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Modulation of brain oscillations during fundamental visuo-spatial processing: A comparison between female collegiate badminton players and sedentary controls

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A B S T R A C T

Objectives: The present study aimed to investigate the difference in fundamental cognitive processing and neural oscillations between badminton players and sedentary controls.
Design: A cross-sectional design was adopted to address this issue.
Methods: We compared time-frequency electroencephalographic (EEG) activity from collegiate female badminton players ($n = 12$, aged 20.58 ± 2.75 years) and age-and gender-matched sedentary non-athletic controls ($n = 13$, aged 19.08 ± 2.10 years) when they performed a task that involves visuo-spatial attention and working memory.
Results: We observed that players responded faster than controls on the task without suffering any increase in error responses. Correspondingly, the players, relative to controls, exhibited higher task-related modulations in beta power in the attention condition as well as in theta and beta power in the working memory condition. Notably, the behavior-EEG correlations revealed that better attention performance is associated with lower beta power, while greater working memory is related to higher theta power.
Conclusions: Our results shed light on the mechanisms of athletic superiority in fundamental cognitive functioning: the higher theta synchronization points to a greater engagement of attention, whereas the higher beta desynchronization supports the contribution of processing speed (or motor-related processing) to better performance in athletes. This study extends current understanding by suggesting that enhanced neurocognitive function seen in athletes may transfer to fundamental tasks, giving insight into the generalizability of sport experience to neurocognitive functioning.

Introduction

Elite athletes show not only increased sporting capacity but also superior performance in terms of cognitive brain function (Yarrow, Brown, & Krakauer, 2009). There is increasing evidence that athletes show superiority in a wide range of cognitive processes, including perception, anticipation and decision-making (Mann, Williams, Ward, & Janelle, 2007; Nakata, Yoshie, Miura, & Kudo, 2010; Yarrow et al., 2009). However, many of these studies employed sport-specific designs (Jin et al., 2011, 2010; Mann et al., 2007; Wright, Bishop, Jackson, & Abernethy, 2011; Zoudji, Thon, & Debû, 2010), which raises the concern that sporting knowledge may contaminate this type of cognitive enhancement. Importantly, the evidence so far means it may be hard to understand how “game intelligence” in sports transfers to fundamental cognitive function in daily living, which remains poorly understood (Vestberg, Gustafson, Maurex, Ingvar, & Petrovic, 2012; Voss, Kramer, Basak, Prakash, & Roberts, 2010). Accordingly, here we were interested in whether individuals with long-term participation in competitive sports training would exhibit better cognitive functioning in tasks

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stripped of sport knowledge; that is, it remains possible that the superior cognitive processing in athletes is not only due to benefits as a consequence of sport-related knowledge, but also in part may be due to better fundamental cognition. We believe that investigation along these lines may further the understanding of sport-related neuroplasticity (Voss et al., 2010).

Recently, Vestberg et al. (2012) found that fundamental executive control was positively correlated with the success in soccer two seasons later, indicating the importance of fundamental cognitive functions in sporting performance. More specifically, it was claimed that athletes trained under both physical and cognitive loads show a larger modulatory effect on cognitive function than those trained under each individually (Chan, Wong, Liu, Yu, & Yan, 2011; Wang, Chang, Liang, Shih, et al., 2013). In line with this argument, Overney, Blanke, and Herzog (2008) found that tennis players showed superiority in temporal perceptual processing relative to both triathletes and non-athletes, suggesting sport-related cognitive skills benefit through training (e.g., temporal processing in tennis). Interestingly, Chaddock, Neider, Voss, Gaspar, and Kramer (2011) reported that athlete and non-athlete differences in processing speed relates to daily multitasking abilities, indicating that higher efficiency in basic information processing for athletes may improve their capacity to perform daily challenges. To further address this issue, additional work is required to explore athletic superiority in information processing using tasks that involve other cognitive components (Chaddock et al., 2011). Thus, athlete-and-control difference in visuo-spatial cognitive processing, which is of importance in sports, was tested in the present study.

In order to test the neural mechanisms underlying differences in visuo-spatial cognition between athletes and non-athletes, a time-frequency analysis of electroencephalographic (EEG) data, which can provide important information about frequency-specific oscillations time-locked to events of interest (Roach & Mathalon, 2008), was used in the current study. Frequency oscillations can be picked up from the scalp through a traditional EEG approach when a large number of neurons fire synchronously within the same frequency band. Task-related bursts of oscillatory activities can thus be interpreted in relation to cognitive performance (Tallon-Baudry & Bertrand, 1999). Previous EEG studies found that oscillations of theta (4–7 Hz) and alpha (8–14 Hz) bands can be seen for factors associated with visuo-spatial processing such as attention or working memory (Bastiaansen, Posthuma, Groot, & de Geus, 2002; Capotosto et al., 2009; Klimesch, 1999; McEvoy, Pellouchoud, Smith, & Gevins, 2001; Roberts, Hsieh, & Ranganath, 2012; Rugg & Dickens, 1982; Ward, 2003). For example, a study with a large number of subjects observed increased theta power in both encoding and retrieval stages during a visuo-spatial working memory task (Bastiaansen et al., 2002), suggesting theta oscillations may be closely related to the processing of encoding and retrieval in memory (Ward, 2003). Importantly, these brain oscillations can reflect individual differences in visuo-spatial processing. Capotosto et al. (2009), using a task requiring visuo-spatial processing, found that intelligence scores had a positive correlation with event-related theta power synchronization. In addition, good memory performance was shown to be associated with an event-related increase in theta power but a decrease in alpha power (Klimesch, 1999). Accordingly, if long-term participation in sport training is associated with differences in fundamental visuo-spatial processing, any differences between athletes and non-athletes may be seen in terms of event-related band power changes. Moreover, prior studies have demonstrated that athletes are able to perform faster simple responses as compared to non-athletes (Chaddock et al., 2011; Voss et al., 2010), indicating athletes may be better at basic motor-related processing (e.g., motor preparation). Faster responses have been associated with lower beta band power (15–30 Hz) (Senkowski, Molholm, Gomez-Ramirez, & Foxe, 2006; Tzagarakis, Ince, Leuthold, & Pellizzer, 2010). Previously it was found that higher beta desynchronization prior to response execution relates to faster processing speed during simple response tasks (Senkowski et al., 2006), suggesting an association of decreased beta power with response facilitation effects. Based on this, we thus further studied beta band power to test whether athletic superiority in cognitive processing is due, in part, to motor-related components, and so gain insight into the possible mechanisms beyond visuo-spatial components underlying any athlete-control differences.

Additionally, although higher modulations of neural oscillations have been related to better cognitive function (Capotosto et al., 2009; Klimesch, 1999), the role of neural efficiency in athletes (Del Percio et al., 2009; Nakata et al., 2010; Yarrow et al., 2009) should be taken into account. Neural efficiency is characterized by optimal performance with minimal cortical resource consumption, which might be achieved through long-term participation in training requiring rapid motor-related processing such as athletic training (Nakata et al., 2010). However, neural efficiency might be linked to sport-specific trained movements (Del Percio et al., 2008; Di Russo, Pitzalis, Aprile, & Spinelli, 2005). Therefore, it is unclear whether athletes could still exhibit higher efficiency in an untrained and non-sport specific cognitive task.

In summary, to examine whether fundamental cognitive function is different in individuals with long-term experience in sports, a modified attention and working memory task that taps visuo-spatial components was administered (Muller & Knight, 2002). We only recruited female participants in order to avoid any gender effect on visuo-spatial processing (Hugdahl, Thomsen, & Ersland, 2006; Vecchi & Girelli, 1998), that may possibly bias any effects of sports training on cognitive function (Voss et al., 2010). We chose badminton players as the athletic group because they are trained yearly in a sport that has intense visuo-spatial demands. They are therefore highly likely to develop superiority in fundamental visuo-spatial cognition as their skill acquisition progresses (Jin et al., 2011, 2010; Lees, 2003) relative to untrained individuals. In accordance with this claim, Tsai (2009), employing a visuo-spatial paradigm, observed that a 10-week racket sport intervention has the capacity to reduce attentional costs induced by an invalid spatial cue in children with developmental coordination disorder (DCD). We also recruited a control group from those who reported having no or only historically little experience in any racket sport and did not partake in regular exercise in at least the 6 months prior to the study.

We firstly hypothesized that badminton players may show better task performance relative to non-athletes because it is suggested that sports training might be a medium for cognitive training that results in more efficient brain function (Voss et al., 2010). Secondly, due to the fact that greater event-related theta synchronization and alpha/beta desynchronization are associated with better visuo-spatial cognition (Capotosto et al., 2009; Klimesch, 1999) or faster motor processing (Senkowski et al., 2006; Tzagarakis et al., 2010), we hypothesized that, if athletic superiority in visuo-spatial processing was found, badminton players might show relatively higher theta power but lower alpha power during task execution. Moreover, if athletes showed better task performance (e.g., faster RTs) on top of motor-related processing, relatively lower beta power prior to motor execution in badminton players would be expected. In contrast, if the neural efficiency (Nakata et al., 2010; Yarrow et al., 2009) in athletes can still be observed in a fundamental cognitive task, the above expected patterns of EEG results would be reversed; that is, lower cortical activities would be seen in athletes during cognitive functioning. To the best of our knowledge, the present study is the first to explore the effects of sporting experience on visuo-spatial processing in young female adults, and more importantly, the first to investigate the possible mechanisms by evaluating brain oscillations.

Methods

Participants

Twenty-eight female university students were recruited. Of these, twelve students were members of the collegiate badminton team (aged 20.58 ± 2.75 years, with training experience of 6.58 ± 2.07 years), while another thirteen students reported no historical specialization in any sport and were sedentary (defined by the estimation of levels of physical activity) at the time of the study (aged 19.07 ± 2.10 years). Two badminton players and one control were excluded from analysis due to excessive artifacts in the electrophysiological data (<20 valid trials) (Kamijo & Takeda, 2013). Thus, analyses were conducted on 25 participants (12 athletes and 13 controls). Additionally, the badminton team won first prize in the National Intercollegiate Athletic Games at the time they participated in the current study, indicating a high level of skill. All participants had normal or corrected-to-normal visual acuity and were right-handed. No individuals reported having a history of neurological problems or cardiovascular diseases, nor were any taking any medications that affect cognitive function. All participants gave informed consent prior to participating and the study was approved by the local ethics committee.

Measures

Estimation of levels of physical activity

A 7-day physical activity recall questionnaire was adapted from Sallis et al. (1985), which can be utilized to estimate and quantify levels of physical activity (Maximova, O'Loughlin, Paradis, Hanley, & Lynch, 2009; Wang, Chang, Liang, Shih, et al., 2013). In the 7-day physical activity recall questionnaire, the experimenter instructed the participants to recall their physical activities in the past 7 days, which estimates the time (hours) spent at different physical activity levels (e.g., light, moderate, high, intense, and sleep). Each level of intensity was indicated by a metabolic equivalent (MET, 1 MET = 1 kcal/kg/hour): sleep = 1 MET, light activity = 1.5 METs [24 h − (sleep + moderate + moderate + high + intense)], moderate = 4 METs (e.g., golf, flexibility), high = 6 METs (e.g., doubles tennis, dancing), intense = 10 METs (singles tennis, swimming, jogging). The Kcal expenditure was calculated by the formula: *Kcal/day = Total physical activity (METs)/7 × weight (kg)*. This questionnaire could thus successfully screen unwanted participants (i.e., physically active non-athletes or physically inactive athletes) that would potentially bias the results (Wang, Chang, Liang, Shih, et al., 2013). Athletes and sedentary controls were excluded according to the following two criteria: (1) for the athletic group: those who engaged in their training programs less than three times per week; (2) for the control group, those who spent more than 2 h per week exercising at the intensity of moderate or higher (Wang, Chang, Liang, Chiu, et al., 2013; Wang, Chang, Liang, Shih, et al., 2013).

Non-delayed and delayed matching-to-sample tests

The current study employed a non-delayed and a delayed matching-to-sample test which consisted of one visuo-spatial attention (non-delay) condition and one visuo-spatial working memory (delay) condition (Muller & Knight, 2002; Wang et al., in press). This type of paradigm allows the investigation of differences in visuo-spatial capacity for different populations (Muller & Knight, 2002; Tsai, Chang, Hung, Tseng, & Chen, 2012).

The paradigm was programmed using STIM2 software (Neuroscan Ltd, El Paso, TX, USA). All stimuli were presented on a 21-inch cathode-ray tube display against a black background. Similar to Muller and Knight (2002)'s study, the stimulus consisted of a 9-mm-diameter red dot randomly presented at one of 50 possible locations within a 3.8° × 7.4° grey rectangle, which was either in the center of the screen or 5.9° to the left or right of the central fixation point. The procedure is illustrated in Fig. 1.

Visuo-spatial attention (non-delay) condition

In the attention condition, two rectangles were presented on the screen simultaneously: one was placed in the center and another was placed either left or right of the center (Fig. 1, non-delay task). The stimuli were presented for 180 ms, a duration typically shorter than voluntary saccade latency, so minimizing the possibility of unwanted eye movements affecting the results (Muller & Knight, 2002; Tsai, Chang, et al., 2012). In this condition, participants were required to discriminate whether the red dots in the two different rectangles were spatially identical or not.

Visuo-spatial working memory (delay) condition

In the working memory condition, the first stimulus (S1) was presented for 180 ms on either the right or left of the central fixation (.5° × .5°), and the second stimulus (S2) appeared for 500 ms in the center of the screen and replaced the fixation during the 1.5 s-delay (Fig. 1, Delay task). Thus, participants were required to encode the red (in web version) dot position in the first stimulus (S1), and to maintain its current spatial location for 1.5 s, and then to decide whether the position of the red dot in the second stimulus (S2) was the same.

Before performing the task, participants were instructed that accuracy and speed were equally important. If the spatial positions of the stimuli seemed identical (matching), participants had to press the "K" key with their index finger, whereas to press the "L" key if it they thought the stimuli were different (non-matching, 6.4 mm diagonal difference), using their middle finger on a computer keyboard. Feedback (correct, incorrect, no response) was provided based on their responses. A total of 216 trials were included in the whole task procedure, which was divided into three consecutive blocks of 72 trials that comprised randomized non-delayed and delayed conditions with equal probability. They were encouraged to take a 3-to-5-minute break between blocks.

Procedure

All participants took part in the experimental procedure that included two phases: the first phase consisted of the 7-day physical activity recall questionnaire and the second phase was comprised of the cognitive task. Only eligible participants who passed the criterion for the questionnaire went on to perform the cognitive task. During the cognitive test, participants were seated comfortably in a dimly lit and soundproof room in front of a screen positioned at eye level at a distance of approximately 100 cm. The duration of the total experimental procedure was approximately 1 h. Before the formal test, the experimenter explained the task procedure and ensured the participants understood the task with a practice block. Additionally, the participants were instructed to avoid saccades with regard to the laterally presented stimuli. After being familiarized with the whole procedure, participants then performed the task while behavioral and EEG data were recorded.

EEG recording

The electroencephalographic recording procedure was similar to previous studies (Tsai, Chang, et al., 2012; Tsai, Wang, & Tseng, 2012). EEG activity was recorded using a Syn-Amps EEG amplifier and the Scan 4.3 package (Neuroscan Inc., El Paso, TX, USA) with 32

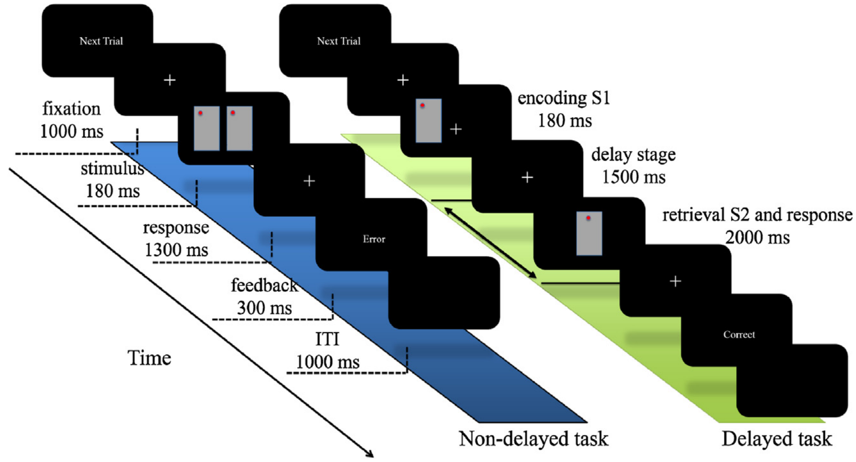

Fig. 1. Illustration of the non-delay and delayed matching-to-sample task. Two different conditions were presented using this paradigm: (1) a non-delayed condition where two stimuli were presented simultaneously (2) a delayed condition which consisted of two stimuli with a 1.5 s delay in between. Feedback was given according to the accuracy of subjects' responses.

electrodes mounted in an elastic cap (Quik-Cap; Compumedics, Neuroscan Inc.) designed for the International 10–20 System. A reference electrode was placed on the mastoid and a ground electrode on the mid-forehead on the Quik-Cap. Horizontal and vertical electro-oculograms were recorded bipolarly from the superolateral right canthus, and below and lateral to the left eye connected to the system reference to monitor eye movements. Electrode impedances were kept below 5 kΩ. Electroencephalography data were acquired with an analog–digital rate of 500 Hz/channel, filtered with a Butterworth bandpass filter (0.1–50 Hz). (Tsai, Chen, et al., 2014; Tsai, Wang, 2014)

Data analysis

Behavioral data

All participants' descriptive characteristics (including age, height, weight, BMI, and estimated physical activity level) were measured using means and standard deviations, and group differences were analyzed using independent *t*-tests. For task performance, a two-way [2 (groups: athletes, controls) × 2 (conditions: attention, working memory)] mixed design, factorial, and repeated-measures ANOVA with a Bonferroni adjustment for multiple comparisons was conducted to analyze the percentage accuracy and correct-trial RTs, neither of which violated the assumptions of the ANOVA. In addition, to test whether the group effect was due to a benefit of exercise in general, in terms of levels of physical activity, rather than a sport-specific training effect, we conducted a correlation analysis (Pearson correlation) to examine the relationship between the task performance and levels of physical activity. We used the accuracy-adjusted reaction time (mean response time/accuracy), which considers measures of both accuracy and RT performance (Townsend & Ashby, 1983), to define the overall task performance. This approach has been suggested to help rule out the possible influences of any behavioral strategy on task performance (e.g., speed-accuracy trade-off) (Getzmann, Falkenstein, & Gajewski, 2013). The significance level was set at $p \leq .05$. All analysis was completed using the SPSS 18.0 Software System.

Time-frequency analysis

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) scripts. Because it is suggested that visuo-spatial processing involves the fronto-parietal network (Corbetta & Shulman, 2002; McEvoy et al., 2001), we selected the midline fronto-parietal cluster (Fz, FCz, Cz, CPz, Pz) for analysis to test the effects of sport on visuo-spatial processing in our group of participants. The offline ocular-corrected EEG data were locked to the stimulus onset, and were segmented into epochs: (1) for the attention (non-delayed) condition, −1000 to 1000 ms relative to the stimulus onset; (2) for the working memory (delayed) condition, 1000 ms before the encoding stimulus onset (S1), and lasting until 1000 ms after the retrieval stimulus (S2). Trials containing artifacts exceeding ±150 uV (Lo et al., 2013) were discarded. Power 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 50 Hz (Roach & Mathalon, 2008). Oscillatory power, defined as the square of the modulus of the resulting complex number, was then averaged across trials. The averaged oscillatory power of each condition for each participant was rescaled by the baseline value from 500 to 50 ms before the stimulus onset, and taking the log 10 transform of this quotient (dB). All trials were averaged for each condition. The different condition types, attention (non-delay) and working memory (delay), was analyzed separately due to the different epoch windows. First, a one sample *t*-test was conducted to see whether the rescaled power was significantly different relative to baseline and a $p < .05$ with false discovery rate (FDR) correction was set for the level of significance. For examinations of group effects, power oscillations in times of interest (e.g., we defined regions between "post-stimulus" and "pre-response" with regard to stimulus onset; 100–400 ms in the non-delay and 100–500 ms in the delay condition) for each frequency band (e.g., theta: 4–7 Hz; alpha: 8–14 Hz; beta: 15–30 Hz) were averaged and separately submitted to independent *t*-tests. The reason for use of this selected time window was to avoid any spectral leakage from stimulus presentation and response execution. In addition, we also tested group effects on theta power in the encoding stage in the delay condition. To achieve this, values within the theta band from 100 to 400 ms with regard to stimulus were averaged and submitted to an independent *t*-test. The significance level was set at $p \leq .05$ with SPSS 18. Finally, correlation between behavioral data (accuracy-adjusted reaction time: mean response time/accuracy) and oscillatory EEG power was tested to gain insight into the possible neural mechanisms being most associated with task performance. The significance level was set at $p \leq .01$ (uncorrected).

Results

Participant demographics

Participant demographic data and their levels of physical activity are provided in Table 1. Demographic variables including age, $t(23) = 1.55$, $p = .135$, $d = .62$, height, $t(23) = .64$, $p = .530$, $d = .02$, weight, $t(23) = .14$, $p = .892$, $d = .06$, and BMI, $t(23) = .00$, $p = .997$, $d = .00$, did not differ between groups. There was a significant group difference for the levels of physical activity, $t(23) = 5.85$, $p < .001$, $d = 2.36$.

Behavioral performance

Accuracy

Accuracy was defined as the percentage of correct responses. As can be seen in Table 2, the data showed a main effect for condition, $F(1,23) = 6.95$, $p = .015$, $\eta_p^2 = .23$, indicating the spatial demand may be higher in the working memory (delayed) condition relative to the attention (non-delayed) condition. However, no significant effect was found for group, $F(1,23) = .39$, $p = .54$, $\eta_p^2 = .02$ and nor was there a group by condition interaction, $F(1,23) = .10$, $p = .759$, $\eta_p^2 = .00$, suggesting athletes and controls had comparable ability in identifying the difference in spatial locations.

Reaction time

Table 2 shows the mean RT across groups and conditions. A significant main effect was observed across conditions, $F(1,23) = 391.78$, $p < .001$, $\eta_p^2 = .95$, with shorter RTs for the attention condition and longer RTs for the working memory condition. Additionally, we found a main effect for group, $F(1,23) = 8.03$, $p = .009$, $\eta_p^2 = .26$. RTs with the athletes much shorter compared to controls, suggesting athletes can identify the similarity/differences in spatial positions more quickly. Finally, there was no significant condition × group interaction, $F(1,23) = 2.06$, $p = .026$, $\eta_p^2 = .08$.

Task performance and levels of physical activity

In this analysis, a correlation analysis between task performance (accuracy-adjusted RT) and levels of physical activity across participants was conducted to test whether the physical activity level is a confounding variable that may potentially bias the sporting effect on cognitive functioning. We found that the accuracy-adjusted RT didn't correlate with levels of physical activity in either the attention ($r = -.0.90$, $p = .669$) or in the working memory condition ($r = -.18$, $p = .396$) across subjects, indicating that levels of physical activity may not directly account for the group effect of task performance in the present study.

Time-frequency analysis

Attention (non-delayed) condition

As represented in Fig. 2a, we mainly found both groups showed increased theta power ($p < .05$, FDR) after the stimulus presentation. However, we observed a decrease in beta power ($p < .05$, FDR) for athletes and a decrease in alpha power ($p < .05$, FDR) for controls. The group effect with independent *t*-test revealed that athletes showed relatively lower beta power than controls ($-.49 \pm .85$ dB vs. $.30 \pm .76$ dB) [$t(23) = -2.44$, $p = .23$], whereas such an effect was not found for either theta ($2.20 \pm .87$ dB vs. 1.80 ± 1.52 dB) [$t(23) = .81$, $p = .428$] or alpha power ($-.15 \pm .98$ dB vs. $-.45 \pm 1.39$ dB) [$t(23) = .62$, $p = .544$] (Fig. 2a, left panel).

Table 1
Demographics of participants in each group.

Group	Athletes ($n = 12$)	Controls ($n = 13$)
Age (year)	20.58 (2.75)	19.08 (2.10)
Height (m)	1.62 (.03)	1.61 (.04)
Weight (kg)	55.17 (6.22)	54.69 (10.37)
BMI (kg/m^2)	20.99 (2.33)	20.98 (3.37)
Kilocalorie expenditure (Kcal/d)	2547.17 (272.69)	1798.58 (356.83)
Training experience (year)	6.58 (2.07)	–

Note: The number in parenthesis is standard deviation.

Table 2
Behavioral performance results for badminton players and non-athletic controls.

Conditions		Athletes ($n = 12$)	Controls ($n = 13$)
Non-delayed	Accuracy (%)	92.88 (3.66)	92.28 (5.76)
	Response times (ms)	496.95 (52.91)	577.25 (85.66)
Delayed	Accuracy (%)	89.86 (6.08)	88.45 (4.84)
	Response times (ms)	766.87 (47.17)	810.64 (58.23)

Note: The number in parenthesis is standard deviation.

Working memory (delayed) condition

As Fig. 2b shows in the memory retrieval stage, both groups showed decreased alpha activity at a time approximating to the response execution ($p < .05$, FDR), but only athletes showed increased theta ($p < .05$, FDR) and decreased beta ($p < .05$, FDR) activity relative to baseline in this stage. The group effect with an independent *t*-test showed that athletes had relatively stronger theta power (1.62 ± 1.27 dB vs. $-.30 \pm 2.12$ dB) [$t(23) = 2.72$, $p = .12$] and lower beta power (-1.45 ± 1.02 dB vs. $-.42 \pm 1.32$ dB) [$t(23) = -2.17$, $p = .40$] than controls in this stage. However, no such effect was found for alpha power (-1.24 ± 1.81 dB vs. -1.22 ± 1.67 dB) [$t(23) = -.32$, $p = .974$].

In the encoding stage (Fig. 2c), only athletes exhibited increased theta power with regard to baseline in the memory encoding stage ($p < .05$, FDR), whereas the controls did not. The group effect revealed that athletes had significantly higher theta power than controls (2.01 ± 1.07 dB vs. $-.30 \pm 1.26$ dB) [$t(23) = 3.55$, $p = .002$].

Correlation between behavioral and EEG data

Pearson correlation analysis was performed to see whether the EEG oscillatory activities were correlated with task performance (accuracy-adjusted RT: mean RT/accuracy). As illustrated in Fig. 3a, in the attention condition, we found a positive correlation between beta band power (15–22 Hz) and accuracy-adjusted RT ($p < .01$, uncorrected) appropriately at a time window ranging from 200 to 400 ms post stimulus onset. In the working memory condition, we found that theta power (7 Hz) was negatively correlated with accuracy-adjusted RT ($p < .01$, uncorrected) during both encoding (about 200 ms–400 ms post stimulus onset; Fig. 3b) and retrieval stages (about 500 ms–600 ms post stimulus onset; Fig. 3c).

Discussion

The purpose of the present study was to investigate the modulatory effect of sport experience on fundamental cognitive function that taps visuo-spatial processing. To address this issue, we adopted a modified cognitive task which required no sport-related knowledge (Muller & Knight, 2002) to assess the differences in visuo-spatial attention and working memory between athletes trained under intense visuo-spatial loading (i.e., badminton players) and sedentary controls. In addition, to explore the neural mechanisms underlying athlete-control differences, EEG time-frequency analysis was performed.

Our primary findings showed that athletes responded faster relative to controls in both visuo-spatial attention and working memory conditions despite no accuracy difference being seen. The

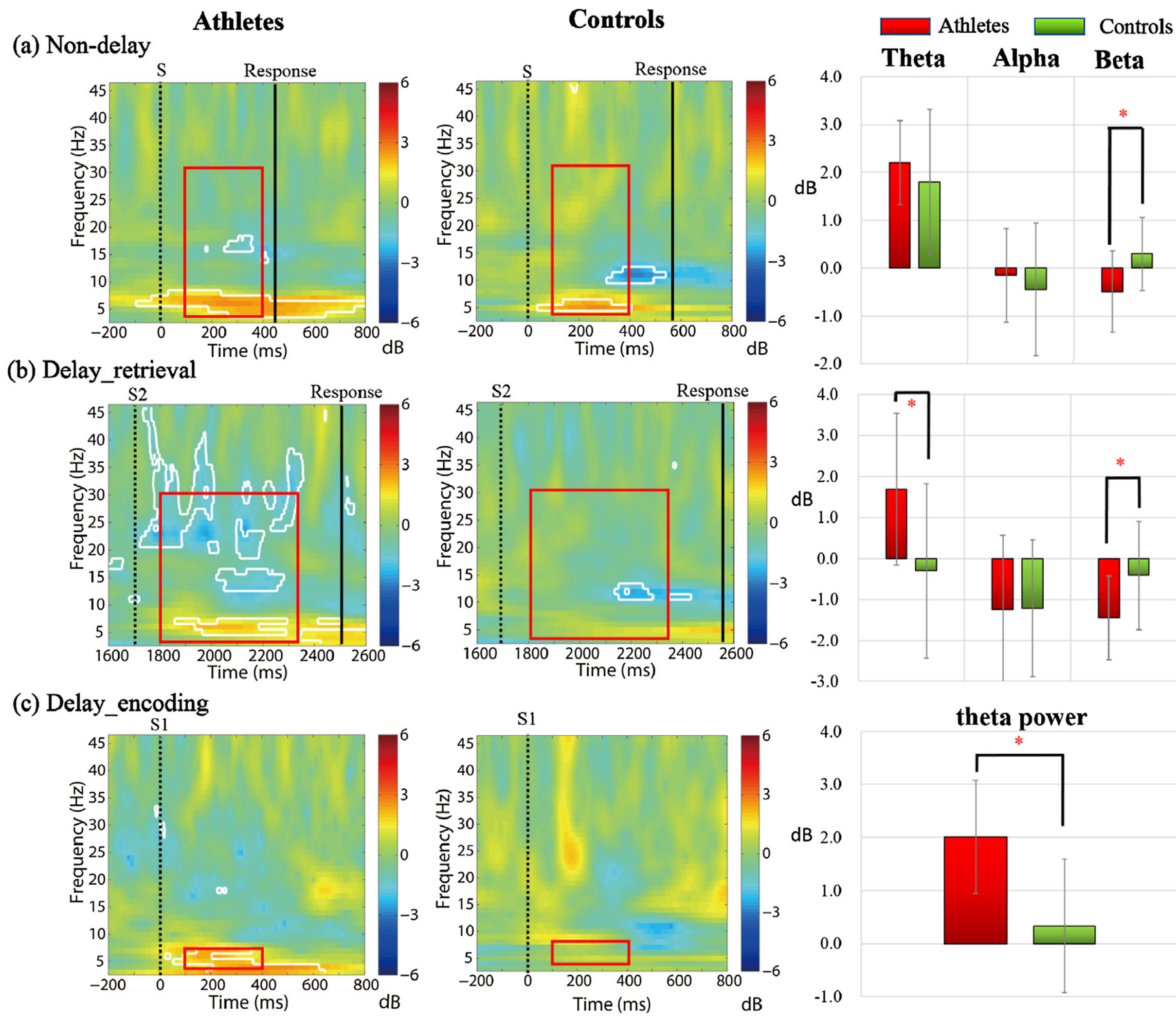

Fig. 2. Time-frequency representation of event-related spectral perturbation power (dB) from fronto-parietal network (Fz, FCz, Cz, CPz, Pz) in (a) Non-delay and (b) retrieval stage and (c) encoding stage in the Delay condition. The white-lined enclosed areas denote the significant power changes relative to baseline in athletes (dB, $p < .05$, FDR) (left panel) and in controls (dB, $p < .05$, FDR) (middle panel). Red-lined boxes in the left and middle panels indicate the region of interest for averaged band power (theta, alpha, and beta) tested in the statistical analysis in the right panels. The black dotted line denotes the stimulus onset for each condition (S indicates the stimulus in non-delay condition; S1 indicates the encoding S1 whereas S2 indicates retrieval S2 in the delay condition). The color of the graph specifies the direction of power intensity in the left and middle panels. The red asterisks denote $p < .05$ in the right panels. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

time-frequency characteristics demonstrated that, relative to controls, (1) in the attention condition, athletes presented lower beta power; (2) in the working memory condition, athletes showed higher power in theta but lower power in beta. Critically, we also observed that task performance was positively associated with beta power in the attention condition, while being inversely correlated with theta power in the working memory condition. To this end, the results in the current study may be indicative of an athlete-and-control difference in modulation on fundamental cognitive functioning.

Behavioral results

In terms of behavioral performance, although no accuracy difference being seen, athletes responded faster relative to controls in both visuo-spatial attention and working memory conditions. These results demonstrate that athletes were able to maintain superior celerity for both types of visuo-spatial cognitive processing without incurring any increase in error responses. This is probably due to the fact that sport training has the capacity to produce a general enhancement of processing speed (Chaddock et al., 2011; Voss et al., 2010), and we further extended this argument allied to visuo-spatial cognition. A similar finding is changes in inhibitory control seen for fencing and is consistent with this argument. Di Russo, Taddei, Apnile, and Spinelli (2006), using a go/no-go task without a sport-related context, observed that fencers had shorter go/no-go discriminative reaction times compared to non-athletic controls. The authors interpreted this as a training-induced facilitation in inhibitory control because the attention switch from unwanted planned actions to new appropriate actions is of importance in fencing. In fact, for successful performance, badminton players must process a large amount of visuo-spatial information within a constrained time window to make response selection and execute actions appropriately and quickly, which may result in superior deployment of visuo-spatial attention to critical sport-specific information (Jin et al., 2011, 2010; Wright et al., 2011). Similar to this, even without a sport-specific context, our results showed superior cognitive processing related to visuo-spatial representation in athletes, suggesting the enhanced cognitive skills acquired via sport training might transfer to a fundamental task,

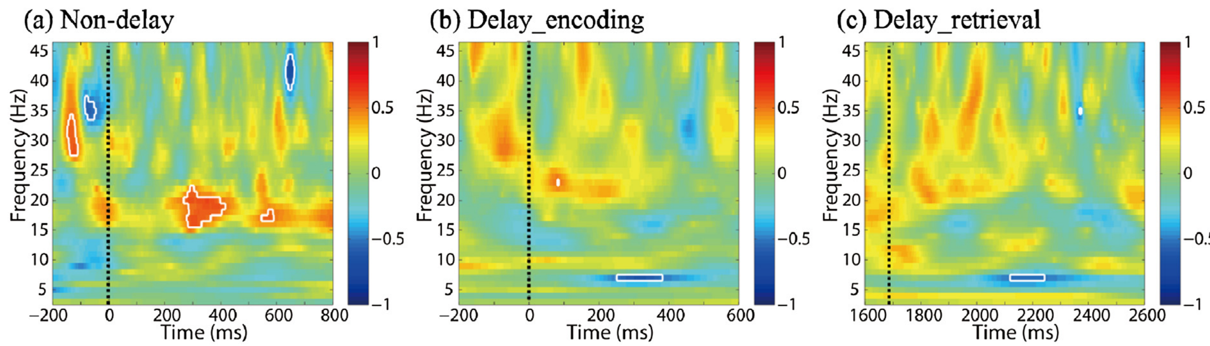

Fig. 3. Behavior-power correlation in cluster (Fz, FCz, Cz, CPz, Pz) of interest in the attention (non-delay) and working memory (encoding and retrieval in delay conditions) conditions across participants: (a) the enclosed area shows the correlation between beta power and accuracy-adjusted reaction time in attention condition (*t*-values, $p < .01$, uncorrected), (b) the enclosed area shows the association between theta power and accuracy-adjusted reaction time during encoding stage in working memory conditions (*t*-values, $p < .01$, uncorrected), (c) the enclosed areas shows the association between theta power and accuracy-adjusted reaction time during retrieval stage in working memory conditions (*t*-values, $p < .01$, uncorrected). The color of the graph specifies the direction of r-square. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

further supporting the claim proposed by the meta-analysis study (Voss et al., 2010) or the virtual task study (Chaddock et al., 2011). Importantly, the absence of a correlation of the physical activity levels with task performance across participants suggests that this effect may be the nature of the sport practice (i.e., badminton training) rather than general exercise (i.e., physical activity levels) that is important for the visuo-spatial task.

One thing should be considered with caution is that data collected here could be argued to be consistent with athletic superiority affecting processing speed (Chaddock et al., 2011; Voss et al., 2010) rather than a specific visuo-spatial effect. However, the psychophysiological measures suggested that athletes did in fact employ different neural processes. Additionally, previously one study has suggested enhanced effects of exercise training on visuo-spatial processing (Tsai, 2009). This study demonstrated that children with DCD developed more efficiency in inhibition of invalid spatial information after a 10-week table tennis training program.

Time-frequency EEG results

In the attention condition, both of the groups showed an event-related increased theta power following the presentation of the stimulus, which may be due to the processing of visuo-spatial information (Capotosto et al., 2009). However, group comparison revealed no differences in the strength of theta power, suggesting that the athletic superiority in attention performance may not be attributed to the ability to process visuo-spatial information. In addition, although only the controls showed a significant decrease in alpha power relative to baseline, we did not observe group difference in alpha power. Given that alpha suppression reflects active information processing (Klimesch, Sauseng, & Hanslmayr, 2007) and is associated with cognitive loads (Klimesch, 1999), the levels of task difficulty may be comparable for both groups, which is supported by their accuracy performance. Surprisingly, we found that athletes presented relatively lower beta power than controls after target presentation, and additionally, the lower beta power were associated with faster accuracy-adjusted processing speed. This finding may lend support to the studies reporting that higher beta-band desynchronization prior to responses relates to fast response speeds (Senkowski et al., 2006; Tzagarakis et al., 2010), demonstrating the relationship between lower beta power and higher motor preparation that results in faster processing speed. This is also in agreement with an animal model proposing that this type of behavior and cortical activity relationship may reflect top-down modulation in visuo-motor processing (Zhang, Wang, Bressler, Chen, & Ding, 2008). Therefore, the present evidence may imply that better motor-related (i.e., motor preparation; Wang, Chang, Liang, Shih, et al., 2013) rather than attentional processing in athletes contributes to more rapid reaction to visuo-spatial stimuli than controls in a simple visuo-spatial attention condition.

On the other hand, athletes showed significantly higher theta but lower beta power than controls in the working memory condition. This may imply that athletes increased their attention to encode new visuo-spatial information and enhanced preparation in speed-related motor responses, whereas these processes may be weaker in controls. This findings is in accordance with the study (Hung, Spalding, Santa Maria, & Hatfield, 2004), using event-related potential (ERP) approaches, showing that racket players (i.e., table tennis) outperformed nonathletic controls on a visuo-spatial attention task along with greater visual attention and motor preparation, as evidenced by their larger amplitude of N1 and lateralized readiness potentials (LRPs). Crucially, the behavior-EEG correlation across participants showed that oscillatory theta power during both encoding and retrieval was positively associated with task performance, that is, the higher the theta power the better the performance in working memory condition. This finding is in accordance with previous studies using a visuo-spatial task showing a positive relationship between theta power and task performance (Rugg & Dickens, 1982) or intelligent scores (Capotosto et al., 2009). Thus, although higher motor preparation can be seen in athletes, as revealed by lower levels of beta power, greater visuo-spatial encoding and retrieval during working memory processing may mostly account for the athlete-control differences in the working memory condition. In sum, these data suggest that participation in sport training may be related to superior visuo-spatial and motor-related processing, which can be observed in both behavior and cortical activities.

However, the present findings appear to contradict the neural efficiency hypothesis that lower cortical activities in the athletes than non-athletes can be seen during cognitive processing (Del Percio et al., 2009; Nakata et al., 2010; Yarrow et al., 2009). For example, Del Percio et al. (2009) observed that athletes exhibited global reduction of cortical activation, reflected by lower alpha and beta event-related desynchronization (ERD), when performing sport-specific visuo-motor skills (e.g., pistol shot) relative to non-athletic controls, indicating higher brain efficiency or economy in athletes. One possibility for these opposite findings may be the differences in the nature of cognitive tasks between the current and prior studies (e.g., fundamental tasks vs. sport-specific cognitive tasks). Previously it has been shown that athletic expertise can influence the neural processing of sport-relevant information. One recent study by Woods, Hernandez, Wagner, and Beilock (2014) reported that expert athletes showed increased activity at the areas of inferior frontal gyrus (IFG) and parietal operculum when passively listening to the sounds of their own sports. These findings may imply that, relative to novices, experts selectively process the sporting domain-specific information that links to a particular motor program in a more efficient manner. In other words, sporting experience would enable athletes to trigger the sporting knowledge required to perform a challenge at a lower cost (Zoudji et al., 2010). Specifically, Di Russo et al. (2005) found that the amplitudes of motor-related cortical potentials (MRCPs) were smaller in the trained hand rather than in the untrained hand, suggesting the effect of neural efficiency may rely on specific training experience (Del Percio et al., 2008; Nakata et al., 2010). Along with this logic, the domain-general or fundamental task employed in our study might preclude the athletes from gaining such cognitive or motor benefits of sport experience, thus demonstrating higher cortical activities in athletes during cognitive processing. Indeed, our data is in agreement with that of Hung et al. (2004). They utilized a fundamental cued RT task and found the amplitudes of contingent negative variation (CNV), a biomarker of motor preparation, were larger in table tennis players than in the non-athletic controls, indicating that the players may prepare their motor responses by employing a compensatory strategy. In line with this, stronger N2 amplitudes were observed in fencers relative to non-athletes in a fundamental go/no-go task (Di Russo et al., 2006). As such, converging evidence may suggest the athletic superiority in terms of neural efficiency might not be observed in untrained tasks or tasks without sport-related knowledge because there no sporting clues in the fundamental tasks for the athletes to use for enhancement of response efficiency (e.g., to activate the programmed responses associated with sport experience). Nevertheless, future studies may need to systematically address this speculative possibility.

In addition, despite the fact that we found athletes had better fundamental cognition at both behavioral and brain levels, it is important to note that there is a possibility that individuals who have better visuo-spatial cognitive function may be more likely to pursue or be successful in sports where this is presumably of benefit, such as badminton training. While we consider this to be unlikely and the difference seen to be a consequence of sport training, a cross-sectional study design prevents any conclusion of a causal effect of sport experience on the task performance. It is thus beneficial for future investigations using longitudinal designs to clarify this issue.

While the present findings shed light on the possible mechanisms of sport training on fundamental cognitive function in terms of visuo-spatial processing, there are some limitations to the interpretations that necessitate caution. For example, as a result of the gender effect on visuo-spatial processing (Hugdahl et al., 2006; Vecchi & Girelli, 1998) or sport-induced cognitive changes (Voss et al., 2010), the present findings may differ from studies comparing the athlete-control differences in male participants. Thus, it would be of interest to test the interaction between sports training and gender effects on visuo-spatial processing. Moreover, although the utility of self-reported physical activity on this type of study have been shown (Wang, Chang, Liang, Chiu, et al., 2013; Wang, Chang, Liang, Shih, et al., 2013), future studies may use more objective measures such as aerobic fitness which is likely to be more reliable than self-report estimations (Barnes, Yaffe, Satariano, & Tager, 2003). For example, the positive effect of aerobic fitness on visuo-spatial cognition (e.g., Stroth, Hille, Spitzer, & Reinhardt, 2009) may cause the differences between athletes and non-athletes. Although we observed no correlation between levels of physical activity and task performance, to further address this, recruiting aerobic-matched controls or additional athletic controls would be beneficial for future investigations. This may help better test the effects of exercise in general.

Conclusions

The present study, by using behavioral and time-frequency approaches, showed that individuals who partake in long-term participation in sport training for a sport with high visuo-spatial demands (e.g., badminton players) might show better visuo-spatial processing in a young female population. In particular, the present data extends the understanding of athletic superiority in fundamental cognitive functions by revealing its associated neural oscillations. We observed that badminton players outperformed nonathletic control on visuo-spatial cognitive tasks with the data consistent with faster processing speed in athletes. The possible neural mechanisms underlying this effect may be due to better preparation of their speeded reactions to visuo-spatial attention and greater attention to encoding and retrieval processing during visuo-spatial working memory. Although our data is inconsistent with the neural efficiency hypothesis in athletes (Del Percio et al., 2009), we believe that one possible source of this discrepancy relates to differences in the nature of tasks between our and previous investigations. In summary, cognitive functions may relate to sports participation, and this would be useful for those who have cognitive difficulties such as aging population or individuals with attention deficit hyperactivity disorder.

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