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RESEARCH ARTICLE

The interactive effects of physical fitness and acute aerobic exercise on electrophysiological coherence and cognitive performance in adolescents

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Abstract The current study examined the effects of physical fitness and aerobic exercise on cognitive functioning and coherence of the electroencephalogram in 30 adolescents between the ages of 13 and 14 years. Participants were first classified as fit or unfit and then performed a modified Eriksen flanker task after a bout of acute exercise and after a period of relaxation. Analysis of behavioural differences between the fit and unfit groups revealed an interaction between fitness levels and acute physical exercise. Specifically, fit participants had significantly faster reaction times in the exercise condition in comparison with the rest condition; unfit, but not fit, participants had higher error rates for NoGo relative to Go trials in the rest condition. Furthermore, unfit participants had higher levels of lower alpha, upper alpha, and beta coherence in the resting condition for NoGo trials, possibly indicating a greater allocation of cognitive resources to the task demands. The higher levels of alpha coherence are of particular interest in light of its reported role in inhibition and effortful attention. The results suggest that physical fitness and acute exercise may enhance cognition by increasing the efficacy of the attentional system.

Keywords EEG · Coherence · Fitness · Exercise · Cognitive performance

Introduction

Extensive research has highlighted the benefits of regular exercise for physical health and well-being (Colcombe and Kramer 2003). More recently, the beneficial effects of physical fitness on cognitive functioning have been examined. Many studies in this area have focused on elderly adults with an emphasis on the protective function of physical activity in the context of age-related cognitive decline (Churchill et al. 2002). The benefits observed largely pertain to executive control (Colcombe and Kramer 2003), a critical high-level system involved in the orchestration of human cognition and action (Norman and Shallice 1986). Executive control plays an important role in action planning, switching, and inhibition (Royall et al. 2002) and shows a high degree of interindividual variability in its functionality (Kiefer et al. 2005). Although both acute bouts of exercise and physical fitness established over longer period of time have been shown to enhance cognitive functioning, the effects of physical fitness appear larger and more robust (Colcombe and Kramer 2003; Stroth et al. 2009). Nevertheless, a recent meta-analysis revealed that cognitive performance during, immediately after, and after a delay of up to 20 min of acute bouts of exercise was enhanced and that these effects are largest for older adults and school-age children relative to the population as a whole (Chang et al. 2012). However, less is known about the neurophysiological changes that may account for the benefits of exercise on

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cognitive performance in children, and whether or not the effects of acute exercise are any different for fit and unfit children. In the current study, we therefore examined the effects of an acute bout of exercise on electroencephalogram (EEG) coherence and behavioural performance of fit and unfit participants between the ages of 13 and 14 years.

Acute exercise, long-term fitness, and cognitive function in children

Given that children and adolescents are an important target for programs in physical education, it is desirable to know more about the short- and long-term effects of physical exercise in this population. Researchers have employed correlational and experimental study designs to examine the relationship between physical fitness and performance on cognitive tasks. A meta-analysis by Sibley and Etnier (2003) reported global cognitive benefits of physical exercise on cognitive functioning in children and adolescents in both correlational and experimental studies. Recent correlational studies have also examined more specific cognitive and physiological effects of exercise in pre-adolescent children. For example, Hillman et al. (2009) examined executive functioning differences between higher- and lower-fit pre-adolescent children (average age 9.4 years). Higher fitness levels were associated with superior executive functioning performance across different conditions of the Erikson flanker task, and also with larger P3 amplitudes of the event-related potential (ERP) in response to stimuli. As the P3 ERP component is an electrophysiological index of attentional allocation (Polich 1987), this finding suggests that increased allocation of attentional resources during the encoding of stimuli was related to better performance in the physically fitter children. These findings are consistent with previous research (Hillman et al. 2005), which has reported enhanced behavioural performance as well as shorter P3 latencies and larger P3 amplitudes in physically fitter children. Higher levels of physical fitness in adolescence have also been found to modulate ERP components associated with executive control such as the N2 ERP component (Stroth et al. 2009; Themanson et al. 2006). In addition to fitness, acute bouts of exercise may increase cognitive performance, regardless of prior exercise regimes (Zervas et al. 1991). Finally, exercise programmes across several weeks have also been shown to improve executive functioning in children and adolescents (Tuckman and Hinkle 1986; Hinkle et al. 1993; Davis et al. 2007).

Effects of acute exercise and long-term fitness on brain function

The neurobiological mechanisms that underlie the beneficial effects of acute and chronic exercise and fitness on cognitive performance in children are still poorly understood. Animal models highlight possible mechanisms through which exercise may influence neurological development, increase neurological efficiency, and enhance cognitive performance. The processes of neural adaptation induced by exercise comprise an increase in regional blood flow (Endres et al. 2003), promotion of brain vascularization (Pereira et al. 2007), an increase in levels of brain-derived neurotrophic factor (BDNF), as well as up-regulation of genes associated with cellular plasticity (Vaynman and Gomez-Pinilla 2006). Moreover, the induction of hippocampal neurogenesis, particularly in the dentate gyrus following physical exercise has been observed in adult (Van Praag et al. 1999a, b; Llorens-Martín et al. 2006) as well as juvenile mammals (Lou et al. 2008). As a result of these neuroplastic changes, brain function is more efficient and adaptive thereby supporting better learning and performance in animals (cf. Cotman and Berchtold 2002). These findings from animal studies have been widely confirmed in human participants (Dierks et al. 2000; Neeper et al. 1995; Pereira et al. 2007).

The neurobiological changes induced by exercise and fitness might influence distributed, but coordinated brain activities, which may be critical for understanding the effects of exercise on cognitive performance. Possible candidates are neural assemblies, that is, distributed networks of neurons transiently linked by reciprocal dynamic connections. The assumption is that particular behaviours are associated with a relatively stable activation pattern of the relevant assemblies and that synchronous oscillations mediate both local interactions between neural networks and long-range interactions between cortical areas (Schnitzler and Gross 2005). Physical exercise may improve cognition by modulating temporal functional connections between cell assemblies that support task performance. Although the operation of neural assemblies is difficult to capture in real time, the millisecond temporal resolution of electroencephalography and the use of coherence analysis to examine synchronous oscillations of electrical activity across scalp locations suggests that EEG coherence measures offer one way of assessing the operation of neural assemblies.

In line with this assumption, acute exercise manipulations have been shown to affect oscillatory activity in the human EEG (Bailey et al. 2008; Moraes et al. 2007). For example, studies have reported that exercise increases oscillatory activity in the alpha range during subsequent cognitive performance, often localized to the right frontal hemisphere (Petruzzello and Landers 1994). This activity is thought to reflect a state of decreased cortical activity associated with relaxation and decreased anxiety (Boutcher 1993). However, no studies to date have examined changes in EEG coherence in fit and unfit participants at rest and in response to acute physical exercise.

Electroencephalogram coherence analysis offers an opportunity to assess the functional connectivity of cortical regions while tasks are being performed. Coherence between two EEG signals, which is the squared cross-correlation in the frequency domain between two EEG time series measured simultaneously at different scalp locations (Nunez 1981), has been interpreted as a measure of the degree of synchronization between brain signals of certain brain regions. Patterns of high coherence between EEG signals recorded at different scalp sites have a functional significance because they are correlated with different kinds of cognitive information processing, like memory, language, concept retrieval, and music processing (Sarnthein et al. 1998; Weiss et al. 1999; Weiss et al. 1998; Weiss and Rappelsberger 2000). Most important for the purpose of the present study is that group differences in coherence levels have been linked with levels of cognitive ability (Jiang and Zheng 2006; Deeny et al. 2009). Hence, changes in EEG coherence as a function of acute exercise and fitness may be an important mechanism underlying the beneficial effects of exercise on cognitive performance.

The current study

The current study examined the effects of physical fitness levels and acute aerobic exercise on cognitive performance and EEG coherence in a sample of 30 adolescents between the ages of 13 and 14 years. The cognitive performance task used was a modified version of the Erikson flanker task (Eriksen and Eriksen 1974, Ruchsow et al. 2004). In the Go/NoGo version of the task, participants had to respond to specific target letters, but withhold the response to others. The flanking letters either indicated the same, compatible response mode as the target letter (Go or NoGo) or a different, incompatible response mode. Physical fitness was assessed by a continuous-graded maximal exercise test, to validly identify individual fitness levels. Participants were then divided by means of a median split into relatively fit and unfit groups within our sample. The acute bout of exercise was realized by using a 20-min workout on a stationary bike at a moderate intensity.

As physical fitness produced more consistent and robust effects in comparison to acute exercise in previous reports (Lardon and Polich 1996; Themanson and Hillman 2006), we expected that physical fitness would enhance behavioural performance and modulate EEG coherence measures reflecting the underlying efficiency of cortical processing. Specifically, it was hypothesized that higher physical fitness would be associated with shorter reactions times (RTs) and lower error rates (ER) compared to lower physical fitness. It was also hypothesized that acute aerobic exercise would positively affect performance to a lesser extent.

With regards to EEG coherence, we predicted that greater effort would be required by the unfit group and would therefore result in higher levels of coherence in response to the Erikson flanker task. Similarly, we predicted that the acute exercise condition would increase cortical processing efficiency and thus result in lower levels of EEG coherence in comparison with the rest condition. The alpha band frequencies were of particular interest in this regard, given that previous research has associated alpha modulation with inhibition (Jokisch and Jensen 2007) and lower alpha specifically with effortful attention (Klimesch 1999). At the same time, in light of research from both human and animal studies supporting a role for neuronal synchronization in the gamma band underlying feature binding, learning, and memory (Herrmann et al. 2010; Jensen et al. 2007; Rieder et al. 2011), we also explored the possibility that fitness- and acute exercise-related differences would be observed in gamma coherence. While current theory and research suggests that gamma synchronization may be critical during the formation of new neural assemblies that undergird learning, theta is known to be involved in memory processing and has been related to gamma (gamma appearing during particular phases within the theta cycle) in studies using intracortical recordings (Mormann et al. 2005) and EEG recording (Demiralp et al. 2007). In order to better understand the influence of fitness and acute exercise on coherence, the current study examines coherence effects across groups and stimulus conditions in the delta, theta, alpha, beta, and gamma range.

Methods

Participants

Thirty healthy adolescents participated in the present study. Participants were recruited through the local administration of secondary schools and were invited to participate in the study by means of an information event at school during class. Mean age was 14.2 years (SD = 0.5). All participants were right-handed and had normal, or corrected to normal vision. Participants were carefully screened and did not show any signs of a history of neurological or psychiatric disorders or medication intake. Participants were divided into two groups according to a median split of the fitness distribution. This was performed for boys and girls separately in order to keep the gender distribution equal in each group. Fifteen adolescents (ten boys and five girls) were classified as “fit” and fifteen adolescents (nine boys and six girls) were classified as “unfit”. With regard to participants' age, height, and weight, no significant differences between the groups existed. All adolescents received information material in order to fully inform their parents. They were allowed to participate after their legal guardian had permitted informed consent. The present study was carried out in accordance with the ethical review board at the University of Ulm, Germany.

Study design

During a regularly scheduled physical education class, participants underwent a maximal incremental cycling test on an electrically braked stationary cycle ergometer to assess physical fitness via individual maximal exercise performance. This exercise test was conducted in order to plan an individually adjusted bout of exercise with heart rate control. Bouts of exercise were planned at 60 % of the individual's maximal heart rate, representing about 50–60 % of maximum oxygen uptake (Wasserman and McIlroy 1964), leading to a workout at a moderate but brisk intensity.

Participants were then assigned to the study with two recording sessions, one following a 20-min bout of exercise and one following a 20-min period of rest. During both sessions, participants came into the laboratory and watched a movie, during the cycling workout as well as during the resting condition. They participated in both conditions in a random order within an exact 7-day interval, at the same day of the week, at the same time of the day to avoid differences in preceding activities or circadian distortions. During both sessions, participants were prepared for the EEG recordings and subsequently performed the 20-min-exercise condition or the resting condition, sitting on the cycling ergometer for 20 min in both conditions to keep them as similar as possible. Afterwards, they performed an Eriksen flanker task with EEG recordings.

Fitness testing

The fitness test was performed 1 week before the recording sessions started. The participating adolescents completed a continuous-graded maximal exercise test during physical education class, with the test administered by members of the research team. The testing protocol started with a resistance of 25 W. Every 2 min, the watt-load of the dynamometer was then increased in 25 W intervals, while the participant maintained the pedalling rate constant at 60 rotations per minute. Grades were continuously increased until the participant reached subjective exhaustion and stopped pedalling. At each interval (every 2 min), the investigator metered and documented heart rates from the monitor the subject was wearing (Polar Electro®, Buettelborn, Germany, Model F6). Heart rate at each interval up to maximal heart rate, absolute time pedalling on the bike (in seconds) as well as maximal watt performance was documented on a record sheet for each subject separately. Maximal watt performance on the dynamometer was then related to the body mass index (BMI) to establish a standardized value for physical fitness, controlling for body mass and size (Armstrong and Welsman 2007). Participants were then divided by means of a median split into relatively fit and unfit groups within our sample. However, as fitness norms are not available for this test, the absolute fitness level cannot be determined in our participants. The median fitness score for girls was 7.11 and the median fitness score for boys was 8.42. For participants' demographic variables and fitness parameters, see Table 1.

Table 1 Means (SDs) of participants' demographic and exercise variables for fit and unfit groups separately, and *p* value for *t* test differences between groups

	Fit ($N = 15$)	Unfit ($N = 15$)	*p* value
Age (years)	14.29 (.48)	14.32 (.70)	.86
Body weight (kg)	50.81 (9.41)	56.63 (16.25)	.24
Height (cm)	1.64 (.07)	1.61 (.09)	.45
BMI	19.49 (3.44)	19.90 (3.18)	.73
Max. duration of exercise (s)	616 (154.5)	546 (157.8)	.22
Max. watt performance of exercise	168 (31.99)	138 (24.76)	.008
Watt/BMI ratio	8.91 (1.21)	6.78 (0.87)	<.0001

Cognitive task

We combined a Go/NoGo task with an Eriksen flanker paradigm, which has been used in several earlier studies (e.g. Ruchsow et al. 2005). Eight different letter strings (congruent: BBBBB, DDDDD, VVVVV, and UUUUU; incongruent: BBDBB, DDBDD, UUVUU, and VVUVV) were presented on a computer screen in randomized order. Subjects had to focus on the target letter in the middle of an array and had to press a response key upon the appearance of the letters B and U (Go condition) and to withhold key press upon the appearance of D and V (NoGo condition). Instructions equally emphasized speed and accuracy. Responses were executed with the index finger of their dominant hand. Letter strings were signalized by a warning stimulus (fixation cross) presented for 600 ms centrally on the screen before the imperative stimuli in the form of letter strings appeared. Each letter combination was presented for a total of 480 ms, with the target letter in the middle of the array appearing after a 320 ms delay with a duration of 80 ms. Subjects received feedback according to their performance 750 ms after key press. As feedback stimuli, we used the German expressions for "correct", "false", and "faster". Feedback stimuli were presented for 500 ms. The inter-trial-interval was 2,600 ms. In each trial, participants received a reward for correct responses and were penalized for errors (5 points per trial). In the end, the greatest amount of points was calculated, and the winner was promised a reward. Before the main experiment, subjects had a training period of 12–20 trials. The whole experiment consisted of five blocks of 120 trials each (300 Go trials; 300 NoGo trials). The behavioural data collected was response latency in ms from the presentation of the target stimulus (Go trials) and response accuracy in terms of percentage of correct responses (Go- and NoGo trials). Participants were seated in a comfortable chair in a sound-attenuating, electrically shielded booth. The whole experiment lasted about 3 h, including exercise/rest sessions, pauses, electrode placement, and removal of electrodes.

EEG recording and coherence calculation

Electroencephalogram was continuously recorded using 39 channels mounted in an elastic cap (Easy Cap, Herrsching, Germany). Electrodes were positioned according to the extended 10–20 system. All electrodes were referenced to an electrode at the left earlobe and re-referenced to average reference off-line. Eye movements were registered by vertical and horizontal EOG. Electrode impedances were kept below 5 kΩ. The EEG was amplified by Neuroscan Synamps amplifiers (bandwidth DC-50 Hz; 50 Hz notch filter) and A/D converted with 12-bit resolution at a rate of 250 Hz and digitally low-pass filtered with 16 Hz and digitally high-pass filtered with 0.10 Hz.

Incorrect responses were excluded from the analysis. The data of participants with fewer than 10 usable epochs for each condition type were removed from the analysis. This led to the removal of three participants. The remaining epochs were separated into stimulus categories. Coherence values were calculated using an EEG sample frame duration of 0.512 s (i.e. 512 samples). A mean coherence value was then calculated by applying this frame to 200 different EEG samples, each centred at a different post-stimulus time ranging from +400 to +800 ms post-stimulus, and by calculating the mean coherence across all such frames for each stimulus category for each participant.

The particular coherence metric used in this study was the event-related linear coherence (ERLCOH) which is a measure of the synchronization in activity between two electrode sites. As part of the process of calculating the ERLCOH, the inter-trial linear coherence (ITLC) is removed. The subtraction of ITLC should result in the intrinsic synchronization between the two electrode sites being reported.

Event-related linear coherence was computed for 18 intra-regional electrode pairings for 3 regions; frontal (Fp1, F7, F3, Fp2, F8, F4), temporal (T7, TP7, FT7, T8, TP8, FT8), and parietal (CP3, P3, P7, CP4, P4, P8). Average intra-regional coherence scores were computed for the three regions. The linear coherence with ITC subtracted was computed for six frequencies: delta 0.5–3 Hz, theta 3–5 Hz, lower alpha 5–9 Hz, upper alpha 9–12.5 Hz, beta 12.5–30 Hz, and gamma 30–50 Hz, and for congruent, incongruent, Go and NoGo trial and for the film and bike conditions.

Statistical analyses

Coherence for each frequency band was analysed in a series of six separate 2 (Fitness: unfit vs. fit) × 2 (Exercise: rest vs. exercise) × 2 (Trial: Go vs. NoGo) × 2 (Congruency: congruent vs. incongruent) × 3 (Region: frontal, temporal, parietal) mixed-factor analysis of variance (ANOVAs). Behavioural measures (reaction time, error rate) were analysed using a series of two 2 (Fitness: unfit vs. fit) × 2 (Exercise: rest vs. exercise) × 2 (Trial: Go vs. NoGo) × 2 (Congruency: congruent vs. incongruent) ANOVAs.

Results

Behavioural performance

A repeated measures ANOVA on the mean RT (reaction time) of hits (correct Go-responses) revealed a main effect of congruency, $F(1, 28) = 53.60$, $p < .001$, indicating that in congruent trials RT was significantly faster than in incongruent trials. There was no main effect of fitness level or acute exercise on RT. However, a significant Fitness × Exercise effect was observed, $F(1, 28) = 7.27$, $p = .012$. Post hoc contrasts revealed that, although unfit participants showed a trend for a slowing of RTs in the acute exercise condition compared to the rest condition, this effect was not statistically significant, $F(1, 28) = 3.\ 37$, $p = .07$; conversely, fit participants had significantly faster RTs in the exercise condition in comparison with the rest condition, $F(1, 28) = 3.\ 90$, $p = .05$; see Fig. 1.

Analysis of error rates across conditions revealed a main effect of congruency, $F(1, 28) = 51.40$, $p < .0001$, with lower error rates observed in congruent ($M = 7.20$, $SD = 3.84$) relative to incongruent trials ($M = 13.10$, $SD = 7.48$). There was a main effect of Trial, $F(1, 28) = 5.037$, $p < .05$, with lower error rates for Go trials relative to NoGo trials. The interactions Exercise × Trial, $F(1, 28) = 4.54$, $p < .05$; and Fitness × Exercise × Trial, $F(1, 28) = 17.31$, $p < .001$ were significant. The results of follow-up ANOVAs conducted for fit and unfit groups separately revealed a significant Exercise × Trial effect for the unfit group, $F(1, 14) = 16.90$, $p < .001$, and a non-significant Exercise × Trial effect for the fit group, $F(1, 14) = 2.430$, $p = .141$. Post hoc contrasts revealed that revealed that unfit, but not fit, participants showed

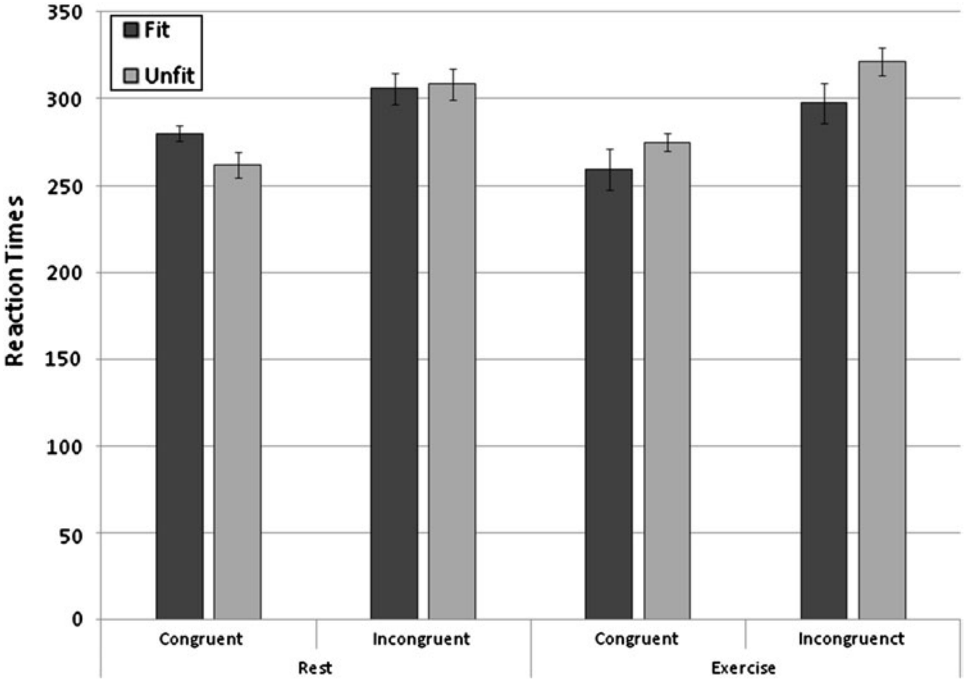

Fig. 1 Reaction times for the fit and unfit groups for the rest and exercise conditions for both congruent and incongruent trials

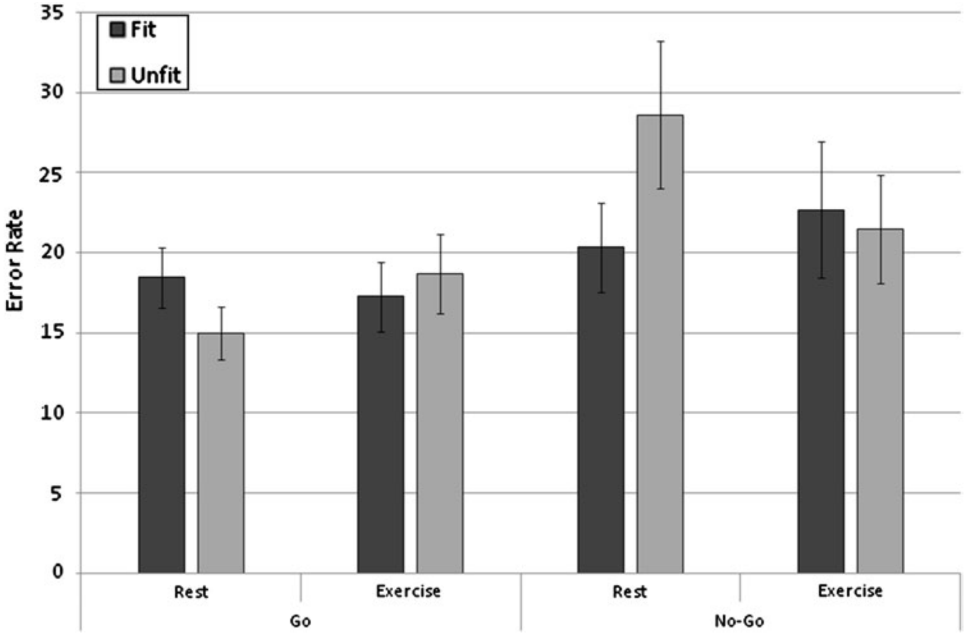

Fig. 2 *Error rates* for the fit and unfit groups for the rest and exercise conditions for both Go and NoGo trials

significantly higher error rates for NoGo relative to Go trials in the rest condition, $F(1, 28) = 11.68$, $p < .005$; see Fig. 2.

EEG coherence

Congruency affected EEG coherence in all six frequency bands examined, but did not interact either with fitness level or the acute exercise condition: Coherence was consistently lower in the congruent ($M = 0.36$, SD = .044) than in the incongruent ($M = 0.37$, SD = .053) condition. This effect was observed in the delta, $F(1, 28) = 34.17$, $p < .001$, theta, $F(1, 28) = 32.78$, $p < .001$, lower alpha, $F(1, 28) = 19.35$, $p < .001$, upper alpha, $F(1, 28) = 21.21$, $p < .005$, beta, $F(1, 28) = 15.54$, $p < .001$, and gamma bands, $F(1, 28) = 12.28$, $p < .005$ (see Table 2). Coherence in the delta, theta, and gamma bands was not significantly influenced by fitness level or acute exercise condition.

Table 2 Mean (SD) coherence in delta, theta, lower alpha, upper alpha, beta, and gamma for the fit and unfit participants in both the rest and exercise condition, for both "Go" and "NoGo" trials and for both the congruent and incongruent trials

	Congruent				Incongruent			
	Rest		Exercise		Rest		Exercise	
	Go	NoGo	Go	NoGo	Go	NoGo	Go	NoGo
Delta								
Fit	.361 (.017)	.393 (.028)	.358 (.019)	.396 (.031)	.399 (.029)	.376 (.021)	.395 (.028)	.368 (.021)
Unfit	.370 (.023)	.397 (.024)	.365 (.022)	.395 (.033)	.400 (.023)	.382 (.026)	.398 (.028)	.380 (.024)
Theta								
Fit	.360 (.017)	.395 (.025)	.354 (.018)	.396 (.026)	.398 (.025)	.377 (.017)	.391 (.025)	.369 (.022)
Unfit	.370 (.022)	.402 (.025)	.364 (.020)	.398 (.029)	.399 (.024)	.388 (.030)	.397 (.025)	.379 (.022)
Lower alpha								
Fit	.349 (.018)	.387 (.022)	.344 (.018)	.385 (.027)	.390 (.020)	.366 (.017)	.376 (.028)	.359 (.022)
Unfit	.362 (.020)	.401 (.031)	.354 (.018)	.392 (.019)	.388 (.028)	.383 (.031)	.389 (.023)	.365 (.021)
Upper alpha								
Fit	.338 (.032)	.370 (.022)	.336 (.020)	.372 (.033)	.374 (.025)	.349 (.021)	.372 (.029)	.348 (.023)
Unfit	.351 (.024)	.390 (.030)	.345 (.029)	.380 (.023)	.379 (.031)	.366 (.030)	.389 (.022)	.352 (.023)
Beta								
Fit	.328 (.032)	.356 (.031)	.330 (.025)	.366 (.032)	.366 (.032)	.329 (.035)	.369 (.032)	.338 (.030)
Unfit	.343 (.020)	.377 (.025)	.344 (.031)	.373 (.030)	.376 (.023)	.349 (.020)	.384 (.031)	.348 (.032)
Gamma								
Fit	.324 (.036)	.349 (.033)	.323 (.039)	.355 (.042)	.365 (.037)	.324 (.040)	.361 (.045)	.322 (.038)
Unfit	.347 (.036)	.375 (.035)	.346 (.039)	.374 (.037)	.384 (.033)	.350 (.032)	.394 (.042)	.347 (.036)

For lower alpha, there was a main effect of Exercise, $F(1, 28) = 4.76$, $p < .05$, with lower coherence in the exercise relative to rest condition. We also found a main effect of Trial, $F(1, 28) = 11.47$, $p < .05$, with lower coherence in the Go relative to the NoGo trials. A significant Congruency × Region interaction effect, $F(2, 56) = 4.78$, $p < .05$, indicated lower coherence in congruent relative to incongruent trials over some scalp regions. Subsequent separate ANOVAs in each scalp region yielded a significant congruency effect in the frontal, $F(1, 28) = 14.27$, $p < .005$, and parietal regions, $F(1, 28) = 4.74$, $p < .05$, but not in the temporal region, $F(1, 28) = 1.14$, $p > .05$. Most importantly, similar to the behavioural data a significant Fitness × Exercise × Trial interaction effect was observed for lower alpha, $F(1, 28) = 4.67$, $p < .05$ (see Fig. 3). The results of follow-up ANOVAs conducted for fit and unfit groups separately revealed that the Trial × Exercise effect for unfit group approached significance, $F(1, 14) = 3.393$, $p = .08$, but did not for fit group, $F(1, 14) = 1.322$, $p = .269$. Results of post hoc contrasts revealed that unfit participants had significantly lower coherence in the exercise relative to the rest condition for NoGo trials, $F(1, 28) = 5.31$, $p < .05$. Conversely, there was a trend for fit participants to show lower coherence in the exercise relative to the rest condition for Go trials, $F(1, 28) = 3.22$, $p = .08$. Differences between other conditions were not significant.

For upper alpha, a main effect of trial type was observed, $F(1, 28) = 4.53$, $p < .05$, with lower coherence in the Go relative to the NoGo trials. There was a Congruence × Region interaction effect, $F(2, 56) = 4.90$, $p < .05$, with lower coherence in congruent relative to incongruent trials observed in the frontal, $F(1, 28) = 9.87$, $p < .005$, and parietal regions, $F(1, 28) = 4.33$, $p < .05$, but not in the temporal region, $F(1, 28) = 0.16$, $p > .05$. Most importantly, the Fitness × Exercise × Trial interaction effect was significant, $F(1, 28) = 4.23$, $p < .05$. The results of follow-up ANOVAs conducted for fit and unfit groups separately revealed a significant Exercise × Trial interaction effect for the unfit group, $F(1, 14) = 4.55$, $p = .05$, but not the fit group, $F(1, 14) = 0.31$, $p = .59$. Post hoc contrasts for the unfit participants revealed higher coherence in NoGo relative to Go trials in the rest condition, $F(1, 28) = 6.85$, $p < .01$, and no difference between Go and NoGo trials in the exercise condition, $F(1, 28) = 0.04$, $p > .05$. Also, while unfit participants tended to show higher coherence than fit participants across the exercise and rest conditions for both Go and NoGo trials, this difference was statistically significant only in the resting condition for NoGo trials, $F(1, 28) = 4.19$; $p < .05$.

Similarly, there was a Fitness × Exercise × Trial interaction effect for Beta, $F(1, 28) = 4.61$, $p < .05$. Follow-up ANOVAs conducted for fit and unfit groups separately

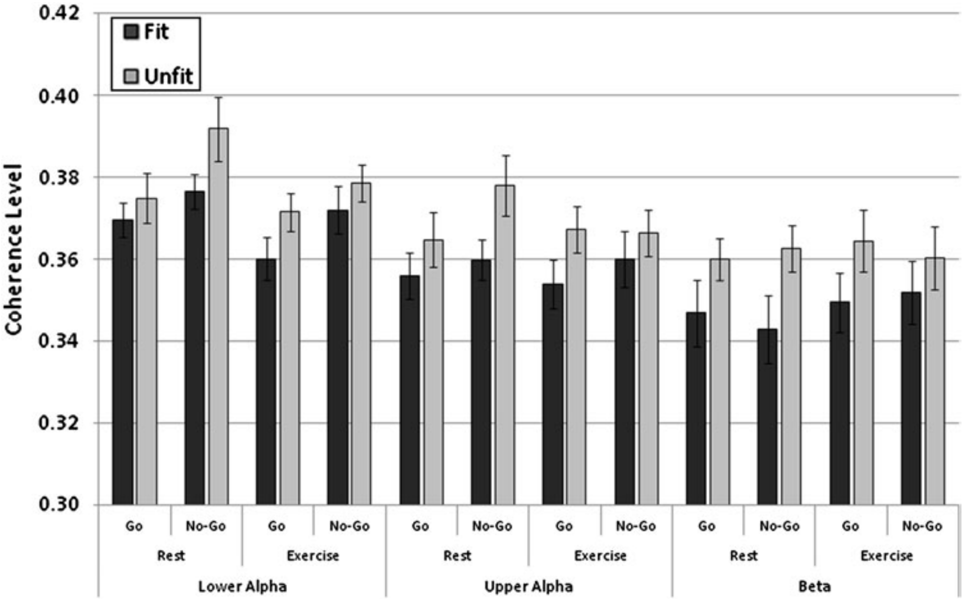

Fig. 3 *Lower alpha*, *upper alpha*, and *beta* coherence levels for the fit and unfit groups for the rest and exercise conditions for both Go and NoGo trials

yielded a trend for a Trial × Exercise interaction in the fit group, $F(1, 14) = 3.17$, $p = .09$, but not in the unfit group $F(1, 14) = 1.96$, $p = .18$. Results of post hoc contrasts revealed that, while unfit participants tended to show higher coherence than fit participants, this difference reached statistical significance only in the resting condition for NoGo trials, $F(1, 28) = 3.88$, $p < .05$.

Coherence-performance correlations

To relate EEG coherence with performance, we computed coherence-performance maps (Collins et al. 2010). Specifically, Pearson's product moment correlations between error rates and coherence values were computed for each electrode pairing separately for each condition and each frequency band across fit and unfit participants. The significant correlations are illustrated in the coherence maps in Fig. 4. Red lines indicate positive correlations, and blue lines indicate negative correlations ($p < .05$). Patterns of coherence-performance relations are clearly different across conditions. The results of these analyses revealed that higher coherence was associated with higher error rates across a number of different performance conditions. These results are discussed in more detail below.

Discussion

The current study examined behavioural performance and EEG coherence of fit and unfit adolescent participants during a modified Eriksen flanker task after both acute exercise and a resting condition. Analysis of behavioural data revealed an interaction between fitness levels and acute physical exercise for both RT and error rate. More specifically, high fit participants had significantly faster RTs in the exercise condition in comparison with the rest condition. Furthermore, unfit, but not fit, participants had higher error rates for NoGo relative to Go trials in the resting condition. Significant EEG coherence differences between fit and unfit participants were observed during NoGo trials in the resting condition. Notably, unfit participants had higher coherence than fit participants in the upper alpha and beta bands in response to NoGo trials in the resting condition. More generally, when coherence effects were combined across lower alpha, upper alpha, and beta results indicated higher coherence in the unfit relative to the fit participants. Furthermore, while acute exercise was associated with a reduction in lower alpha relative to rest in the sample as a whole, post hoc analysis of interaction effects revealed that these effects were only significant in the unfit participants, who showed lower coherence in the lower alpha band in the exercise relative to the rest condition for NoGo trials. Consistent with previous research which has revealed reduced neural activity as a function of congruency in the Erikson flanker task (Colcombe et al. 2004), congruency affected EEG coherence in the current study in all six frequency bands examined, with consistently lower coherence observed in the congruent relative to the incongruent condition. For lower and upper alpha, lower coherence in congruent relative to incongruent trials was observed in the frontal region and the parietal region, but not the temporal region. However, the congruency effect did not interact with fitness or acute exercise.

As both physical fitness and exercise may enhance cognitive performance (Hillman et al. 2008) and higher levels of coherence reflect higher cognitive effort (Deeny et al.

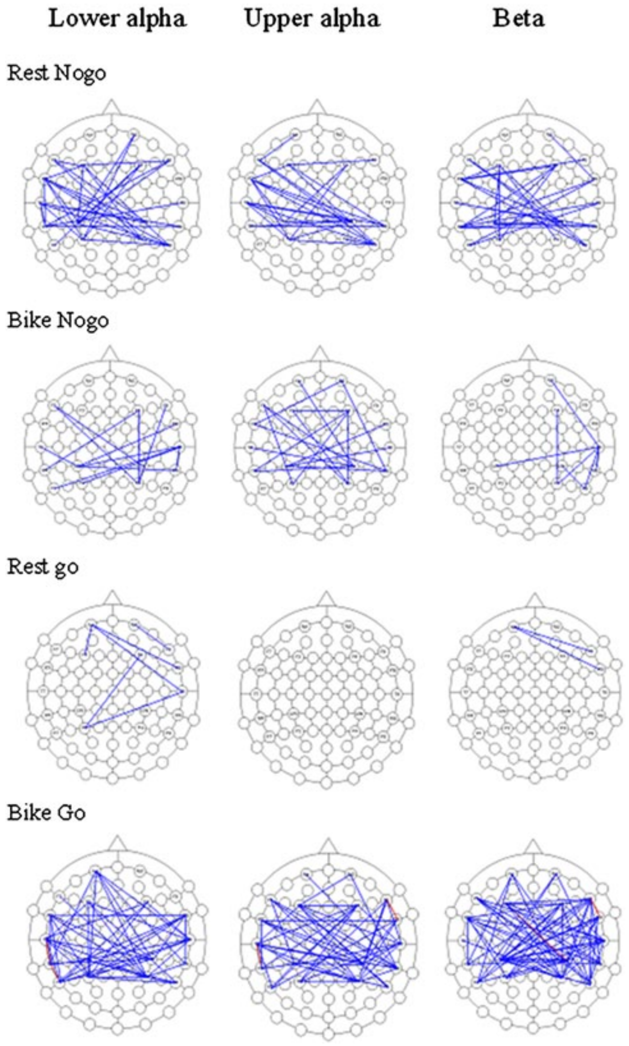

Fig. 4 Significant coherence-performance (*error rate*) correlations for lower alpha, upper alpha, and beta for rest and exercise conditions, for Go and NoGo trials. *Blue lines* indicate positive correlations and *red lines* indicate negative correlations ($p < .05$). All electrode pairing between: P7, TP7, T7, FT7, F7, P8, TP8, T8, FT8, F8, Fp1, F3, CP3, P3. Fp2, F4, CP4, and P4 were examined (153 pairings) (colour figure online)

2003), we predicted that the unfit adolescents would show higher levels of coherence in response to task demands, particularly during the resting condition. These hypothesised differences between fit and unfit participants were observed in the current study for upper alpha and beta coherence. One interpretation of these results is that the unfit group were exerting a greater amount of effort than the fit group. The higher levels of physical fitness in the fit group may have facilitated greater cortical efficiency, particularly when the flanker task was performed after the resting condition, with fewer cognitive resources needed to maintain performance in comparison with unfit individuals. As the group differences were less pronounced after a bout of exercise, this suggests that acute exercise might improve cognitive performance efficiency particularly in less fit individuals (see also Colcombe and Kramer 2003). This interpretation is consistent with the finding that unfit, but not fit, adolescents had higher error rates for NoGo relative to Go trials in the resting condition, whereas in the acute exercise condition, there were no differences in error rates between groups.

In contrast to the presently observed beneficial effects of exercise and fitness on executive functioning and EEG coherence in adolescents, some earlier studies assessing the effects of exercise on general intelligence in children and adolescents reported little positive gain associated with exercise intervention programmes lasting weeks and months (see Tomporowski et al. 2008 for a review). However, changes in cognitive performance were measured via global IQ tests, which may not be sensitive enough to detect specific changes in cognitive functioning associated with exercise and fitness levels (e.g. Hillman et al. 2005, 2009).

Exercise and fitness affected EEG coherence in the alpha and beta bands. Previous research has highlighted the importance of alpha modulation during inhibition tasks (Jokisch and Jensen 2007) and beta band power has been implicated in effortful attention (Klimesch 1999). The unfit group in the current study had the highest coherence levels in the NoGo trials of the resting condition suggesting that a combination of being unfit, not exercising, and performing a trial that required the inhibition of a response (Kiefer et al. 1998) demanded the greatest allocation of cognitive resources. Conversely, being fit, in the exercise condition, and performing a Go trail was associated with the lowest coherence level suggesting this was the least cognitively demanding combination.

Although the sample size of the current study was small, which had implications for the power of our statistical analyses, behavioural and coherence effects we observed suggest that, overall, unfit adolescents may perform cognitive tasks at the same level as fit participants in certain conditions (exercise condition, Go trials), but possibly at the expense of greater cortical effort reflected in higher coherence. In situations where attentional demands are high, relatively higher levels of coherence were coupled with higher error rates in the unfit group, suggesting a link between higher coherence and higher error rates in the sample as a whole. The results of coherence-performance mapping (Collins et al. 2010) confirmed that higher error rates were associated with higher coherence across a number of different performance conditions, and were strongest in the NoGo rest and Go exercise condition. These effects are interesting as they suggest that, in the sample as a whole higher coherence in lower alpha, upper alpha and beta was associated with greater difficulty withholding a key press upon the appearance of NoGo stimuli in the rest condition, and an increased tendency to erroneously withhold a key press upon the appearance of the Go stimuli in the acute exercise condition. Although the effects were weaker, it should also be noted that higher coherence, particularly in lower and upper alpha, was associated with poorer NoGo performance in the exercise condition, and the only correlations observed between coherence and performance in the Go rest condition were negative. Nevertheless, future research should seek to examine if the relationship between EEG coherence and behavioural performance in adolescents is moderated by acute exercise, physical fitness levels, and the nature of task requirements. One possibility suggested from the current study is that, although the task was reasonably difficult in general, with error rates of 15–30 % across conditions, participants with higher EEG coherence may have found different aspects of the task more or less difficult in different conditions. Future research should also seek to examine if physical fitness training interventions serve to increase cortical efficiency and cognitive performance, specifically, by altering the synchronous oscillations of electrical activity across scalp locations.

It is unclear to what degree effects of exercise on EEG coherence and behavioural performance would be comparably observed in children and adolescents. Some researchers suggest that physical activity may produce more global effects in children in comparison with those observed in the adult population (Hillman et al. 2005). Notably, younger children, whose frontal lobes are characterized by an earlier stage of maturation, have greater difficulty inhibiting irrelevant stimuli and focusing attention on relevant stimuli (Ridderinkhof and van der Molen, 1995). With maturation comes an increased ability to manage interference (Travis 1998), and perform better on executive control tasks (Diamond and Taylor 1996), due in part to increases in the efficiency of the supporting brain structures. Exercise can influence a number of processes that affect neurological development; for example, the production of neurotrophins involved in the regulation of neuron production and differentiation (Vaynman and Gomez-Pinilla 2006), and synaptogenesis (Huttenlocher and Dabholkar 1997). The impact of fitness and both chronic and acute exercise interventions on EEG coherence and behavioural performance may thus be different for younger children and adolescence, that is, depending on their current stage of neurological and cognitive development. Future research should seek to examine the differential impact of fitness and exercise across the lifespan and thus develop a better understanding of when exercise interventions might be best used to support ongoing development at a neural and cognitive level. While electrophysiological measures provide a window into brain functioning and have excellent temporal resolution, MRI, fMRI and MEG should be used to examine structural and functional changes in the brain associated with both acute and chronic exercise, and examine the link between these changes and behavioural and developmental changes in children and adolescents.

The effects of fitness and both chronic and acute exercise interventions on brain activity and behavioural performance should be replicated in larger samples of children and adolescents while controlling for a variety other factors that might be related to both fitness levels and brain and behavioural measures (e.g. intelligence, academic achievement, socioeconomic status). Also, given that the increased level of arousal induced by physical activity may mediate increased response speed and accuracy (Davranche and Audiffren 2004), future studies need to examine if the arousal effects of exercise differ for children, adolescents and adult samples.

In conclusion, the present study revealed an interaction between an acute bout of exercise and long-term physical fitness in adolescence. Although fit adolescents showed better performance in the Erisken flanker task than unfit adolescents, unfit adolescents, but not fit adolescents benefited from an acute bout of exercise. At a neural level, unfit participants had higher levels of lower alpha, upper alpha, and beta coherence, in particular in the resting condition, possibly indicating a greater allocation of cognitive resources to the task demands. The higher levels of alpha coherence are of particular interest in light of its reported role in inhibition and effortful attention (Klimesch 1999; Jokisch and Jensen 2007). The results suggest that physical fitness and acute exercise may enhance cognition by increasing functionality of the attentional system in adolescence. The present study therefore highlights the importance of intervention programs providing physical exercise for adolescents, which may improve attention and cognitive performance at school and in everyday life.

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