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The Influence of Aerobic Fitness on Top-Down and Bottom-Up Mechanisms of Interference Control

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Objective: Extensive evidence has demonstrated the relationship between aerobic fitness and cognitive function in early adulthood. Little is known, however, about whether the cognitive benefits of aerobic fitness are related to the modulation of top-down or bottom-up mechanisms in the control of executive attention. The present study aimed to shed light on this question by evaluating the phase-locking factor (PLF) of electroencephalogram (EEG) signal during cognitive control. ***Method:*** Higher fit and lower fit young adults performed a neuropsychological test of cognitive control (i.e., Stroop color-naming task) with concurrent EEG recording. ***Results:*** In line with previous literature, behavioral results showed that higher fit individuals performed better on the Stroop task overall. Interestingly, beta phase synchronization was larger during the incongruent condition than the congruent condition for higher fit but not for lower fit individuals, suggesting a more effective use of top-down control in the former. However, no such effect was seen for gamma activity, indicating that bottom-up mechanisms are unlikely to account for the differences in performance explained by fitness levels. ***Conclusion:*** Altogether, these findings suggest that the greater cognitive control observed in higher fit individuals is associated with differences in the control of top-down rather than bottom-up processing, consistent with the hypothesis of selective improvement.

General Scientific Summary
This study investigates the potential mechanism that accounts for the greater cognitive control performance associated with higher fitness levels in young adulthood. Overall, individuals with higher aerobic fitness outperformed their lower fitness counterparts on a test of cognitive control, with greater modulation of neural activity related to top-down attentional control. Although cross-sectional, the present study suggests that maintaining a high level of aerobic fitness may be associated with most efficient brains, which, in turn, may enable better goal-directed behavior, even within high-performing healthy populations.

Keywords: aerobic fitness, top-down control, interference control, phase-locking factor

There is ample evidence supporting the positive relationship between aerobic fitness and cognitive functioning (Åberg et al., 2009; Guiney & Machado, 2013; Hillman, Erickson, & Kramer, 2008). Specifically, studies have rather consistently found that cognitive processes requiring flexibility and top-down cognitive control such as executive functions (Diamond, 2013; Miller & Cohen, 2001) benefit more from enhanced aerobic fitness than other, possibly less complex, cognitive processes (Colcombe & Kramer, 2003; Kawagoe, Onoda, & Yamaguchi, 2017; Khan & Hillman, 2014; Pontifex et al., 2011). This selective effect of fitness level on higher order cognition is known as the selective improvement hypothesis (Kramer et al., 1999).

Most of the knowledge regarding the selective improvement hypothesis, however, has been gained from studies on populations

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whose executive functions are either still maturing (i.e., children) or deteriorating (e.g., elderly adults, adults with cognitive impairments). In contrast, the evidence is less clear in early adulthood. For example, Scisco, Leynes, and Kang (2008) investigated the effect of aerobic fitness on the switching aspect of executive function in young adults and found no effect on behavioral measures regardless of whether switching was required. Similarly, Kamijo, O'Leary, Pontifex, Themanson, and Hillman (2010) did not observe greater performance across different levels of working memory load (i.e., set size) during a Sternberg task in aerobically fit young adults compared with less fit individuals. Still, there is an increasing number of reports pointing out the beneficial effect of enhanced or maintained aerobic fitness on cognitive health in young adults (Åberg et al., 2009; Hansen, Johnsen, Sollers, Stenvik, & Thayer, 2004; Themanson, Pontifex, & Hillman, 2008; Wang, Shih, & Tsai, 2016). Given the importance of executive functions in everyday tasks (e.g., goal-directed behavior; Mäntylä, Karlsson, & Marklund, 2009), and, arguably, the increasing cognitive demands of modern society, finding valid means to enhance cognition could be beneficial to many individuals in various settings, including professional, academic, and social environments.

The lack of strong evidence for higher executive functions in young adults with higher aerobic fitness may be due to the wide range of cognitive tasks used across studies. Executive functions refer to the collection of top-down mental processes necessary for goal-directed cognition and behavior (Diamond, 2013), which has been proposed to cover three core processes including inhibitory control, working memory, and cognitive flexibility (Diamond, 2013; Etnier & Chang, 2009; Wang & Tsai, 2016). Although there is no clear behavioral evidence regarding the cognitive benefits of enhanced aerobic fitness on working memory (Kamijo et al., 2010) and cognitive flexibility (i.e., task switching; Scisco et al., 2008) in young adults, some studies have suggested an association with the inhibitory control aspect of executive functions, in particular, interference control (Dupuy et al., 2015; Song et al., 2016; Themanson et al., 2008). Thus, investigating the effect of interference control to address this theoretical question might have the potential to refine our understanding of the selective improvement hypothesis, and further extend its relevance to early adult populations.

Interference control, also referred to as inhibitory control of attention, is a process that enables an individual to selectively attend to a stimulus, while suppressing attention to goal-irrelevant stimuli (Diamond, 2013). One specific neuropsychological task, the Stroop task (Stroop, 1935), has become a classic to investigate the interference control aspect of executive functions. In a typical Stroop task, subjects are asked to name the ink color of color-word stimuli when the two dimensions of information are congruent (e.g., "RED" printed in red font) or incongruent (e.g., "RED" printed in green font). Because semantic information interferes with color naming, participants typically show greater error rates and slower responses on incongruent trials than on congruent trials (Gajewski & Falkenstein, 2015; MacLeod, 1991), which is known as the Stroop interference effect.

Recent research on the relationship between aerobic fitness and Stroop interference control has reported equivocal findings, preventing any strong inference regarding the selective improvement hypothesis among healthy young subjects. Dupuy et al. (2015) observed that high-fitness individuals exhibited faster response times (RTs) than low fitness individuals in the condition with higher level of Stroop interference, whereas Song et al. (2016) found that aerobic fitness was selectively related to processing speed only in the trials with lower level of interference. Thus, it remains unclear whether aerobic fitness is related to more efficient interference control during a Stroop task.

It is worth noting that the Stroop interference effect can be interpreted as competition between two stimulus aspects (color and word) for a priority in information processing (Milham, Banich, & Barad, 2003). This tradeoff is assumed to be related to the interplay of top-down and bottom-up processing during goal-directed behavior (Melcher & Gruber, 2006). Top-down processing allows focusing on task-relevant information (color font), while task-irrelevant information (word meaning) is appropriately suppressed. In the incongruent condition of a Stroop task, automatic word reading induces lexical processing, which interferes with the task at hand (MacLeod & MacDonald, 2000). Such interruption on task performance can also be interpreted as a result of the bottom-up influences of task-irrelevant information (Melcher & Gruber, 2006). That is, if attention is too easily captured by bottom-up processes (i.e., word meaning), performance can appear fragmented. By contrast, the associated automaticity would be expected to result in a bottom-up facilitating effect for the color-word congruent trials. Consistent with this idea, superior performance in the Stroop incongruent condition for high fit individuals (Dupuy et al., 2015) might reflect better use of top-down attentional control; in contrast, better performance of high fit individuals in the congruent condition might be related to a bottom-up attentional facilitation (Song et al., 2016). The extent to which these fitness-related performance differences are modulated by top-down or bottom-up mechanisms is currently unknown, and more work is thus needed to make sense of the discrepancies reported in the literature.

Typical behavioral outcomes result from end-state processes occurring after a series of covert cognitive processes. To further inform the covert mechanisms responsible for behavioral change, this study used electroencephalogram (EEG) synchronization to probe the top-down and bottom-up mechanisms underlying Stroop interference. Several macaque and human studies have demonstrated that oscillatory beta and gamma phase synchronizations are crucial for bottom-up and top-down control of attention (Buschman & Miller, 2007; Michalareas et al., 2016; Phillips & Takeda, 2009, 2010; Richter, Thompson, Bosman, & Fries, 2017). In the macaque study, Buschman and Miller (2007) reported greater beta synchronization during conjunction search requiring top-down control than feature search tapping bottom-up attention, whereas the pattern of results was opposite in the gamma band. Consistent with this finding, young adults were found to exhibit greater beta band synchronization during conjunction search (Phillips & Takeda, 2009), whereas greater gamma synchronization was found during feature search in elderly adults (Phillips & Takeda, 2010). These findings can be understood as age-related differences in the use of top-down and bottom-up control of attention (Phillips & Takeda, 2010). These earlier investigations thus provided evidence for the two modes of attentional control: gamma activity for bottom-up processing and beta activity for top-down processing. Interestingly, such modulations of EEG phase synchronization seem to be associated with the difference in levels of physical activity (Kamijo & Takeda, 2013; Kamijo, Takeda, & Hillman, 2011) and aerobic fitness (Kamijo, Takeda, Takai, & Haramura, 2016). To elaborate, these studies indicate that individuals with higher levels of physical activity or aerobic fitness have superior brain functional connectivity during tasks requiring a greater amount of top-down control of attention, as evidenced by greater modulation of phase synchronization at the beta frequency band. In contrast, physical activity levels seem less sensitive to gamma activity, an index of bottom-up control processes (Kamijo et al., 2011). This evidence is also in line with the selective improvement hypothesis (Colcombe & Kramer, 2003), and demonstrates the utility of EEG oscillations to explore the cognitive benefits of enhanced aerobic fitness.

The overall aim of this study was to refine our understanding of the relationship between aerobic fitness and executive functions in young adults, by measuring top-down and bottom-up mechanisms during a Stroop task via the examination of PLF values of EEG. Behaviorally, we assessed both mean-level dependent variables (i.e., accuracy and mean reaction time (RT) and intraindividual variability (i.e., RT variability; MacDonald, Nyberg, & Bäckman, 2006) in order to provide converging evidence. RT variability has been shown to have the capacity to reflect levels of interference control (i.e., Stroop interference or flanker interference; Gajewski & Falkenstein, 2015; Wang, Yang, Moreau, & Muggleton, 2017; Wu et al., 2011), and is sometimes more sensitive to aerobic fitness effect than mean RTs (Moore et al., 2013; Wu et al., 2011). For the EEG data, we focused on oscillatory beta (22–34 Hz) and gamma (36–56 Hz) phases across fronto-parietal areas, which have been shown to be associated with top-down and bottom-up controls of attention in human (Kamijo & Takeda, 2013; Kamijo et al., 2011; Phillips & Takeda, 2009, 2010; Phillips, Takeda, & Singh, 2012). Our hypothesis was that greater task-related modulation of EEG PLF values in the beta band would be observed in higher fit individuals relative to their lower fit counterparts, given the association between aerobic fitness and top-down attentional control. In contrast, if fitness-related differences in behavioral performance are associated with bottom-up attentional processes, we would expect a group difference in modulations of PLF values in the gamma band.

Method

Participants

Thirty-six male young adults, aged 21 to 27 years old, were recruited for this study. This age range is similar to those investigating the relationship between aerobic fitness and executive function in young adulthood (Dupuy et al., 2015; Hayes, Forman, & Verfaellie, 2016; Kamijo et al., 2010; Scisco et al., 2008; Song et al., 2016; Themanson & Hillman, 2006). Only male participants were recruited to avoid obscuring the effect of interest with gender-related variability in performance (i.e., greater verbal abilities of female participants; Mekarski, Cutmore, & Suboski, 1996). All participants were right-handed and reported having normal or corrected-to-normal visual acuity. No individual reported any history of neurological problems or cardiovascular diseases, nor were any taking medications known to affect cognitive function. Because of the negative relation of body mass index (BMI) to executive functions (Song et al., 2016), those with a measured BMI >24 kg/m^2 (defined as overweight by the Ministry of Health and Welfare, Taiwan), were excluded. Eligible participants were labeled highernfit or lower fit based on whether their VO_{2max} value fell below the level of average/poor (VO_{2max} <50 ml/kg/min) or above the level of good/excellent (VO_{2max} >52 ml/kg/min), as defined by the American College of Sports Medicine (ACSM, 2013). Such fitness criteria of group classification is similar to the previous investigation (Kamijo et al., 2010). The demographic information for both groups is summarized in Table 1. Informed consent was obtained prior to the study, which was approved by the Human Research Ethics Committee of National Cheng Kung University.

Measures

Cardiorespiratory endurance test. We measured participants' maximal cardiorespiratory endurance with a modified Bruce protocol treadmill test on a Medtrack ST55 Control Treadmill (Quinton Instrument, Bothell, WA). This protocol involved running on a treadmill, with both the speed and slope increasing every 3 min (Kalyani, Ebadi, Mehri, & Jamshidi, 2008), until volitional exhaustion occurred or other criteria were met, as explained in detail below. After becoming familiar with the exercise equipment, each participant was fitted with a head gear and a mouthpiece to collect expired gases using semicomputerized open-circuit spirometry with the logic pathway on a Vmax system (Vmax Spectra Series Model 29, VIASYS Respiratory Care, Yorba Linda, CA), which was required for the measurement of the following respiratory parameters: oxygen uptake (VO_2), minute ventilation (V_E), carbon dioxide output (VCO_2), and respiratory exchange ratio (RER, VO_2/VCO_2), with a sampling interval of 20 s to determine the maximal oxygen uptake during the graded exercise test (GXT). Throughout the GXT, we monitored heart rate and rhythm via electrocardiography (VIASYS Respiratory Care, Yorba Linda, CA) and a Polar heart rate (HR) monitor (RS400, Polar Electro Oy, Finland). Each test section included a 3-min warm up, a GXT on a motor-driven treadmill and cool down. During the VO_{2max} test, we verbally encouraged the participants to continue exercising until exhausted, and the test was terminated based on the following four criteria: (a) indication of maximal exhaustion; (b) peak HR reaching more than 90% of the theoretic age-predicted maximum (220 – age); (c) a plateau in oxygen consumption corresponding to an increase of less than 150 Ml in VO_2 values, despite the increase in exercise workload; or (d) an RER greater than 1.15 (ACSM, 2013; Wang et al., 2016).

Behavioral paradigm. Cognitive testing was conducted on a different day from the cardiovascular endurance test to avoid acute exercise effects. Experimenters ensured that participants had not engaged in any specific activity that may have biased the effects of interest (e.g., exercising or drinking alcohol).

Table 1
Demographics of Participants in Each Group (Standard Deviation in Parentheses)

Group	Higher fit ($n = 18$)	Lower fit ($n = 18$)
Age (year)	22.56 (1.89)	22.67 (1.91)
BMI (kg/m^2)	21.80 (1.37)	21.50 (1.39)
VO_{2max} (ml/kg/min)[a]	62.42 (5.47)	45.58 (4.09)

Note. BMI = body mass index.
[a] Significant difference between groups, $p < .001$.

We used a computer version of the color-naming Stroop test, programmed using E-prime (Psychology Software Tools, Sharpsburg, PA). A two-choice version of the Stroop task, which has been demonstrated to induce a clear Stroop interference in both young and older adults (Brink & McDowd, 1999), was adopted in this study in order to minimize the influence of response selection on task performance. In addition, given the evidence that semantic significantly interferes with color naming (Gajewski & Falkenstein, 2015) while color interferes very little with word reading, possibly because reading is a heavily trained and highly automated process in literate adults (MacLeod, 1991; Stroop, 1935), this study adopted the color-naming condition to investigate the effect of aerobic fitness on neurocognitive functioning associated with Stroop interference. The stimuli were two color names in Chinese presented as "紅" (red) and "綠" (green). All stimuli were presented with a 4.5 × 4.5 cm letters in the center of a 21-in. cathode-ray tube display against a black background at an 80-cm distance. In the incongruent condition, the color of the word in the display was different from its word meaning, whereas in the congruent condition the meaning of the word and its color matched. A single test block consisted of 50% incongruent and 50% congruent trials, in a randomized order. We adopted the 50% congruency in order to reduce the influence of trial numbers on PLF measures (Cohen, 2014). Two blocks of 120 trials, for a total 240 trials, were presented for each participant, with a rest period of 2 min between blocks. Each stimulus appeared on the screen until the participant responded, and the next stimulus appeared 1.5 to 2 s after the response. Participants were instructed to respond as quickly and accurately as possible with a button press of their index ("N" key) and middle ("M" key) fingers of right hand on a computer to the color while ignoring word meaning. The stimulus-response pairs were counterbalanced across participants.

All participants performed the Stroop task with simultaneous electrophysiological recording (see below). After a practice block of 10 trials to ensure that the participants had understood the task instruction, the formal test was administered to allow for collection of behavioral performance along with EEG data.

EEG Recording

The electroencephalographic recording procedure was performed in a manner similar to previous studies (Wang et al., 2014; Wang, Tsai, et al., 2015). EEG activity was recorded using a Nu-Amps EEG amplifier and the Scan 4.5 package (Neuroscan, El Paso, TX) with 32 electrodes mounted in an elastic cap (Quik-Cap; Compumedics, Neuroscan, El Paso, TX) designed for the International 10–20 System. The average of the bilateral mastoids served as the online reference and the forehead served as ground. In addition, two sets of bipolar electrodes were placed on the upper and lower sides of the left eye, and near the outer canthi of both eyes in order to monitor vertical and horizontal eye movements. Electrode impedances were kept below 10 kΩ. Electroencephalography data were acquired with an analogue-digital rate of 1,000 Hz per channel, filtered with a Butterworth bandpass filter (0.1–70 Hz), a 60-Hz notch filter, and written continuously to a hard disk for subsequent offline analysis (Wang, Lo, et al., 2015).

Data Reduction and Statistical Analyses

Behavioral data. E-prime 2.0 (Psychology Software Tools, Sharpsburg, PA) was used to record RTs (in milliseconds) and accuracy. RTs were excluded from all analyses if they were from: (a) nonresponse trials, (b) error trials, and (c) trials with latencies more than three standard deviations above the mean latency value on correct trials. Thus, only mean RTs and RT variability in the eligible trials were used for further analysis. RT variability was computed as the standard deviation of RTs across trials (Papenberg, Hämmerer, Müller, Lindenberger, & Li, 2013; Wang, Yang, et al., 2017).

A 2 (groups: higher-fit, lower-fit) × 2 (conditions: congruent, incongruent) mixed analysis of variance (ANOVA) with Bonferroni adjustment for multiple comparisons was conducted to analyze accuracy, RTs and RT variability for correct responses. The significance level was set at $p \leq .05$. Partial η^2 (η_p^2), a measure of effect size, was used to complement significance testing, with the following standards used to determine the magnitude of the effect size: 0.01–0.059 typically indicates a small effect, 0.06–0.139 a medium effect, and >0.14 a large effect (Cohen, 1973). Moreover, the Stroop interference, which represents the interference between top-down and bottom-up processes, was calculated as the differences in accuracy, mean RTs, and RT variability between incongruent and congruent conditions. Group comparisons were investigated using independent *t* tests. All analyses were completed using SPSS 18.0.

Time-frequency analysis of EEG. This study examined the top-down and bottom-up mechanisms during interference processing by measuring the modulation of phase synchrony in EEG signal during a Stroop task. The examination of PLF values has been suggested to have sufficient test–retest reliability for use in assessing clinical neurophysiological changes in human (Fründ, Schadow, Busch, Körner, & Herrmann, 2007). This analysis was performed using SPM8 for MEG/EEG (Wellcome Department of Cognitive Neurology, London, UK; www.fil.ion.ucl.ac.uk/spm/) and custom Matlab (MathWorks, Natick, MA) scripts (Hsu, Tseng, Liang, Cheng, & Juan, 2014; Wang, Lo, et al., 2015; Wang, Tseng, Liu, & Tsai, 2017). Only data collected from correct trials were analyzed. Prior to the time-frequency analysis, ocular artifacts were corrected from the EEG signal with a regression-based algorithm implemented in the Neuroscan Edit 4.5 software (Neuroscan, El Paso, TX; Semlitsch, Anderer, Schuster, & Presslich, 1986). Although there is no single best approach for removing all artifacts (Urigüen & Garcia-Zapirain, 2015), the regression-based approach has been widely employed in recent EEG studies (Pontifex, Miskovic, & Laszlo, 2017), suggesting its utility in removing ocular artifacts from EEG signals. Continuous EEG data were locked to the target onset and were segmented into epochs from −1,500 to 1,500 ms relative to this time point. Trials containing artifacts with amplitudes exceeding ±150 μV were discarded. The final number of trials included in the subsequent analysis were 111.97 ± 5.27 trials (lower fit group: 111.39 ± 5.83; higher fit group: 112.57 ± 4.73) in the congruent condition and 110.06 ± 5.81 trials (lower fit group: 108.72 ± 6.99; higher fit group: 111.38 ± 4.12) in the incongruent condition.

PLF estimates were computed by a continuous Morlet wavelet transform (Morlet wavelet factor = 6) of single-trial data for the frequency band ranging from 2 to 60 Hz (Roach & Mathalon, 2008). PLF measures the temporal consistency of the phase value for a given frequency band at each time point across trials (Roach & Mathalon, 2008). PLF varies from 0 to 1, where 0 indicates absence of any EEG phase consistency across trials, and 1 indicates identical EEG phase consistency across trials (Delorme & Makeig, 2004; Wang, Yang, et al., 2017). In line with previous EEG studies in human (Kamijo & Takeda, 2013; Kamijo et al., 2011, 2016; Phillips & Takeda, 2009, 2010), the electrodes around midline fronto-parietal regions (Fz, Cz, Pz) were crusted here for the subsequent analysis.

According to the visual inspection of the time-frequency representation of the EEG signal in which evident beta and gamma activities were seen (Figure 1A), top-down processes were evaluated by averaging the evoked beta (22–34 Hz) response to the stimuli in the 100–200 ms poststimuli onset, whereas by averaging the evoked gamma (36–56 Hz) response 100–150 ms poststimuli onset for the bottom-up process. A 2 (Group: higher-fit, lower-fit) × 2 (conditions: congruent, incongruent) mixed ANOVA with Bonferroni correction for multiple comparisons was conducted on PLF values, separately for gamma and beta bands. The significance level was set at $p \leq .05$.

Results

Participant Demographics

Participant demographic data are shown in Table 1. Demographic variables including age, $t(35) = .21$, $p = .836$, and BMI, $t(35) = -.02$, $p = .983$, did not differ between higher fit and lower fit groups. The VO$_{2\text{max}}$ level was 62.42 ± 4.47 ml/kg/min on average for the higher fit group and 45.58 ± 4.09 ml/kg/min for the lower fit group, and the difference was significant, $t(35) = -10.78$, $p < .001$. These findings confirm the absence of heterogeneity between groups, except for aerobic fitness levels.

Behavioral Performance

Table 2 shows accuracy, mean RTs, and RT variability across groups and conditions. We detail each of these measures hereafter.

Accuracy. Participants had higher accuracy for congruent trials compared with incongruent ones (congruent: 97.86 ± 3.01% vs. incongruent: 96.32 ± 3.10%), $F(1, 34) = 12.81$, $p = .001$, $\eta_p^2 = .27$. However, the main effects of group ($F(1, 34) = .03$, $p = .856$) and Group × Condition interaction ($F(1, 34) = 1.24$, $p = .727$) were not significant.

Mean RTs. Participants had faster RTs for congruent trials compared with incongruent ones (congruent: 394.20 ± 44.92 ms vs. incongruent: 417.10 ± 61.76 ms), $F(1, 34) = 34.74$, $p < .001$, $\eta_p^2 = .51$. In addition, we found a significant main effect of group ($F(1, 34) = 5.13$, $p = .030$, $\eta_p^2 = .13$), with shorter RTs for the higher- fit group relative to the lower fit group (higher fit: 386.86 ± 35.74 ms vs. lower fit: 424.45 ± 35.74 ms). However, the Group × Condition interaction ($F(1, 34) = 3.32$, $p = .077$) was not significant.

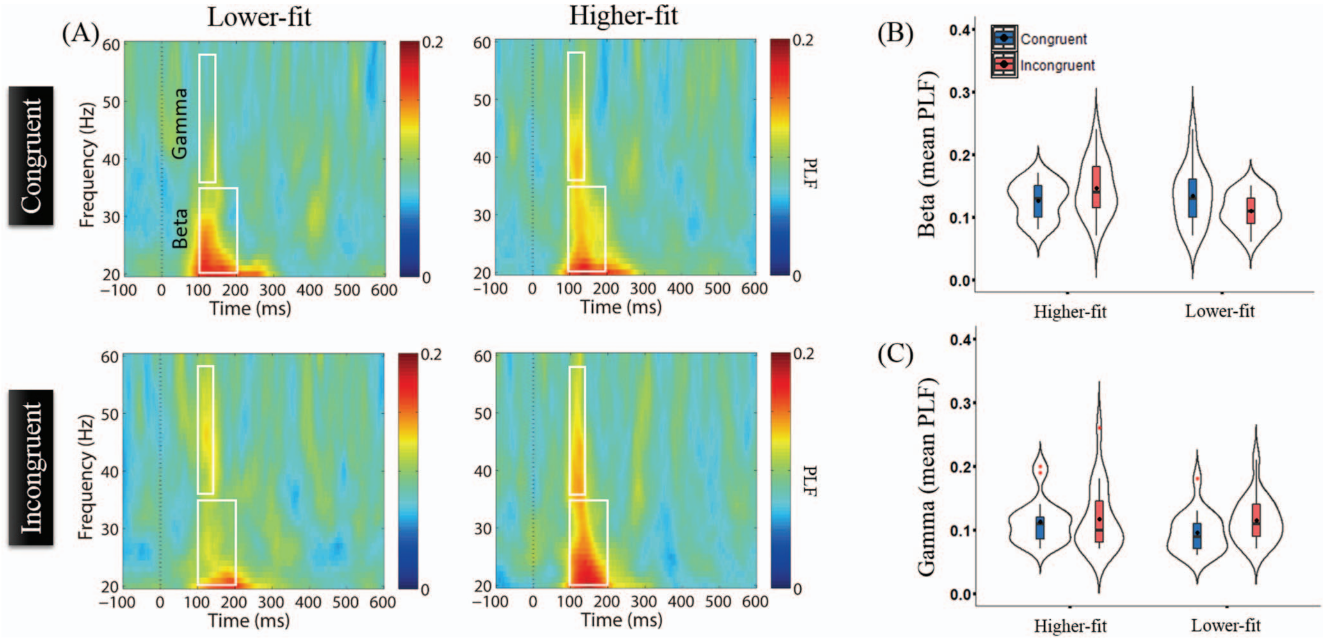

Figure 1. (A) Group average phase-locking factor (PLF) values across fronto-parietal electrodes (Fz, Cz, Pz) for each condition (congruent, incongruent) and group (higher fit and lower fit) during the Stroop task. The white line rectangles denote the areas of interest for evoked beta (22–34 Hz) and gamma responses (36–56 Hz) used in the statistical analysis. The plot shows the distribution (violin) of mean values of EEG phase synchronization in beta (B), and gamma bands (C) together with the mean (box central dot), median (box central line), first and third quartile (box edges), minimum and maximum (whiskers), and outliers (outside dots). The zero time point denotes the onset of the stimulus. See the online article for the color version of this figure.

Table 2
Behavioral and EEG Performance Results for Each Group

Conditions	Higher fit (n = 18)	Lower fit (n = 18)
Congruent		
Accuracy (%)	97.74 (3.99)	97.97 (1.93)
Response time (ms)	378.95 (32.57)	409.46 (51.00)
RT variability (ms)	77.69 (18.84)	98.54 (30.37)
Beta PLF	.13 (.03)	.13 (.04)
Gamma PLF	.11 (.03)	.09 (.03)
Incongruent		
Accuracy (%)	96.77 (3.25)	95.87 (2.96)
Response time (ms)	394.77 (40.33)	439.44 (71.90)
RT variability (ms)	94.12 (22.62)	128.16 (42.29)
Beta PLF	.15 (.04)	.11 (.03)
Gamma PLF	.12 (.05)	.11 (.03)

Note. The number in parenthesis is the standard deviation. RT = response time; PLF = phase-locking factor; EEG = electroencephalogram.

Trial-to-trial RT variability. Participants had smaller RT variability for congruent trials compared with incongruent ones (congruent: 88.12 ± 30.37 ms vs. incongruent: 111.14 ± 37.62 ms), $F(1, 34) = 43.58$, $p < .001$, $\eta_p^2 = .56$. Moreover, the main effect of group was also significant ($F(1, 34) = 8.64$, $p = .006$, $\eta_p^2 = .20$), with lower RT variability for the higher fit group than for the lower fit group (higher fit: 85.91 ± 18.77 ms vs. lower fit: 113.35 ± 34.89 ms). The Condition × Group interaction was not significant ($F(1, 34) = 3.57$, $p = .067$).

Stroop interference scores. The independent *t* tests revealed that the higher fit group exhibited marginally smaller Stroop interference in both mean RT (higher fit: 15.82 ± 16.27 ms versus lower fit: 29.98 ± 28.67 ms, $t(34) = 1.82$, $p = .077$, Cohen's d = .61) and RT variability (higher fit: 16.43 ± 18.01 ms versus lower fit: 29.51 ± 23.48 ms $t(34) = 1.89$, $p = .067$, Cohen's d = .63). However, the same effect on accuracy performance was not significant (higher fit: 0.01 ± 0.02 versus lower fit: 0.02 ± 0.03, $t(34) = 1.32$, $p = .196$).

Phase-Locking Factors (PLFs)

Beta PLFs. Figure 1A shows the time-frequency plots of the PLF of beta (22–34 Hz) around fronto-parietal electrodes (Fz, Cz, Pz) for each condition and group, and Figure 1B presents mean beta values for the region of interest for each condition and group.

As can be shown in Table 2, although neither main effects of condition ($F(1, 34) = .00$, $p = .989$) nor group ($F(1, 34) = 2.48$, $p = .124$) was observed, the effect of Condition × Group interaction reaches the significance level ($F(1, 34) = 9.24$, $p = .005$, $\eta_p^2 = .21$). Bonferroni-corrected post hoc analysis ($p = .0125$) comparing the condition difference within group revealed a greater beta PLF in the incongruent condition than in the congruent condition for the higher fit group ($p = .012$). Such a difference in condition, however, was not observed for the lower fit group ($p = .089$). Post hoc analyses with Bonferroni correction ($p = .0125$) comparing group difference across conditions showed no group-level difference in beta PLF for the congruent condition ($p = .604$), whereas we observed a significant effect for the incongruent condition ($p = .004$).

Gamma PLFs. Figure 1A shows the time-frequency plots of the PLF of gamma (36–56 Hz) at fronto-parietal sites (Fz, Cz, Pz) for each condition and group, and Figure 1C presents mean gamma values for the regions of interest for each condition and groups. The results revealed no significant main effect of condition ($F(1, 34) = 4.07$, $p = .052$), group ($F(1, 34) = 1.11$, $p = .299$), and a nonsignificant Condition × Group interaction ($F(1, 34) = 1.70$, $p = .201$; see Table 2).

Discussion

Executive functions are sensitive to individual differences in aerobic fitness and, as we observed in this study, this can be related to differences in neural oscillation associated with interference control even in healthy, early adulthood. PLF measures of EEG proved to be a valid approach for investigating neural synchrony in top-down and bottom-up processes during cognitive functioning. We found superior behavioral performance and greater interference-related modulation on beta PLFs but not gamma PLFs for the higher- fit group compared with lower fit individuals. Thus, PLFs in EEG appear to be related to the benefits of aerobic fitness on interference control processes: one important aspect of executive function. Importantly, these suggest differences in top-down rather than bottom-up processes as a mechanism underlying fitness-related differences in cognitive performance.

Behavioral Performance

Our results showed that all three behavioral indices were sensitive to the Stroop effect. Lower accuracy, slower RT, and larger variability were observed in the incongruent condition compared with the congruent condition, possibly because word reading significantly interferes with color naming (Gajewski & Falkenstein, 2015; MacLeod, 1991). These findings are in line with a large body of previous research (Gajewski & Falkenstein, 2015; Song et al., 2016; Stroop, 1935) as well as with a study using a two-choice version of the Stroop task (Brink & McDowd, 1999), suggesting that the Stroop task was reliably administered in the present study.

In terms of accuracy performance, although a clear Stroop effect was observed, fitness levels did not modulate accuracy performance as well as the Stroop interference score on accuracy. One possible explanation may be a celling effect, given that both groups performed with relatively high accuracy across both congruent and incongruent conditions (congruent: 97.86 ± 3.01% vs. incongruent: 96.32 ± 3.10%). Thus, future studies are warranted to systematically address this issue by using Stroop tasks with various levels of response choice.

Previous studies using mean RTs on the relationship between Stroop task performance and aerobic fitness in young adults lacked consistency (Dupuy et al., 2015; Song et al., 2016). For example, young adults with a high level of aerobic fitness responded faster in trials that included interference in one study (Dupuy et al., 2015), but responded faster in trials that did not include interference in another (Song et al., 2016). The present study showed faster responses for the higher fit group than for the lower fit group, regardless of congruency level. In order to provide supplemental evidence regarding whether aerobic fitness is related to the interference between top-down and bottom-up processes, we calculated the Stroop interference score by subtracting mean RT when the color and the color name were congruent from those that are incongruent. The results revealed a marginal main effect of group, suggesting that individuals with a higher level of aerobic fitness might be experiencing lower interference during the Stroop task, though it remains to be confirmed.

Rather than just measuring the central tendency parameters of task performance, we also examined trial-by-trial response variability (West, Murphy, Armilio, Craik, & Stuss, 2002; Wu et al., 2011). This measure helps prevent erroneous inference, given that mean-level assessments may be flawed or imprecise when variability increases (MacDonald, Li, & Bäckman, 2009; MacDonald et al., 2006). For example, Bellgrove, Hester, and Garavan (2004), using a go/no-go response inhibition paradigm, found that individual differences in go RT variability can predict inhibitory success unexplained by mean go RT. In the current study we found a smaller response variability in the higher fit group relative to that of the lower fit group across congruent and incongruent trials, a result in line with findings by Wu et al. (2011), who reported less variability in high fit preadolescents than their low fit peers, regardless of levels of flanker congruency. Similarly, research in elderly populations has shown that individuals with a higher level of physical activity are more stable in overall Stroop performance than their inactive counterparts (Gajewski & Falkenstein, 2015). Altogether, these findings suggest that higher levels of aerobic fitness are associated with greater response stability in performance during tasks requiring variable interference control. Given that smaller within-individual performance variability has been linked to better top-down regulation of attention during tasks involving executive control (Bellgrove et al., 2004; Nakata, Sakamoto, & Kakigi, 2012; West et al., 2002), our behavioral data might indicate that enhanced fitness benefits young adults, by efficiently regulating attentional control during interference-related processing. In line with this argument, we also observed that higher fit individuals showed marginally smaller Stroop interference on response variability relative to their lower fit counterparts, perhaps reflecting less demand for interference control to maintain task performance.

PLF Analysis of EEG

Despite the fact that the behavioral observation revealed some interesting findings, the lack of interaction between fitness levels and congruency does not fully support the association of higher fitness level with more efficient Stroop performance. One possible explanation is that the effect of aerobic fitness on interference control cannot be fully grasped by investigating behavioral data. Examination of the subtle aspects of cognitive processing that contribute to task performance may therefore provide further insights, which may be inaccessible via behavioral measures alone. Accordingly, this study evaluated PLFs in EEG to explore the interplay of top-down and bottom-up processes when performing the Stroop task, which may help elucidate the mechanism underlying the relation of fitness to behavioral performance. We specifically focused on beta bands (22–34 Hz) and gamma bands (36–56 Hz) because phase synchrony across fronto-parietal areas in these frequency bands has been associated with top-down and bottom-up control processes (Buschman & Miller, 2007; Kamijo & Takeda, 2013; Kamijo et al., 2011, 2016; Phillips & Takeda, 2009, 2010).

Beta PLFs. The analyses revealed that beta PLF values were greater for the incongruent condition than the congruent condition in the higher fit group only. This finding is consistent with prior evidence showing that greater beta band synchrony in the condition requiring greater amounts of executive control is only observed in individuals with higher levels of physical activity (Kamijo & Takeda, 2013; Kamijo et al., 2011) or aerobic fitness (Kamijo et al., 2016). Prior research using visual search tasks have demonstrated that beta band synchrony was greater in a conjunction search condition, in which participants were required to inhibit task-irrelevant information, than in a feature search condition (Buschman & Miller, 2007; Phillips & Takeda, 2009). The authors interpreted these findings as evidence that beta phase reflects top-down control processes. Accordingly, the greater Stroop congruency-related modulation on beta PLF values we observed in the higher-fit group may reflect an enhanced regulation of top-down attentional control on the processes related to focusing attention to task-relevant information (e.g., ink color) or to inhibiting the task-irrelevant information (e.g., word meaning). The absence of such beta phase modulation in the lower fit group may be indicative of weaker top-down attentional processes.

Our findings are also in line with the idea that aerobic fitness is related to differences in the adoption of cognitive control strategies (Kao et al., 2017; Pontifex et al., 2011). According to the dual mechanism of control framework (Braver, 2012), cognitive control operates via two theoretically separable models: “proactive control” and “reactive control.” Proactive control can be conceptualized as a top-down control process that actively maintains goal-relevant information to bias perception, attention, and action systems before the onset of cognitively demanding events. In contrast, reactive control reflects a late correction mechanism that is implemented in a timely manner when a high interference event arises within the information processing system (Braver, 2012). Applying this idea to performance on the color-naming Stroop task (Braver, 2012), response latencies may be slowed for participants adopting a reactive control strategy in which the task goals were reactivated based upon the detection of interference. By contrast, more efficient responses should be observed when participants have to actively maintain task goals by adopting a proactive control strategy. Interestingly, high fit children were found to be able to constrain their attentional focus and suppress response activation induced by incongruent flankers, which may be attributable to the adoption of a more proactive strategy (Kao et al., 2017). As such, greater regulation of top-down attentional control in higher-fit participants presumably reflects a greater likelihood of proactive control strategies, which allow maintaining task goals active during the task, and lead to more efficient responses.

Furthermore, our EEG findings may also provide further insight into the observed fitness-related differences in intraindividual response variability, given that response variability has been associated with top-down attentional control in previous research (Bellgrove et al., 2004; Nakata et al., 2012; West et al., 2002). To elaborate, smaller response variability along with greater modulation of beta PLF in the higher-fit group—likely due to the increased efficiency in top-down regulation of attention—was associated with better interference control during the Stroop task. This is consistent with research showing that enhanced aerobic fitness is beneficial to a variety of aspects of executive control (Hillman et al., 2008; Hwang, Castelli, & Gonzalez-Lima, 2017), possibly as a result of the upregulation of top-down attentional control (Themanson & Hillman, 2006; Themanson et al., 2008).

We should also point out that there is evidence against top-down processing of executive function. For example, in a recent animal study, Bedwell, Billett, Crofts, and Tinsley (2014) observed a direct connection from prefrontal cortex to sensory-motor cortex, which contrasts with the traditional model of hierarchical organization (Botvinick, 2008). Therefore, although earlier EEG investigations (Kamijo & Takeda, 2013; Kamijo et al., 2011; Phillips & Takeda, 2009) have demonstrated the role of top-down control in executive functioning, and the fact that we show evidence for the association between aerobic fitness and interference control as evidenced by frontal beta PLF, further studies are required to explore whether other functional connectivity characteristics can better explain the superior executive functioning associated with higher aerobic fitness levels.

Gamma PLFs. This study also examined whether the superior cognitive performance of higher fit individuals relates to differences in bottom-up attentional control. In the Stroop task, the impact of task-irrelevant information (i.e., the automaticity of word reading) on behavioral performance might be caused by disruption of bottom-up influences (Melcher & Gruber, 2006). Thus, if attention is easily influenced by task-irrelevant information, performance is expected to decrease during incongruent trials. The same effect, however, would elicit a bottom-up facilitation for the congruent trials. Following this rationale, it is particularly informative to examine whether aerobic fitness modulates bottom-up processes during the Stroop task.

Indeed, aerobic fitness has recently been reported to be associated with bottom-up processing of novel nontargets. Using a visual oddball task and event-related potentials analysis, Kamijo, Takeda, Takai, and Haramura (2015), found that low fit children exhibited higher miss rates (i.e., did not respond to the target), along with greater P3a amplitude, than their high fit peers. P3a is typically elicited by rare and salient distractor stimulus (Kok, 2001; Pontifex, Hillman, & Polich, 2009) and has been shown to change as a function of salient level (Yago, Corral, & Escera, 2001). Thus, P3a is believed to reflect involuntary attentional orientation to task-irrelevant stimulus (Polich, 2007). The authors concluded that children with lower fitness might have inefficient inhibition of involuntary attentional orientation to task-irrelevant information, as reflected by stronger P3a (Kamijo et al., 2015).

In contrast, our findings revealed that the modulation of gamma PLF values was not different between higher fit and lower fit participants, suggesting that the superior task performance of higher fit individuals could not be explained by differences in the control of bottom-up attentional processes. One plausible explanation is that the capacity to process task-irrelevant stimuli is age-dependent (Wetzel, Widmann, Berti, & Schröger, 2006). For example, Wetzel et al. (2006), using an auditory distraction paradigm, found that the deviant P3a was absent in adults when they were instructed to ignore the distractor sounds (i.e., changes in pitch that were not relevant to the task). By contrast, the deviant sounds still induced a clear P3a in children even though they tried to ignore distractor sounds and focus on the task. Moreover, a significant increase in fronto-parietal gamma-band synchronization in feature search compared with conjunctive search was observed in older adults (Phillips & Takeda, 2010) but not in young adults (Phillips & Takeda, 2009), perhaps reflecting a greater bias toward bottom-up driven attentional in the elderly population. Accordingly, if bottom-up attentional processes less affect performance in healthy adulthood, there might be little room for fitness-related improvements (i.e., ceiling effect). This argument is consistent with the finding that the P3a component is not modulated by fitness level in healthy young adults (Pontifex et al., 2009; Scisco et al., 2008). Further investigation of this relationship would allow a better understanding of the benefits of enhanced fitness on bottom-up interference control in children and the elderly.

Taken together, our findings are in line with previous research showing a positive relation between physical activity and beta—but not gamma—phase (Kamijo et al., 2011), suggesting that physical activity levels influence top-down, but not bottom-up, attentional control. It is perhaps not surprising that we did not found evidence of the relationship between aerobic fitness and bottom-up attentional control using EEG PLF, given that the present study did not show an effect of trial type for the gamma band, possibly due to dissimilarities between human and animal models (Phillips & Takeda, 2009) or the fact that young adults are more likely to rely on a top-down strategy than a bottom-up strategy, resulting in reduced susceptibility to task-irrelevant distractors (Phillips & Takeda, 2009, 2010).

Limitations of the Present Study

There are several limitations to the present study. First, interference control was the only aspect, among a set of executive functions, investigated in the present study. A broader range of tasks tapping various executive processes could allow more detailed explanations of the link between aerobic fitness and top-down/bottom-up attentional control. Our choice to restrict the present study to interference control was deliberate, however, and motivated by previous literature, to allow precise, well-informed hypotheses. Second, this study only evaluated subjects' aerobic fitness without considering the specific types of exercise they engaged in. Given previous work showing that activities that involve both complex motor and fitness components may better benefit cognitive functioning (Moreau, 2013; Moreau, Clerc, Mansy-Dannay, & Guerrien, 2012), future studies could also explore whether exercise type plays an important role in modulating top-down or bottom-up control of attention. Moreover, and despite our attempt to control for gender influence on the effect of interest, future studies are needed to replicate and extend upon our findings, for example by testing the interactive effect of gender and fitness on the top-down and bottom-up mechanisms underlying executive functioning. Lastly, our experimental design was cross-sectional, thus limiting causal interpretations from the observed findings. A prospective intervention study would allow circumventing this issue by directly investigating whether changes in aerobic fitness actually induce changes in EEG oscillations.

Conclusion

Our findings extend upon previous work by demonstrating that the effect of aerobic fitness on interference control can be appreciated in early adulthood (Dupuy et al., 2015; Song et al., 2016; Themanson & Hillman, 2006). Individuals with a higher level of aerobic fitness showed faster responses and smaller response variability in a color-naming Stroop task relative to their lower fit peers. Furthermore, the higher-fit group also showed marginally smaller Stroop interference scores on mean RTs and response variability along with greater modulation of beta phase synchronization, which we argue might be due to differences in the use of top-down control processes. The present study provides additional evidence that fitness-related differences in interference control relate differently to top-down and bottom-up mechanisms, in line with the selective improvement hypothesis.

References

Åberg, M. A. I., Pedersen, N. L., Torén, K., Svartengren, M., Bäckstrand, B., Johnsson, T., . . . Kuhn, H. G. (2009). Cardiovascular fitness is associated with cognition in young adulthood. *Proceedings of the National Academy of Sciences of the United States of America, 106,* 20906–20911. http://dx.doi.org/10.1073/pnas.0905307106

American College of Sports Medicine (ACSM). (2013). *ACSM's resource manual for guidelines for exercise testing and prescription* (7th ed.). Philadelphia, PA: Lippincott Williams & Wilkins.

Bedwell, S. A., Billett, E. E., Crofts, J. J., & Tinsley, C. J. (2014). The topology of connections between rat prefrontal, motor and sensory cortices. *Frontiers in Systems Neuroscience, 8,* 177. http://dx.doi.org/10.3389/fnsys.2014.00177.eCollection2014

Bellgrove, M. A., Hester, R., & Garavan, H. (2004). The functional neuroanatomical correlates of response variability: Evidence from a response inhibition task. *Neuropsychologia, 42,* 1910–1916. http://dx.doi.org/10.1016/j.neuropsychologia.2004.05.007

Botvinick, M. M. (2008). Hierarchical models of behavior and prefrontal function. *Trends in Cognitive Sciences, 12,* 201–208. http://dx.doi.org/10.1016/j.tics.2008.02.009

Braver, T. S. (2012). The variable nature of cognitive control: A dual mechanisms framework. *Trends in Cognitive Sciences, 16,* 106–113. http://dx.doi.org/10.1016/j.tics.2011.12.010

Brink, J. M., & McDowd, J. M. (1999). Aging and selective attention: An issue of complexity or multiple mechanisms? *The Journals of Gerontology: Series B: Psychological Sciences and Social Sciences, 54B,* P30–P33. http://dx.doi.org/10.1093/geronb/54B.1.P30

Buschman, T. J., & Miller, E. K. (2007). Top-down versus bottom-up control of attention in the prefrontal and posterior parietal cortices. *Science, 315,* 1860–1862. http://dx.doi.org/10.1126/science.1138071

Cohen, J. (1973). Eta-squared and partial eta-squared in fixed factor ANOVA designs. *Educational and Psychological Measurement, 33,* 107–112. http://dx.doi.org/10.1177/001316447303300111

Cohen, M. X. (2014). *Analyzing neural time series data. Theory and practice*. Cambridge, MA: MIT Press.

Colcombe, S., & Kramer, A. F. (2003). Fitness effects on the cognitive function of older adults: A meta-analytic study. *Psychological Science, 14,* 125–130. http://dx.doi.org/10.1111/1467-9280.t01-1-01430

Delorme, A., & Makeig, S. (2004). EEGLAB: An open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *Journal of Neuroscience Methods, 134,* 9–21. http://dx.doi.org/10.1016/j.jneumeth.2003.10.009

Diamond, A. (2013). Executive functions. *Annual Review of Psychology, 64,* 135–168. http://dx.doi.org/10.1146/annurev-psych-113011-143750

Dupuy, O., Gauthier, C. J., Fraser, S. A., Desjardins-Crèpeau, L., Desjardins, M., Mekary, S., . . . Bherer, L. (2015). Higher levels of cardiovascular fitness are associated with better executive function and prefrontal oxygenation in younger and older women. *Frontiers in Human Neuroscience, 9,* 66. http://dx.doi.org/10.3389/fnhum.2015.00066

Etnier, J. L., & Chang, Y. K. (2009). The effect of physical activity on executive function: A brief commentary on definitions, measurement issues, and the current state of the literature. *Journal of Sport & Exercise Psychology, 31,* 469–483. http://dx.doi.org/10.1123/jsep.31.4.469

Fründ, I., Schadow, J., Busch, N. A., Körner, U., & Herrmann, C. S. (2007). Evoked γ oscillations in human scalp EEG are test-retest reliable. *Clinical Neurophysiology, 118,* 221–227. http://dx.doi.org/10.1016/j.clinph.2006.09.013

Gajewski, P. D., & Falkenstein, M. (2015). Long-term habitual physical activity is associated with lower distractibility in a Stroop interference task in aging: Behavioral and ERP evidence. *Brain and Cognition, 98,* 87–101. http://dx.doi.org/10.1016/j.bandc.2015.06.004

Guiney, H., & Machado, L. (2013). Benefits of regular aerobic exercise for executive functioning in healthy populations. *Psychonomic Bulletin & Review, 20,* 73–86. http://dx.doi.org/10.3758/s13423-012-0345-4

Hansen, A. L., Johnsen, B. H., Sollers, J. J., III, Stenvik, K., & Thayer, J. F. (2004). Heart rate variability and its relation to prefrontal cognitive function: The effects of training and detraining. *European Journal of Applied Physiology, 93,* 263–272. http://dx.doi.org/10.1007/s00421-004-1208-0

Hayes, S. M., Forman, D. E., & Verfaellie, M. (2016). Cardiorespiratory fitness is associated with cognitive performance in older but not younger adults. *The Journals of Gerontology: Series B, Psychological Sciences and Social Science, 71,* 474–482. http://dx.doi.org/10.1093/geronb/gbu167

Hillman, C. H., Erickson, K. I., & Kramer, A. F. (2008). Be smart, exercise your heart: Exercise effects on brain and cognition. *Nature Reviews Neuroscience, 9,* 58–65. http://dx.doi.org/10.1038/nrn2298

Hsu, T. Y., Tseng, P., Liang, W. K., Cheng, S. K., & Juan, C. H. (2014). Transcranial direct current stimulation over right posterior parietal cortex changes prestimulus alpha oscillation in visual short-term memory task. *NeuroImage, 98,* 306–313. http://dx.doi.org/10.1016/j.neuroimage.2014.04.069

Hwang, J., Castelli, D. M., & Gonzalez-Lima, F. (2017). The positive cognitive impact of aerobic fitness is associated with peripheral inflammatory and brain-derived neurotrophic biomarkers in young adults. *Physiology & Behavior, 179,* 75–89. http://dx.doi.org/10.1016/j.physbeh.2017.05.011

Kalyani, M. N., Ebadi, A., Mehri, S. N., & Jamshidi, N. (2008). Comparing the effect of Fire-fighting protective clothes and usual work clothes on aerobic capacity (Vo2max). *Pakistan Journal of Medical Sciences, 24,* 678–683.

Kamijo, K., O'Leary, K. C., Pontifex, M. B., Themanson, J. R., & Hillman, C. H. (2010). The relation of aerobic fitness to neuroelectric indices of cognitive and motor task preparation. *Psychophysiology, 47,* 814–821.

Kamijo, K., & Takeda, Y. (2013). Physical activity and trial-by-trial adjustments of response conflict. *Journal of Sport & Exercise Psychology, 35,* 398–407. http://dx.doi.org/10.1123/jsep.35.4.398

Kamijo, K., Takeda, Y., & Hillman, C. H. (2011). The relation of physical activity to functional connectivity between brain regions. *Clinical Neurophysiology, 122,* 81–89. http://dx.doi.org/10.1016/j.clinph.2010.06.007

Kamijo, K., Takeda, Y., Takai, Y., & Haramura, M. (2015). Greater aerobic fitness is associated with more efficient inhibition of task-irrelevant information in preadolescent children. *Biological Psychology, 110,* 68–74. http://dx.doi.org/10.1016/j.biopsycho.2015.07.007

Kamijo, K., Takeda, Y., Takai, Y., & Haramura, M. (2016). The relationship between childhood aerobic fitness and brain functional connectivity. *Neuroscience Letters, 632,* 119–123. http://dx.doi.org/10.1016/j.neulet.2016.08.051

Kao, S. C., Drollette, E. S., Scudder, M. R., Raine, L. B., Westfall, D. R., Pontifex, M. B., & Hillman, C. H. (2017). Aerobic fitness is associated with cognitive control strategy in preadolescent children. *Journal of Motor Behavior, 49,* 150–162. http://dx.doi.org/10.1080/00222895.2016.1161594

Kawagoe, T., Onoda, K., & Yamaguchi, S. (2017). Associations among executive function, cardiorespiratory fitness, and brain network properties in older adults. *Scientific Reports, 7,* 40107. http://dx.doi.org/10.1038/srep40107

Khan, N. A., & Hillman, C. H. (2014). The relation of childhood physical activity and aerobic fitness to brain function and cognition: A review. *Pediatric Exercise Science, 26,* 138–146. http://dx.doi.org/10.1123/pes.2013-0125

Kok, A. (2001). On the utility of P3 amplitude as a measure of processing capacity. *Psychophysiology, 38,* 557–577. http://dx.doi.org/10.1017/S0048577201990559

Kramer, A. F., Hahn, S., Cohen, N. J., Banich, M. T., McAuley, E., Harrison, C. R., . . . Colcombe, A. (1999). Ageing, fitness and neurocognitive function. *Nature, 400,* 418–419. http://dx.doi.org/10.1038/22682

MacDonald, S. W. S., Li, S. C., & Bäckman, L. (2009). Neural underpinnings of within-person variability in cognitive functioning. *Psychology and Aging, 24,* 792–808. http://dx.doi.org/10.1037/a0017798

MacDonald, S. W. S., Nyberg, L., & Bäckman, L. (2006). Intra-individual variability in behavior: Links to brain structure, neurotransmission and neuronal activity. *Trends in Neurosciences, 29,* 474–480. http://dx.doi.org/10.1016/j.tins.2006.06.011

MacLeod, C. M. (1991). Half a century of research on the Stroop effect: An integrative review. *Psychological Bulletin, 109,* 163–203. http://dx.doi.org/10.1037/0033-2909.109.2.163

MacLeod, C. M., & MacDonald, P. A. (2000). Interdimensional interference in the Stroop effect: Uncovering the cognitive and neural anatomy of attention. *Trends in Cognitive Sciences, 4,* 383–391. http://dx.doi.org/10.1016/S1364-6613(00)01530-8

Mäntylä, T., Karlsson, M. J., & Marklund, M. (2009). Executive control functions in simulated driving. *Applied Neuropsychology, 16,* 11–18. http://dx.doi.org/10.1080/09084280802644086

Mekarski, J. E., Cutmore, T. R. H., & Suboski, W. (1996). Gender differences during processing of the Stroop task. *Perceptual and Motor Skills, 83,* 563–568. http://dx.doi.org/10.2466/pms.1996.83.2.563

Melcher, T., & Gruber, O. (2006). Oddball and incongruity effects during Stroop task performance: A comparative fMRI study on selective attention. *Brain Research, 1121,* 136–149. http://dx.doi.org/10.1016/j.brainres.2006.08.120

Michalareas, G., Vezoli, J., van Pelt, S., Schoffelen, J. M., Kennedy, H., & Fries, P. (2016). Alpha-beta and gamma rhythms subserve feedback and feedforward influences among human visual cortical areas. *Neuron, 89,* 384–397. http://dx.doi.org/10.1016/j.neuron.2015.12.018

Milham, M. P., Banich, M. T., & Barad, V. (2003). Competition for priority in processing increases prefrontal cortex's involvement in top-down control: An event-related fMRI study of the Stroop task. *Cognitive Brain Research, 17,* 212–222. http://dx.doi.org/10.1016/S0926-6410(03)00108-3

Miller, E. K., & Cohen, J. D. (2001). An integrative theory of prefrontal cortex function. *Annual Review of Neuroscience, 24,* 167–202. http://dx.doi.org/10.1146/annurev.neuro.24.1.167

Moore, R. D., Wu, C. T., Pontifex, M. B., O'Leary, K. C., Scudder, M. R., Raine, L. B., . . . Hillman, C. H. (2013). Aerobic fitness and intra-individual variability of neurocognition in preadolescent children. *Brain and Cognition, 82,* 43–57. http://dx.doi.org/10.1016/j.bandc.2013.02.006

Moreau, D. (2013). Motor expertise modulates movement processing in working memory. *Acta Psychologica, 142,* 356–361. http://dx.doi.org/10.1016/j.actpsy.2013.01.011

Moreau, D., Clerc, J., Mansy-Dannay, A., & Guerrien, A. (2012). Enhancing spatial ability through sport practice: Evidence for an effect of motor training on mental rotation performance. *Journal of Individual Differences, 33,* 83–88. http://dx.doi.org/10.1027/1614-0001/a000075

Nakata, H., Sakamoto, K., & Kakigi, R. (2012). The relationship between reaction time and response variability and somatosensory no-go potentials. *European Journal of Applied Physiology, 112,* 207–214. http://dx.doi.org/10.1007/s00421-011-1973-5

Papenberg, G., Hämmerer, D., Müller, V., Lindenberger, U., & Li, S. C. (2013). Lower theta inter-trial phase coherence during performance monitoring is related to higher reaction time variability: A lifespan study. *NeuroImage, 83,* 912–920. http://dx.doi.org/10.1016/j.neuroimage.2013.07.032

Phillips, S., & Takeda, Y. (2009). Greater frontal-parietal synchrony at low gamma-band frequencies for inefficient than efficient visual search in human EEG. *International Journal of Psychophysiology, 73,* 350–354. http://dx.doi.org/10.1016/j.ijpsycho.2009.05.011

Phillips, S., & Takeda, Y. (2010). Frontal-parietal synchrony in elderly EEG for visual search. *International Journal of Psychophysiology, 75,* 39–43. http://dx.doi.org/10.1016/j.ijpsycho.2009.11.001

Phillips, S., Takeda, Y., & Singh, A. (2012). Visual feature integration indicated by pHase-locked frontal-parietal EEG signals. *PLoS ONE, 7,* e32502. http://dx.doi.org/10.1371/journal.pone.0032502

Polich, J. (2007). Updating P300: An integrative theory of P3a and P3b. *Clinical Neurophysiology, 118,* 2128–2148. http://dx.doi.org/10.1016/j.clinph.2007.04.019

Pontifex, M. B., Hillman, C. H., & Polich, J. (2009). Age, physical fitness, and attention: P3a and P3b. *Psychophysiology, 46,* 379–387. http://dx.doi.org/10.1111/j.1469-8986.2008.00782.x

Pontifex, M. B., Miskovic, V., & Laszlo, S. (2017). Evaluating the efficacy of fully automated approaches for the selection of eyeblink ICA components. *Psychophysiology, 54,* 780–791. http://dx.doi.org/10.1111/psyp.12827

Pontifex, M. B., Raine, L. B., Johnson, C. R., Chaddock, L., Voss, M. W., Cohen, N. J., . . . Hillman, C. H. (2011). Cardiorespiratory fitness and the flexible modulation of cognitive control in preadolescent children. *Journal of Cognitive Neuroscience, 23,* 1332–1345. http://dx.doi.org/10.1162/jocn.2010.21528

Richter, C. G., Thompson, W. H., Bosman, C. A., & Fries, P. (2017). Top-down beta enhances bottom-up gamma. *The Journal of Neuroscience, 37,* 6698–6711. http://dx.doi.org/10.1523/JNEUROSCI.3771-16.2017

Roach, B. J., & Mathalon, D. H. (2008). Event-related EEG time-frequency analysis: An overview of measures and an analysis of early gamma band phase locking in schizophrenia. *Schizophrenia Bulletin, 34,* 907–926. http://dx.doi.org/10.1093/schbul/sbn093

Scisco, J. L., Leynes, P. A., & Kang, J. (2008). Cardiovascular fitness and executive control during task-switching: An ERP study. *International Journal of Psychophysiology, 69,* 52–60. http://dx.doi.org/10.1016/j.ijpsycho.2008.02.009

Semlitsch, H. V., Anderer, P., Schuster, P., & Presslich, O. (1986). A solution for reliable and valid reduction of ocular artifacts, applied to the P300 ERP. *Psychophysiology, 23,* 695–703. http://dx.doi.org/10.1111/j.1469-8986.1986.tb00696.x

Song, T. F., Chi, L., Chu, C. H., Chen, F. T., Zhou, C., & Chang, Y. K. (2016). Obesity, cardiovascular fitness, and inhibition function: An electrophysiological study. *Frontiers in Psychology, 7,* 1124. http://dx.doi.org/10.3389/fpsyg.2016.01124.eCollection2016

Stroop, J. R. (1935). Studies of interference in serial verbal reactions. *Journal of Experimental Psychology, 18,* 643–662. http://dx.doi.org/10.1037/h0054651

Themanson, J. R., & Hillman, C. H. (2006). Cardiorespiratory fitness and acute aerobic exercise effects on neuroelectric and behavioral measures of action monitoring. *Neuroscience, 141,* 757–767. http://dx.doi.org/10.1016/j.neuroscience.2006.04.004

Themanson, J. R., Pontifex, M. B., & Hillman, C. H. (2008). Fitness and action monitoring: Evidence for improved cognitive flexibility in young adults. *Neuroscience, 157,* 319–328. http://dx.doi.org/10.1016/j.neuroscience.2008.09.014

Urigüen, J. A., & Garcia-Zapirain, B. (2015). EEG artifact removal-state-of-the-art and guidelines. *Journal of Neural Engineering, 12,* 031001. http://dx.doi.org/10.1088/1741-2560/12/3/031001

Wang, C. H., Lo, Y. H., Pan, C. Y., Chen, F. C., Liang, W. K., & Tsai, C. L. (2015). Frontal midline theta as a neurophysiological correlate for deficits of attentional orienting in children with developmental coordination disorder. *Psychophysiology, 52,* 801–812. http://dx.doi.org/10.1111/psyp.12402

Wang, C. H., Shih, C. M., & Tsai, C. L. (2016). The relation between aerobic fitness and cognitive performance. *Journal of Psychophysiology, 30,* 102–113. http://dx.doi.org/10.1027/0269-8803/a000159

Wang, C. H., & Tsai, C. L. (2016). Physical activity is associated with greater visuospatial cognitive functioning regardless of the level of cognitive load in elderly adults. *Journal of Sport & Exercise Psychology, 38,* 69–81. http://dx.doi.org/10.1123/jsep.2015-0221

Wang, C. H., Tsai, C. L., Tseng, P., Yang, A. C., Lo, M. T., Peng, C. K., . . . Liang, W. K. (2014). The association of physical activity to neural adaptability during visuo-spatial processing in healthy elderly adults: A multiscale entropy analysis. *Brain and Cognition, 92,* 73–83. http://dx.doi.org/10.1016/j.bandc.2014.10.006

Wang, C. H., Tsai, C. L., Tu, K. C., Muggleton, N. G., Juan, C. H., & Liang, W. K. (2015). Modulation of brain oscillations during fundamental visuo-spatial processing: A comparison between female collegiate badminton players and sedentary controls. *Psychology of Sport and Exercise, 16,* 121–129. http://dx.doi.org/10.1016/j.psychsport.2014.10.003

Wang, C. H., Tseng, Y. T., Liu, D., & Tsai, C. L. (2017). Neural oscillation reveals deficits in visuospatial working memory in children with developmental coordination disorder. *Child Development, 88,* 1716–1726. http://dx.doi.org/10.1111/cdev.12708

Wang, C. H., Yang, C. T., Moreau, D., & Muggleton, N. G. (2017). Motor expertise modulates neural oscillations and temporal dynamics of cognitive control. *NeuroImage, 158,* 260–270. http://dx.doi.org/10.1016/j.neuroimage.2017.07.009

West, R., Murphy, K. J., Armilio, M. L., Craik, F. I. M., & Stuss, D. T. (2002). Lapses of intention and performance variability reveal age-related increases in fluctuations of executive control. *Brain and Cognition, 49,* 402–419. http://dx.doi.org/10.1006/brcg.2001.1507

Wetzel, N., Widmann, A., Berti, S., & Schröger, E. (2006). The development of involuntary and voluntary attention from childhood to adulthood: A combined behavioral and event-related potential study. *Clinical Neurophysiology, 117,* 2191–2203. http://dx.doi.org/10.1016/j.clinph.2006.06.717

Wu, C. T., Pontifex, M. B., Raine, L. B., Chaddock, L., Voss, M. W., Kramer, A. F., & Hillman, C. H. (2011). Aerobic fitness and response variability in preadolescent children performing a cognitive control task. *Neuropsychology, 25,* 333–341. http://dx.doi.org/10.1037/a0022167

Yago, E., Corral, M. J., & Escera, C. (2001). Activation of brain mechanisms of attention switching as a function of auditory frequency change. *NeuroReport: For Rapid Communication of Neuroscience Research, 12,* 4093–4097. http://dx.doi.org/10.1097/00001756-200112210-00046

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