms, $S.D.=82$) compared with neutral ($M=475$ ms, $S.D.=77$), trials. However, no significant Fitness ($P's\geq 0.29$) or Session ($P's\geq 0.40$) effects were observed. Response accuracy analyses revealed the predicted significant effect of Congruency, $F(1,26)=34.74$, $P<0.001$, $\eta^2=.56$, with reduced accuracy for incongruent ($M=91\%$ correct, $S.D.=7\%$), compared with neutral ($M=94\%$ correct, $S.D.=6\%$), trials. No significant Fitness ($P's\geq 0.33$) or Session ($P's\geq 0.11$) effects were observed (see Table 3).

Response slowing

To verify that the data conformed to the expected response slowing on trials following an error, an analysis of RT on error trials and correct trials following error trials was conducted. As expected, results indicated significantly slower

RT on correct trials following error trials ($M=472$ ms, $S.D.=71$) compared with RT on error trials ($M=408$ ms, $S.D.=67$), $F(1,26)=56.46$, $P<0.001$, $\eta^2=.69$. Thus, a Fitness \times Accuracy analysis was conducted, which indicated a significant two-way interaction, $F(1,26)=8.96$, $P<0.01$, $\eta^2=.26$. Post hoc Tukey tests revealed a significant Accuracy effect for the higher-fit group, with longer RT for correct trials following error trials ($M=492$ ms, $S.D.=80$) than for correct trials following matched-correct trials ($M=433$ ms, $S.D.=65$). This finding indicates that higher-fit individuals showed significantly more response slowing following error trials compared with correct trials matched for RT (see Fig. 4). In contrast, no significant Accuracy effect was observed for lower-fit individuals when comparing RT on correct trials following error ($M=452$ ms, $S.D.=57$) and matched-correct ($M=436$ ms, $S.D.=62$) trials. Alternately, a significant Fitness effect was present for RT on correct trials following error trials, with higher-fit

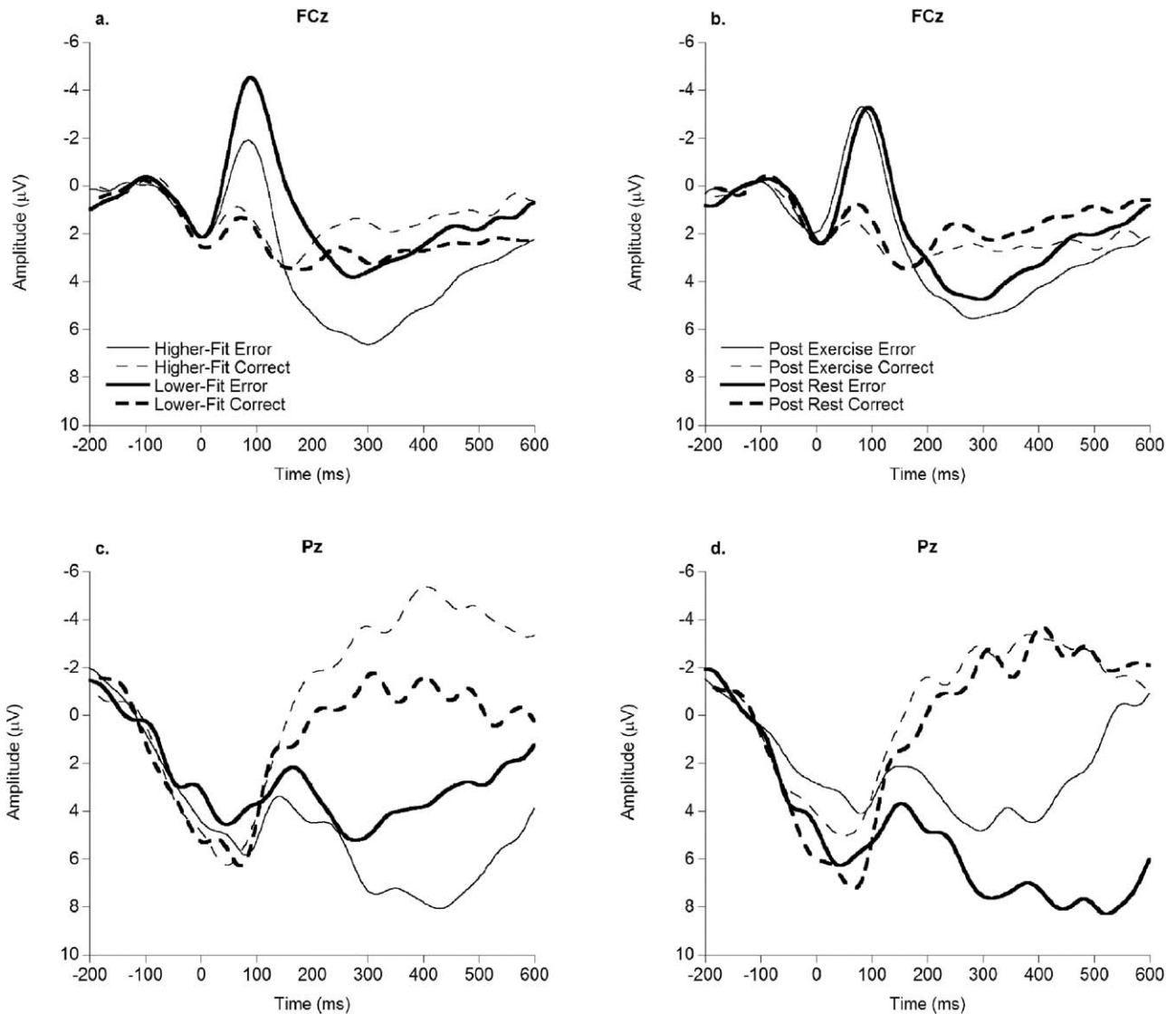


Fig. 2. Grand averaged response-locked waveforms for cardiorespiratory fitness (left side) and acute exercise effects (right side) on error and correct trials at the FCz and Pz electrode sites.

participants showing significantly longer RT compared with lower-fit individuals, suggesting increased response slowing following error trials for higher-fit participants relative to lower-fit participants. This Fitness effect was not observed for RT on correct trials following matched-correct trials (see Fig. 4).

DISCUSSION

The present study substantiated previous research on cardiorespiratory fitness influences on cognitive performance and extended this literature to action monitoring. Higher-fit individuals exhibited relatively smaller ERN amplitude than lower-fit adults, corroborating neuroimaging research indicating a relative decrease in ACC activation for aerobically trained individuals (Colcombe et al., 2004), as well as research showing decreased ERN amplitude for physically active adults (Themanson et al., in press). Additionally,

higher-fit individuals displayed both relatively larger P_e amplitude and relatively greater post-error response slowing than lower-fit individuals, suggesting an increase in both neural and behavioral post-error adjustments in top-down attentional control. Alternatively, findings revealed no relationship between a 30-minute acute bout of moderately-hard treadmill exercise and measures of performance, or neuroelectric indices of action monitoring during task performance, acquired approximately 40 min after the acute bout of exercise.

Given current views of ERN as a neuroelectric index of action monitoring processes triggered by the detection of task errors and/or response conflict, the analysis of the ERN provided a test of the relative contribution of action monitoring processes during task execution for higher- and lower-fit individuals. Analyses revealed a relationship between levels of cardiorespiratory fitness and ERN ampli-

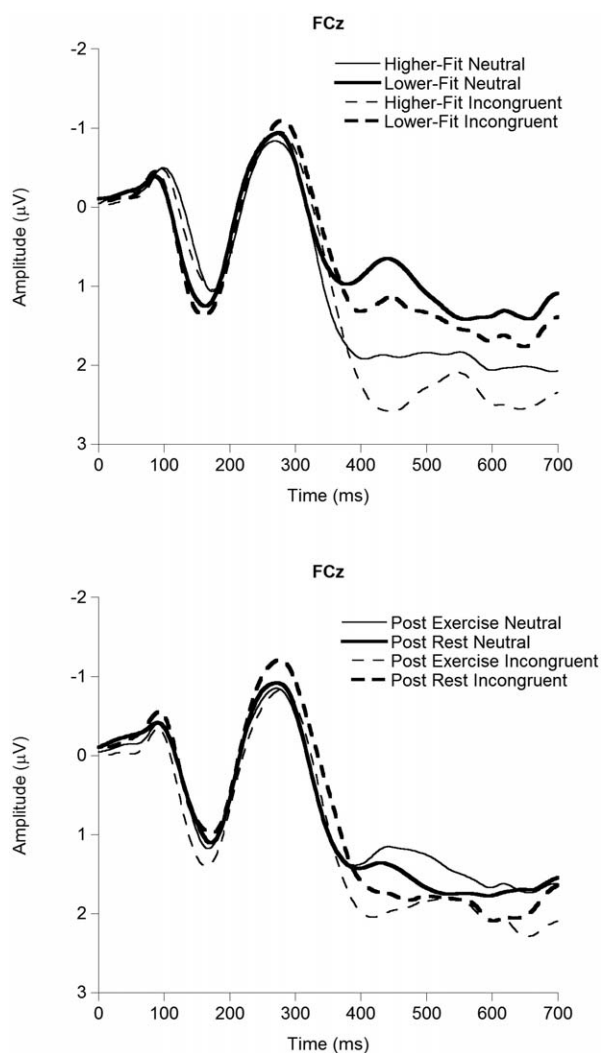


Fig. 3. Grand averaged stimulus-locked waveforms by congruency for cardiorespiratory fitness and acute exercise effects on correct trials at the FCz electrode site.

tude. Specifically, higher-fit individuals exhibited relatively decreased ERN amplitudes compared with lower-fit individuals, with no decrements in task performance (i.e. fit participants did not exhibit reduced response accuracy or increased response latency in conjunction with this reduction in ERN amplitude). This suggests that cardiorespiratory fitness may be associated with increased top-down attentional control during task execution, with a concomitant reduction in task-related response conflict. By extension, this reduction in conflict leads to decreased activation of the system designed to respond to indicants of task performance problems, resulting in reduced ERN amplitude. This is consistent with the conflict monitoring theory proposed by Botvinick et al. (2001), which suggests a reduction in conflict is evidenced in a relative reduction in the ACC and ERN activation. For example, activation of action monitoring processes in the ACC during Stroop task performance has been decreased by manipulations increasing top-down attentional control (Carter et al., 2000).

Moreover, Colcombe et al. (2004) have demonstrated a similar reduction in ACC activation during a flanker task in aerobically fit older adults. In sum, the observed reduction in ERN in higher-fit adults is consistent with these previous observations and suggests that increased top-down attentional control among aerobically fit individuals may decrease activation of action monitoring processes through a concurrent reduction in behavior conflict.

Cardiorespiratory fitness also exhibited an influence on the slowing of responses on subsequent trials following response errors, which further supports the notion that higher-fit individuals exhibit relatively greater amounts of top-down attentional control compared with lower-fit individuals. Specifically, higher-fit individuals evinced longer RT on trials immediately following errors compared with following matched-correct trials; an effect not observed for lower-fit participants. Post-error response slowing is a behavioral indicator of increased recruitment and implementation of additional top-down attentional control to improve behavioral performance on subsequent environmental interactions (Gehring et al., 1993; Kerns et al., 2004). Therefore, the observed increase in post-error response slowing for higher-fit individuals suggests that these individuals may allocate more top-down attentional control following an error than their lower-fit counterparts.

Further, levels of cardiorespiratory fitness were also related to P_e amplitude. Specifically, individuals in the higher-fit group exhibited relatively larger P_e amplitude compared with lower-fit individuals. Given current views of P_e amplitude as a neuroelectric index of post-response evaluation of an error (Davies et al., 2001; Falkenstein et al., 1990), or the allocation of attentional resources toward an error following error commission (Mathewson et al., 2005), this finding provides additional evidence for increased top-down attentional control in higher-fit individuals following an error.

Alternatively, no relationship was observed between levels of cardiorespiratory fitness and N2 amplitude or behavioral measures of pre-response conflict (i.e. interference). Although these findings appear inconsistent with an interpretation based upon reductions in conflict, the lack of an interference effect between the two fitness groups may be due to a floor effect of RT in healthy younger adults. That is, previous research using a switch task (Themanson et al., in press) revealed that physical activity was related to shorter RT on conditions requiring greater amounts of top-down attentional control in older adults, but not younger adults. This supports the contention that younger adults may be performing at maximum efficiency, leaving

Table 3. Mean values (SD) for percentage of correct responses by treatment condition and by group

Condition	Group		Total
	Higher-fit	Lower-fit	
Exercise	90.9 (8.0)	93.4 (5.7)	92.1 (6.9)
Rest	91.9 (7.0)	94.2 (5.4)	93.1 (6.3)
Total	91.4 (7.5)	93.8 (5.3)	

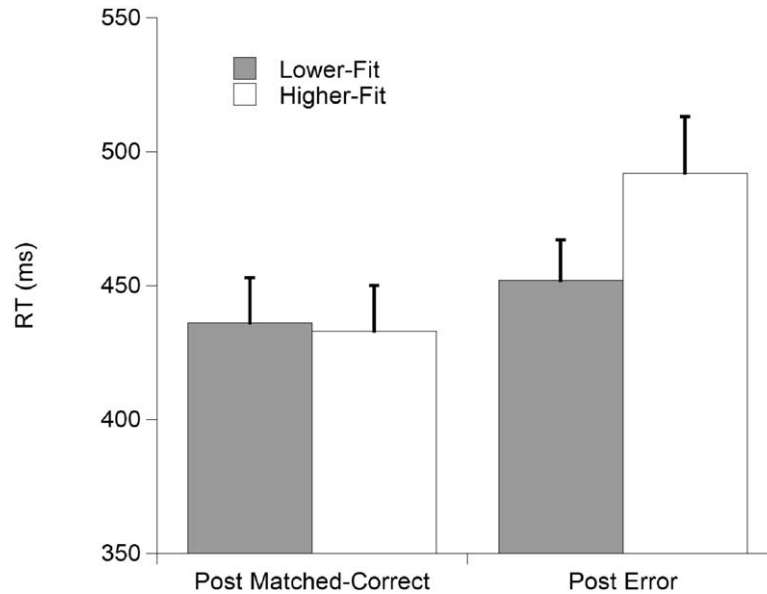


Fig. 4. Average response time for correct trials immediately following error trials and matched-correct trials by cardiorespiratory fitness group.

little room for fitness-related improvements. Additionally, N2 amplitude was not influenced by fitness, suggesting that the influence of fitness on conflict may be specific to errors, processes related to error commission, or post-error adjustments in control in young adults. However, this relationship may be different in studies of response conflict on correct trials during older adulthood (see Colcombe et al., 2004).

Collectively, the present findings suggest increased top-down attentional control in higher-fit individuals reduces levels of error-related response conflict and increases levels of post-error attention control. Specifically, reduced ERN amplitude is associated with increased post-error behavioral adjustments in higher-fit individuals, suggesting a more efficient neuroelectric system related to action monitoring processes. This finding corroborates previous research examining physical activity and action monitoring processes (Themanson et al., *in press*) as well as fitness training influences on ACC activation (Colcombe et al., 2004). However, these findings are inconsistent with previous research examining ERN amplitude and post-error adjustments, which has documented increased conflict during error commission with subsequent increased recruitment of top-down attentional control (Gehring et al., 1993; Kerns et al., 2004). This discrepancy in the literature may suggest top-down attentional control modulation associated with action monitoring processes differs for individuals of varying levels of cardiorespiratory fitness. Further, this fitness-difference appears to be specific to error and post-error processes related to conflict and top-down attentional control. Thus, future research is necessary to determine the relationship and extent to which cardiorespiratory fitness is related to action monitoring.

Acute bouts of exercise were observed to be unrelated to neuroelectric and behavioral measures of task performance, suggesting that exercise may not produce a substan-

tial influence on cognitive processes when it is distributed in single, acute bouts. However, cognitive measurements of acute exercise effects on neuroelectric and behavioral indices of action monitoring processes did not take place until approximately 40 min following the acute exercise session. Additionally, all acute bouts of exercise were conducted on a treadmill in this investigation. Future research should assess cognitive processes at multiple durations following acute exercise, examine varying levels of exercise intensity, employ different durations of acute exercise, and utilize diverse modes of exercise to better examine the possible relationship between action monitoring processes and acute exercise.

Limitations

Despite the demonstrated relationships between cardiorespiratory fitness, and neuroelectric and behavioral indices of action monitoring, the lack of random assignment to fitness groups, as well as the cross-sectional nature of this study, limits the strength of the findings because the relationship may be attributable to other factors (e.g. genetics, personality characteristics). Future research should utilize a randomized control design that manipulates cardiorespiratory fitness to avoid the issues associated with self-selection into fitness groups. In spite of these limitations, these data serve as preliminary evidence that adopting a more physically active lifestyle aimed at increasing cardiorespiratory fitness may be associated with cognitive benefits involving action monitoring processes.

CONCLUSION

In sum higher levels of cardiorespiratory fitness were associated with benefit in cognitive processing through an increase in top-down attentional control as measured by reduced ERN amplitude and increased neuroelectric (i.e.

P_e amplitude) and behavioral (i.e. post-error response slowing) corrective actions following errors in higher-fit adults. Alternatively, acute aerobic exercise was not related to neuroelectric or behavioral indices of action monitoring. The current results add to the growing literature on the beneficial relationship of cardiorespiratory fitness on cognitive function and provide a basis for the further exploration of exercise and fitness influences on action monitoring.

REFERENCES

- American College of Sports Medicine (2000) ACSM's guidelines for exercise testing and prescription, 6th ed. New York: Lippincott Williams & Wilkins.
- Bashore TR (1989) Age, physical fitness, and mental processing speed. *Annu Rev Gerontol Geriatr* 9:120–144.
- Bashore TR, Goddard PH (1993) Preservative and restorative effects of aerobic fitness on the age related slowing of mental speed. In: *Adult information processing: Limits on loss* (Cerella J, Rhybash J, Hoyer W, eds), pp 205–228. New York, NY: Academic Press.
- Blumenthal JA, Emery CF, Madden DJ, Schniebolk S, Walsh-Riddle M, George LK, McKee DC, Higginbotham MB, Cobb FR, Coleman RE (1991) Long-term effects of exercise on psychological functioning in older men and women. *J Gerontol Psychol Sci* 46:352–361.
- Borg G (1970) Perceived exertion as an indicator of somatic stress. *Scand J Rehabil Med* 2:92–98.
- Botvinick MM, Braver TS, Barch DM, Carter CS, Cohen JD (2001) Conflict monitoring and cognitive control. *Psychol Rev* 108:624–652.
- Boutcher SH, Landers DM (1988) The effects of vigorous exercise on anxiety, heart rate, and alpha activity of runners and nonrunners. *Psychophysiology* 25:696–702.
- Carter CS, Braver TS, Barch DM, Botvinick MM, Noll D, Cohen JD (1998) Anterior cingulate cortex, error detection, and the online monitoring of performance. *Science* 280:747–749.
- Carter CS, Macdonald AM, Botvinick M, Ross LL, Stenger VA, Noll D, Cohen JD (2000) Parsing executive processes: Strategic vs. evaluative functions of the anterior cingulate cortex. *Proc Natl Acad Sci U S A* 97:1944–1948.
- Colcombe S, Kramer AF (2003) Fitness effects on the cognitive function of older adults: A meta-analytic study. *Psychol Sci* 14:125–130.
- Colcombe SJ, Kramer AF, Erickson KI, Scalf P, McAuley E, Cohen NJ, Webb A, Jerome GJ, Marquez DX, Elavsky S (2004) Cardiovascular fitness, cortical plasticity, and aging. *Proc Natl Acad Sci U S A* 101:3316–3321.
- Coles MGH, Scheffers MK, Holroyd CB (2001) Why is there an ERN/Ne on correct trials? Response representations, stimulus-related components, and the theory of error-processing. *Biol Psychol* 56:173–189.
- Compumedics Neuroscan (2003) Offline analysis of acquired data, SCAN 4.3, Vol. II, edition 4.3. [Software manual.] El Paso, TX: Compumedics Neuroscan.
- Davies PL, Segalowitz SJ, Dywan J, Pailing PE (2001) Error-negativity and positivity as they relate to other ERP indices of attentional control and stimulus processing. *Biol Psychol* 56:191–208.
- Dehaene S, Posner MI, Tucker DM (1994) Localization of a neural system for error detection and compensation. *Psychol Sci* 5:303–305.
- Dengel DR, Pratley RE, Hagberg JM, Goldberg AP (1994) Impaired insulin sensitivity and maximal responsiveness in older hypertensive men. *Hypertension* 23:320–324.
- Dustman RE, Emmerson RY, Shearer DE (1990) Electrophysiology and aging: Slowing, inhibition, and aerobic fitness. In: *Cognitive and behavioral performance factors in atypical aging* (Howe ML, Stones MJ, Brainerd CJ, eds), pp 103–149. New York, NY: Springer-Verlag.
- Eriksen BA, Eriksen CW (1974) Effects of noise letters upon the identification of a target letter in a nonresearch task. *Percept Psychophys* 16:143–149.
- Eriksen CW, Schultz DW (1979) Information processing in visual search: A continuous flow conception and experimental results. *Percept Psychophys* 25:249–263.
- Etnier JL, Salazar W, Landers DM, Petruzzello SJ, Han M, Nowell P (1997) The influence of physical fitness and exercise upon cognitive functioning: A meta-analysis. *J Sport Exerc Psychol* 19:249–274.
- Falkenstein M, Hohnsbein J, Hoormann J, Blanke L (1990) Effects of errors in choice reaction tasks and the ERP under focused and divided attention. In: *Psychological brain research* (Brunia CHM, Gaillard AWK, Kok A, eds), pp 192–195. Tilburg, The Netherlands: Tilburg University Press.
- Falkenstein M, Hohnsbein J, Hoormann J, Blanke L (1991) Effects of crossmodal divided attention on late ERP components: II. Error processing in choice reaction tasks. *Electroencephal Clin Neurophysiol* 78:447–455.
- Falkenstein M, Hoormann J, Christ S, Hohnsbein J (2000) ERP components on reaction errors and their functional significance: A tutorial. *Biol Psychol* 51:87–107.
- Falkenstein M, Hoormann J, Hohnsbein J (2001) Changes of error-related ERPs with age. *Exp Brain Res* 138:258–262.
- Gehring WJ, Goss B, Coles MGH, Meyer DE, Donchin E (1993) A neural system for error detection and compensation. *Psychol Sci* 4:385–390.
- Gehring WJ, Knight RT (2000) Prefrontal-cingulate interactions in action monitoring. *Nat Neurosci* 3:516–520.
- Herrmann MJ, Römmler J, Ehlis A-C, Heidrich A, Fallgatter AJ (2004) Source localization (LORETA) of the error-related-negativity (ERN/Ne) and positivity (Pe). *Cogn Brain Res* 20:294–299.
- Hill RD, Storandt M, Malley M (1993) The impact of long-term exercise training on psychological function in older adults. *J Gerontol* 48:12–17.
- Hillman CH, Belopolsky A, Snook EM, Kramer AF, McAuley E (2004) Physical activity and executive control: Implications for increased cognitive health during older adulthood. *Res Q Exerc Sport* 75:176–185.
- Hillman CH, Kramer AF, Belopolsky AV, Smith DP (2006) A cross-sectional examination of age and physical activity on performance and event-related brain potentials in a task switching paradigm. *Int J Psychophysiol* 59:30–39.
- Hillman CH, Snook EM, Jerome GJ (2003) Acute cardiovascular exercise and executive control function. *Int J Psychophysiol* 48:307–314.
- Hillman CH, Weiss EP, Hagberg JM, Hatfield BD (2002) The relationship of age and cardiovascular fitness to cognitive and motor processes. *Psychophysiology* 39:303–312.
- Hogervorst E, Riedel W, Jeukendrup A, Jolles J (1996) Cognitive performance after strenuous physical exercise. *Percept Mot Skills* 83:479–488.
- Holroyd CB, Coles MGH (2002) The neural basis of human error processing: Reinforcement learning, dopamine, and the error-related negativity. *Psychol Rev* 109:679–709.
- Jasper HH (1958) The ten-twenty electrode system of the International Federation. *Electroencephalogr Clin Neurophysiol* 10:371–375.
- Kerns JG, Cohen JD, MacDonald AW III, Cho RY, Stenger VA, Carter CS (2004) Anterior cingulate conflict monitoring and adjustments in control. *Science* 303:1023–1026.
- Kramer AF, Hahn S, McAuley E (2000) Influence of aerobic fitness and the neurocognitive function of older adults. *J Aging Phys Act* 8:379–385.
- Kramer AF, Sowon H, Cohen NJ, Banich MT, McAuley E, Harrison CR, Chason J, Vakil E, Bardell L, Boileau RA, Colcombe A (1999) Ageing, fitness, and neurocognitive function. *Nature* 400:418–419.

- Magnié MN, Bermon S, Martin F, Madany-Lounis M, Suisse G, Muhammad W, Dolisi C (2000) P300, N400, aerobic fitness and maximal aerobic exercise. *Psychophysiology* 37:369–377.
- Mathalon DH, Whitfield SL, Ford JM (2003) Anatomy of an error: ERP and fMRI. *Biol Psychol* 64:119–141.
- Mathewson KJ, Dywan J, Segalowitz SJ (2005) Brain bases of error-related ERPs as influenced by age and task. *Biol Psychol* 70:88–104.
- Meyer DE, Kieras DE (1997) A computational theory of executive cognitive processes and multi-task performance: Part 1. Basic mechanisms. *Psychol Rev* 104:3–65.
- Miltner WHR, Lemke U, Weiss T, Holroyd C, Scheffers MK, Coles MGH (2003) Implementation of error-processing in the human anterior cingulate cortex: A source analysis of the magnetic equivalent of the error-related negativity. *Biol Psychol* 64:157–166.
- Nieuwenhuis S, Ridderinkhof KR, Talsma D, Coles MGH, Holroyd CB, Kok A, van der Molen MW (2002) A computational account of altered error processing in older age: Dopamine and the error-related negativity. *Cogn Affect Behav Neurosci* 2:19–36.
- Norman DA, Shallice T (1986) Attention to action: Willed and automatic control of behavior. In: *Consciousness and self-regulation: Vol. 4, Advances in research and theory* (Davidson RJ, Schwartz GE, Shapiro D, eds), pp 1–18. New York, NY: Plenum Press.
- Rodríguez-Fornells A, Kurzbuch AR, Münte TF (2002) Time course of error detection and correction in humans: Neurophysiological evidence. *J Neurosci* 22:9990–9996.
- Spencer KM, Coles MGH (1999) The lateralized readiness potential: Relationship between human data and response activation in a connectionist model. *Psychophysiology* 36:364–370.
- Themanson JR, Hillman CH, Curtin JJ. Age and physical activity influences on action monitoring during task switching. *Neurobiol Aging*, in press.
- van Veen V, Carter CS (2002) The timing of action-monitoring processes in the anterior cingulate cortex. *J Cogn Neurosci* 14:593–602.
- Yeung N, Cohen JD, Botvinick MM (2004) The neural basis of error detection: conflict monitoring and the error-related negativity. *Psychol Rev* 111:931–959.

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