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Motor expertise modulates neural oscillations and temporal dynamics of cognitive control

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ABSTRACT

The field of motor expertise in athletes has recently been receiving increasing levels of investigation. However, there has been less investigation of how dynamic changes in behavior and in neural activity as a result of sporting participation might result in superiority for athletes in domain-general cognition. We used a flanker task to investigate conflict-related behavioral measures, such as mean reaction time (RT) and RT variability, in conjunction with electroencephalographic (EEG) measures, including N2d, theta activity power, and inter-trial phase coherence (ITPC). These measures were compared for 18 badminton players, an interceptive sport requiring the performance of skills in a fast-changing and unpredictable environment, and 18 athletic controls (14 track-and-field athletes and 4 dragon boat athletes), with high fitness levels but no requirement for skills such as responses to their opponents. Results showed that badminton players made faster and less variable responses on the flanker task than athletic controls, regardless of stimulus congruency levels. For EEG measures, both badminton players and athletic controls showed comparable modulations of conflicting on midfrontal N2 and theta power. However, such an effect on ITPC values was found only for the badminton players. The behavior-EEG correlation seen suggests that smaller changes in RT variability induced by conflicting process in badminton players may be attributable to greater stability in the neural processes in these individuals. Because these findings were independent from aerobic fitness levels, it seems such differences are likely due to training-induced adaptations, consistent with the idea of specific transfer from cognitive components involved in sport training to domain-general cognition.

1. Introduction

Elite performance in sports has long fascinated experts and neophytes alike. This phenomenon has contributed to the growing interest in athletic superiority in perceptual-cognitive skills (Abernethy, 1994; Jin et al., 2011; Mann et al., 2007; Zoudji et al., 2010), in line with the idea that repeated sport practice is associated with better performance on sport-specific tasks (Starkes and Ericsson, 2003).

While a number of studies have investigated whether skills and abilities developed through sport training can be transferred to domain-general cognitive tasks, evidence that this is the case remains mixed. A number of studies have found that athletes outperform non-athlete/novice controls on a variety of domain-general cognitive measures. These include processing speed, selective attention, working memory, and cognitive control (Hung et al., 2004; Moreau, 2013; Verburgh et al., 2014; Voss et al., 2010; Wang et al., 2015c), and raise the possibility of experience-induced neural changes in support of expert behavior (Moreau and Conway, 2013; Voss et al., 2010). Specifically, Vestberg et al. (2012) found that executive functions were superior for higher level soccer players, and also that these differences could predict later athletic performance, supporting the relationship between expertise in sports and enhanced cognitive abilities (Voss et al., 2010). By contrast, a few studies have failed to demonstrate any benefits on domain-general cognition as a consequence of sporting expertise (e.g., Chang et al., 2015; Memmert et al., 2009). In these studies, the authors argued that expertise resulting from sporting performance does not transfer to tasks outside of training.

There are at least two possible explanations for this inconsistency in the literature. First, fitness levels were not well-controlled in previous

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studies (Voss et al., 2010). Most previous studies have typically employed a non-athletic control group (e.g., Alves et al., 2013; Di Russo et al., 2006; Hung et al., 2004; Wang et al., 2015c), which does not rule out enhanced aerobic fitness as a confounding variable in any analysis (Chan et al., 2011). This possibility is supported by Wang et al. (2013b), who found that tennis players outperform sedentary controls in a go/no-go task under high temporal uncertainty, but that this effect was not significant when the tennis players were compared to fitness-matched athletic controls (swimmers in this case), consistent with both fitness and skill-related modulation of performance. Second, mean-level performance alone might not be a sensitive indicator of any sports/exercise effects on domain-general cognition. It is suggested that cognitive performance should not only be evaluated in terms of mean-level performance but that short-term fluctuations in task performance (i.e., intra-individual variability in reaction times, RT variability) should also be considered (MacDonald et al., 2006). Such RT variability has been considered a functional index of the central nervous system (MacDonald et al., 2009; Stuss et al., 2003) that is independent of mean RT (Stuss et al., 2003; Wu et al., 2011). In addition, mean-level performance measures may lead to flawed estimates of the differences between groups as variability increases (MacDonald et al., 2006, 2009). For example, Wu et al. (2011) found that RT variability was significantly lower for a high-fitness group even though the mean RT of task performance (a flanker task in this case) was comparable between high-fitness and low-fitness children. Similarly, in a go/no-go task Di Russo et al. (2010) found differences between two different types of disabled athletes, swimmers and wheelchair basketball players, only in RT variability and not in mean RTs.

To further investigate the effects of sporting expertise on more domain-general cognition we recruited players of an interceptive sport (badminton players), who are required to perform in a fast-changing and unpredictable environment, and athletic controls (track-and-field athletes and dragon boat athletes) trained in a physically demanding but relatively stable environment. Badminton players were selected because previous findings suggest that players involved in interceptive sports have better cognitive control and flexibility in performing tasks, presumably as a consequence of the cognitively demanding elements of their sport and training (Hung et al., 2004; Jin et al., 2011; Overney et al., 2008; Wang et al., 2013a). Importantly, these cognitively demanding factors may also induce training-related structural and functional changes in the brain (Di et al., 2012). Track-and-field and dragon boat athletes were chosen to make up the control group because these are physically demanding sports requiring high aerobic capacity, but are performed in a self-paced manner in relatively predictable environments (Chang et al., 2015; Singh et al., 1995). Behavioral performance in these two groups was measured using a flanker task which has varying levels of cognitive demand (Eriksen and Eriksen, 1974). We hypothesized that, if the superior cognitive performance associated with sports expertise is indeed independent from indices of aerobic fitness, badminton players would show faster and less variable responses on this task when compared to the athletic controls.

In addition to measurement of behavioral performance, we used electroencephalography (EEG) and event-related potentials (ERP) to further examine the effect of sports expertise on temporal dynamics of neural processing during cognitive control. Although a number of studies have investigated ERP components when exploring neural mechanisms underlying the superior behavioral performance seen in athletes (Di Russo et al., 2006; Nakamoto and Mori, 2008; Yamashiro et al., 2015), considerable potentially cognitive-related information that may be contained in the EEG, such as frequency dynamics, is lost as a consequence of the time-domain averaging that this analysis requires. It remains to be determined whether this leads to dismissal of important information (Makeig et al., 2004). Thus, the time-domain averaging approach is limited in terms of elucidation of the complex neural dynamics that may be associated with cognitive superiority in athletes. We therefore conducted a time-frequency analysis of EEG, which allows the investigation of event-related changes in the magnitude (power) and temporal synchronicity (phase) of EEG oscillations at specific frequencies that relate to events of interest (Makeig et al., 2004). Specifically, EEG power reflects the magnitude of the oscillations and is independent from EEG phase (i.e., inter-trial phase coherence, ITPC) that reflects the temporal coordination of cortical processes (Roach and Mathalon, 2008).

We focused on analysis of neural activity associated with cognitive control while performing the flanker task. In terms of ERP analysis, a negative-going deflection, the N2, has been demonstrated to vary as a function of the level of cognitive demand in a flanker task (Hsieh and Lin, 2014; Tillman and Wiens, 2011), and is thought to reflect conflict or attentional control processing during stimulus detection and response execution (Bartholow et al., 2005; Tillman and Wiens, 2011). For frequency and power/phase components, previously a greater theta (4–7 Hz) power and ITPC have been commonly found in cognitively demanding trials of a task, such as incongruent target-noise arrays (Cavanagh et al., 2009; Cohen et al., 2008; Zavala et al., 2013, 2015), indicating that theta oscillation is reliable maker of cognitive control (Nigbur et al., 2011, 2012). As such, these electrophysiological indexes may provide more refined indices of cognitive expertise in athletes. If motor expertise modulates the neural dynamics associated with general cognition, we hypothesized that individual differences in expert behavior would be associated with modulations of the neural activity reflecting cognitive control and would be elevated by difficult trials; namely, group differences in modulating conflict-related N2, theta power, and theta ITPC would be expected.

The present study was therefore designed to help clarify whether expert behavior associated with sports expertise seen in prior research employing central tendency parameters (i.e., mean response latencies or time-averaging analysis of EEG) can also be characterized by trial-to-trial variability of behavioral and neural dynamics. Such investigation has the potential to shed new light into the modulation of inter-trial phase synchrony during higher control processes as a plausible mechanism contributing to changes in response variability, and lay the foundation for future investigations on exploring experience/training-related neuroplastic changes.

2. Methods

2.1. Participants

A total of 36 male university undergraduate and graduate students participated in the study. Of these, 18 students were active players on the collegiate badminton team, an open-skill sport (age 20.56 ± 1.82 years, with professional training experience of 6 years or more), while the remaining 18 students were athletes matched for health, age, gender, and fitness, from other close-skill university sport teams (14 track-and-field athletes and 4 dragon boat athletes; age 20.98 ± 3.37 years, with professional training experience at least 7 years) (Table 1). None of the athletic control group had any professional badminton training experience, nor any significant training in other open-skill sports. In addition, all the athletes were ranked as Division II in the National Intercollegiate Athletic Games at the time of the study. All the participants had normal or corrected-to-normal vision and were right-handed (Chapman and Chapman, 1987). No individuals reported having a history of neurological problems or cardiovascular diseases, nor were any taking medications known to affect cognitive function. In addition, none of the participants showed any symptoms of depression, as measured by the

Table 1
Demographics of participants in each group (standard deviation in parentheses).

Group	Badminton players ($n = 18$)	Athletic controls ($n = 18$)
Age (year)	20.77 (1.90)	20.61 (1.38)
BMI (kg/m2)	21.75 (0.99)	21.29 (1.81)
BDI	3.17 (3.09)	2.89 (2.25)
PACER test (laps)	86.89 (10.61)	88.94 (14.12)

Beck Depression Inventory II (BDI-II, all scored below 13) (Beck et al., 1996). Informed consent was obtained prior to the study, which was approved by the Human Research Ethics Committee of National Cheng Kung University.

2.2. Measures

2.2.1. Aerobic fitness assessment

In order to control for the potential influence of aerobic fitness on cognitive performance (Chan et al., 2011; Wang et al., 2013a), we evaluated participants' aerobic capacity using the Multistage 20-Meter Shuttle Run test, the Progressive Aerobic Cardiovascular Endurance Run (PACER), which has high validity and reliability in field examination of aerobic fitness for healthy young adults and athletes (Hillman et al., 2005; Leger et al., 1988; Welk et al., 2002). According to FITNESSGRAM recommendations, all the participants practiced two trials on the PACER in order to ensure that they were suitably familiarized with performing the test. All of the participants completed the PACER test during their regularly scheduled training programs under the supervision of university coaches, with the test administered by our research assistants.

2.2.2. Behavioral paradigm

Cognitive testing was conducted on a different day from the PACER test to avoid potential acute exercise effects (Tsai et al., 2014). In addition, all of the participants were tested prior to their regular training or on days without training to prevent potential fatigue effects induced by athletic training on task performance (Alves et al., 2013).

An arrow version of the flanker task was employed (see Fig. 1), in which participants were required to respond to a centrally presented target arrow while ignoring flanking arrows, providing measures typically considered indicative of selective attention and cognitive control (Alves et al., 2013). The paradigm was programmed using E-prime 2.0 (Psychology Software Tools, Inc, Sharpsburg, PA). On each trial, a white fixation cross (0.5° × 0.5°) appeared in the center of the screen for 300 ms. The central target arrow with flanking arrows was subsequently displayed. The target arrow pointed either in the same direction as (congruent trial; <<<<< or >>>>>) or in the opposite direction (incongruent trial; <<><< or >><>>) to the flanking arrows. The two trial types were equally distributed within each block so that there were 50% each of congruent and incongruent trials (Alves et al., 2013). Additionally, for 50% of trials the target arrow pointed to the left and for 50% it pointed to the right, evenly divided for the congruent and incongruent trials. Arrows were presented on the screen until either the participant made a response indicating the direction the target pointed or until 2 s had elapsed. Each trial was followed by a blank screen of a duration ranging from 1 000 to 1500 ms. Participants had to focus on the target arrow in the middle of an array and respond as quickly and accurately as possible to its direction by pressing the "N" (left-pointing arrow) or the "M" (right-pointing arrow) button of the keyboard by using the index and middle fingers of their right hand. All arrow strings were presented in white against a black background on a 21-inch cathode-ray tube display.

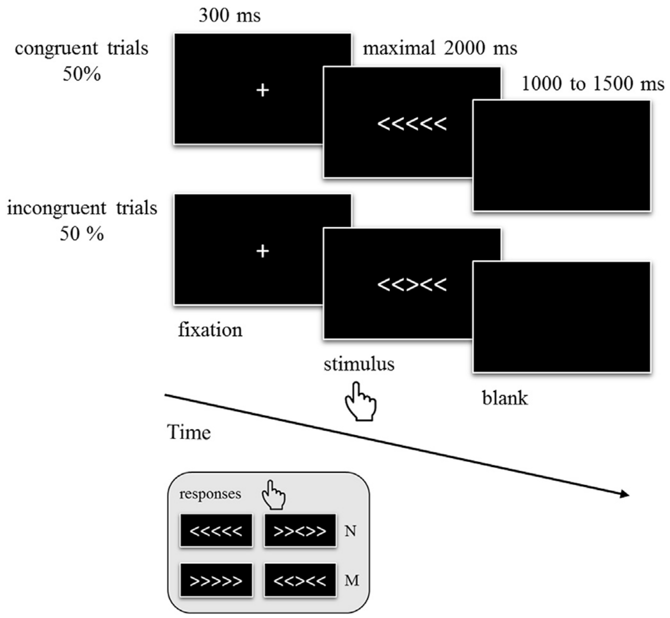

Fig. 1. Eriksen flanker task. Following a 300 ms fixation cross (+), either congruent or incongruent stimuli were displayed focally for a maximal 2000 ms response window. A random blank of 1 000–1500 ms occurred following the participant's response. Participants were instructed to focus on the central arrow and make a response as quickly and accurately as possible to its direction by pressing the "N" (left-pointing arrow) or the "M" (right-pointing arrow) button of the keyboard.

All the participants performed the flanker task with concomitant electrophysiological recording (see below). After a practice block of 10 trials to ensure that the participants had understood the task requirements, the formal trials were administered to allow collection of task RTs and accuracy along with EEG data. Participants completed 2 blocks of the task, each consisting of 120 trials, yielding 120 congruent trials and 120 incongruent trials in total.

2.3. EEG recording

The electroencephalographic recording procedure was performed in a manner similar to the previous studies (Wang et al., 2014, 2015c). EEG activity was recorded using a Nu-Amps EEG amplifier and the Scan 4.3 package (Neuroscan Inc., El Paso, TX, USA) with 32 electrodes mounted in an elastic cap (Quik-Cap; Compumedics, Neuroscan Inc.) designed for the International 10–20 System. The left and right mastoids were used as online references and a ground electrode was placed on the mid-forehead on the Quik-Cap. In addition, two sets of bipolar electrodes were placed on the upper and lower sides of the left eye, and on the canthi of both eyes in order to monitor vertical (VEOG) and horizontal (HEOG) 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 hard disk for subsequent offline analysis (Wang et al., 2015b).

2.4. Data reduction and statistical analyses

2.4.1. Behavioral data

E-prime 2.0 was used to record behavioral performance in terms of RTs (in milliseconds) and accuracy. RTs were excluded from analysis if there were from: (1) non-response trials, (2) error trials, and (3) 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 et al., 2013).

A 2 (groups: badminton players, athletic controls) × 2 (congruency: congruent, incongruent) mixed ANOVA with Bonferroni adjustment for multiple comparisons was conducted to analyze the RTs and RT variability for correct responses with the significance level set at $p \leq .05$. All analyses were carried out using SPSS 18.0.

2.4.2. Event-related potentials data processing

Offline ocular-corrected EEG was first segmented into epochs ranging from −200 ms to 800 ms relative to target onset. The EEG data were then filtered with a digital band-pass of 0.1 and 30 Hz (12 dB/octave) with FIR filter. The FIR filter was adopted because it can achieve linear phase response (Kiebel et al., 2005). The 200 ms pre-target period was used for baseline correction. Data with behavioral errors or artifacts with amplitudes ±100 μV in the HEOG channel and the other channels were discarded. The rest of the resulting artifact-free data was then averaged according to each trial type. We used the difference waveforms (Gajewski and Falkenstein, 2013), calculated by subtracting the individual ERP average from incongruent-stimulus trials from those from congruent-stimulus trials, to assess the effects of flanker type on ERP components. On the basis of previous research (Tillman and Wiens, 2011), we examined the N2-component from electrodes adjacent to frontal and central scalp areas (i.e., Fz, FCz, Cz). Visual inspection of the average ERP waveforms indicated that the flanker N2 (i.e., N2d) was most evident for the time window between 300 and 400 ms following stimulus onset. The mean amplitude and peak latency for these electrodes within this time window were used for the analysis of the N2d component.

The amplitudes as well as latencies of N2d were analyzed using a 3 × 2 mixed ANOVA, with *electrode* (Fz, FCz, CPz) as the within-subjects factor, and *group* (badminton players and athletic controls) as the between-subject factor. When the assumption of sphericity was violated, the significance levels of the *F* ratios were adjusted using the Greenhouse-Geisser correction. The significance level was set at $p \leq .05$. Partial η^2 ($\eta^2{}_p$), 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 to 0.139 a medium effect, and more than 0.14 a large effect (Cohen, 1973). All analyses were completed using SPSS 18.0.

2.4.3. *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 (Hsu et al., 2014; Wang et al., 2015b). Only data collected from correct trials was analyzed. Prior to the time-frequency analysis, we identified large artifacts in the continuous EEG data and set the maximum level for eye-blinks. A correction for eye-blinks was applied to the EEG data, with eye-blink peaks being derived from VEOG by means of regression and correlation (Wang et al., 2017) and these data used to perform eye movement correction for all electrodes. Continuous EEG data were locked to the target onset and were segmented into epochs from −1 500 to 1500 ms relative to this time point. Trials containing artifacts with amplitudes exceeding ±150 μV were discarded. Oscillatory power amplitude and inter-trial phase coherence 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 and Mathalon, 2008). Oscillatory power (the magnitude of the analyzed signal), 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 values from −500 to −300 ms relative to stimulus onset (Nigbur et al., 2012), and taking the log10 transform of this quotient (dB) (dB power = 10 × 10 [power/baseline]), allowed a direct comparison of results of interest across frequencies. ITPC, which is independent of power amplitude changes, measures the temporal consistency of the phase value for a given frequency band at each time point across trials. Phase coherence 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 and Makeig, 2004). A few studies using the flanker paradigm have found that theta power and theta ITPC activities were most evident at midfrontal areas during stimulus conflict (Cavanagh et al., 2009; Padrão et al., 2015; Zavala et al., 2013). Thus, the electrodes around midfrontal region (FZ/FCz/Cz) were clustered here for time-frequency analysis. The log-transformed changes in signal power relative to the baseline, as well as the ITPC values for each time-point and frequency were used as the measures of interest for statistical analysis. To test the *trial type* effect (congruent, incongruent; paired *t*-tests) and *group* effect (badminton players, athletic controls; independent *t*-tests), a $q < .05$ with a false discovery rate (FDR) correction (Benjamini and Yekutieli, 2001) for multiple comparisons was employed.

2.4.4. *Behavior-EEG correlations*

Correlations between behavioral and EEG data were examined to gain insight into the relationship between EEG modulations and conflict-related performance. This has the potential to provide details about the mechanisms that may underlie any differences in conflict processing between the two groups. Therefore, we evaluated the effect of congruency on measured variables by subtracting all dependent variables of the incongruent trials from those of the congruent trials for both behavioral and EEG data. Behavioral data were therefore mean $\mathrm{RT}_{incongruent-congruent}$, and RT $\mathrm{variability}_{incongruent-congruent}$. ERP data consisted of the mean amplitudes of the N2d components acquired from difference waveforms across the electrodes of interest (Fz, FCz, Cz) for incongruent and congruent trials. For time-frequency EEG data, we extracted and averaged the theta power or theta ITPC within the time-frequency matrix that showed a significant flanker effect ($p < .05$) after the paired *t*-tests with FDR correction (see Fig. 5). The results revealed that the flanker effect on theta power was most evident across the theta bands ranging from 4 to 7 Hz within the time window between 300 and 500 ms. Thus, we extracted and averaged the theta power values within this metric for further analysis. On the other hand, evident flanker effect on theta ITPC was observed in the frequency bands across 4–5 Hz within the time window between 200 and 400 ms. Theta ITPC values included within this metric were thus extracted and averaged for further analysis. These variables were used to examine the behavior-EEG correlations using the Pearson product-moment correlation with a significance level set at $p \leq .05$.

3. Results

3.1. *Participant demographics*

Participant demographic data and their levels of physical activity are shown in Table 1. Demographic variables including age, $t(34) = .30$, $p = .765$, BDI, $t(34) = .31$, $p = .760$, PACER test, $t(34) = -.49$, $p = .625$, and body mass index (BMI), $t(34) = 0.93$, $p = 0.357$, did not differ between the badminton players and athletic controls.

3.2. *Behavioral performance*

3.2.1. *Accuracy*

Groups did not differ in terms of accuracy rates when performing the task. Badminton players performed with 97 ± 3% accuracy; athletic controls performed with 98 ± 2% accuracy [$t(34) = -1.49$, $p = 0.146$].

3.2.2. *Mean reaction times*

Fig. 2a illustrates the mean RTs for correct trials across groups and trial types. A significant main effect was observed for trial type [$F(1,34) = 383.26$, $p < .001$, $\eta_p^2 = 0.92$] with shorter RTs for congruent trials compared to incongruent trials, suggesting effective modulation of performance by flanker type. There was also a main effect of group [$F(1,34) = 5.76$, $p = 0.022$, $\eta_p^2 = 0.15$], with the RTs of badminton players lower than those of athletic controls. Additionally, the trial type by group interaction was significant [$F(1,34) = 4.92$, $p = .033$, $\eta_p^2 = 0.13$]. Post-hoc tests revealed that this interaction was explained by marginally significant group effect for congruent trials [$t(34) = -1.96$, $p = 0.058$], compared with a significant effect of group in the incongruent trials [$t(34) = -2.57$, $p = 0.015$].

3.2.3. *Trial-to-trial RT variability*

As illustrated in Fig. 2b, participants had significantly lower RT variability for congruent trials compared to incongruent ones [$F(1,34) = 65.02$, $p < .001$, $\eta_p^2 = 0.66$]. The main effect for group was also significant [$F(1,34) = 6.12$, $p = 0.019$, $\eta_p^2 = 0.15$], with RT variability for badminton players significantly lower than for athletic controls. The trial type by group interaction was not significant [$F(1,34) = 1.66$, $p = .206$, $\eta_p^2 = 0.05$].

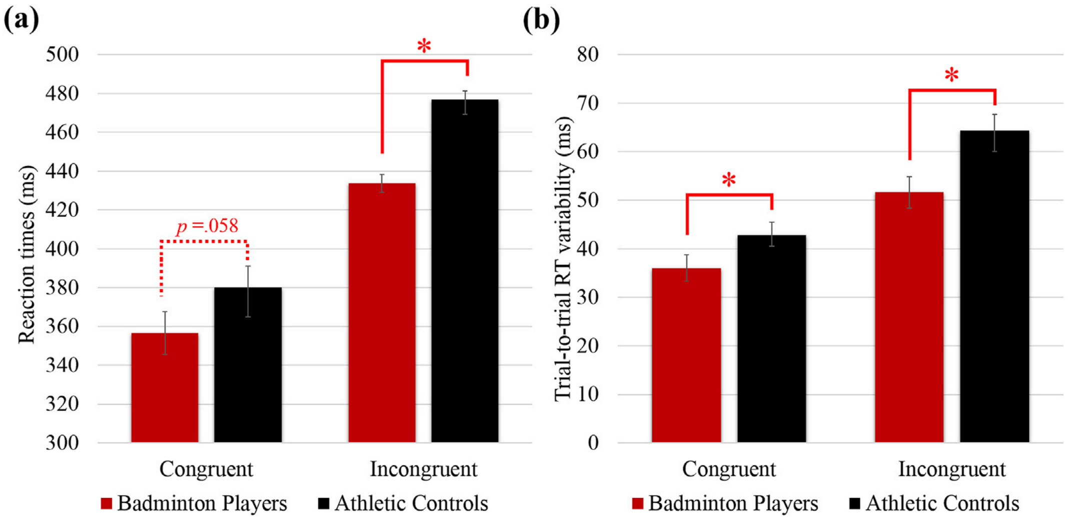

Fig. 2. Behavioral performance (mean ± SE) including (a) mean reaction times (RTs) and (b) trial-to-trial RT variability for the players and controls across congruent and incongruent trials. (a) There was a significant difference in mean RTs between badminton players and athletic controls in the incongruent trials, whereas only a marginal effect was found in the congruent trials. (b) The trial-to-trial RT variability was smaller in badminton players relative to the non-athletic controls in both congruent and incongruent trials. * denotes $p < 05$.

3.3. N2d ERP component

3.3.1. N2d amplitude

N2d is illustrated in Fig. 3. There was a main effect of *electrode* [$F(1,34) = 13.83$, $p < .001$, $\eta_p^2 = 0.29$], with the N2d amplitude significantly smaller at Fz (−1.89 ± 0.41 μV) than at both FCz (−2.56 ± 0.49 μV) ($p = 0.003$) and Cz (−2.89 ± 0.50 μV) ($p < .001$), while no differences were observed between FCz and Cz ($p = 0.123$). The main effect of *group* [$F(1,34) = 0.03$, $p = 0.876$, $\eta_p^2 = 0.00$] (badminton players: −2.37 ± 0.64 μV vs athletic controls: −2.52 ± 0.64 μV) and the interaction between *electrode* and *group* [$F(1,34) = 0.47$, $p = 0.626$, $\eta_p^2 = 0.01$] were not significant.

3.3.2. N2d latency

We did not observe significant main effects of *group* [$F(1,34) = 0.67$, $p = 0.419$, $\eta_p^2 = 0.02$] (badminton players: 337.37 ± 29.83 ms vs athletic controls: 346.98 ± 39.95 ms), *electrode* [$F(1,34) = 0.50$, $p = 0.607$, $\eta_p^2 = 0.02$] (Fz: 340.42 ± 26.19 ms vs FCz: 343.42 ± 27.15 ms vs Cz: 342.69 ± 24.82 ms), and the interaction between *electrode* and *group* [$F(1,34) = 0.30$, $p = 0.74$, $\eta_p^2 = 0.01$] (see Fig. 3).

3.4. EEG time-frequency analysis

3.4.1. Theta power oscillations over the midfrontal area

We investigated changes in spectral EEG power and found that both trial types exhibited similar decreases in alpha (9–13 Hz) and beta (15–30 Hz) oscillatory power after stimulus onset (Fig. 4a and c). In addition, theta power activity showed a significantly greater amplitude in the incongruent trials relative to congruent trials following target onset ($q < .05$ FDR corrected), exhibiting conflict-related processing. These observed effects were similar for both groups and we did not observe any group differences in the event-related power changes across all time points and frequencies (all $qs < .05$ FDR corrected).

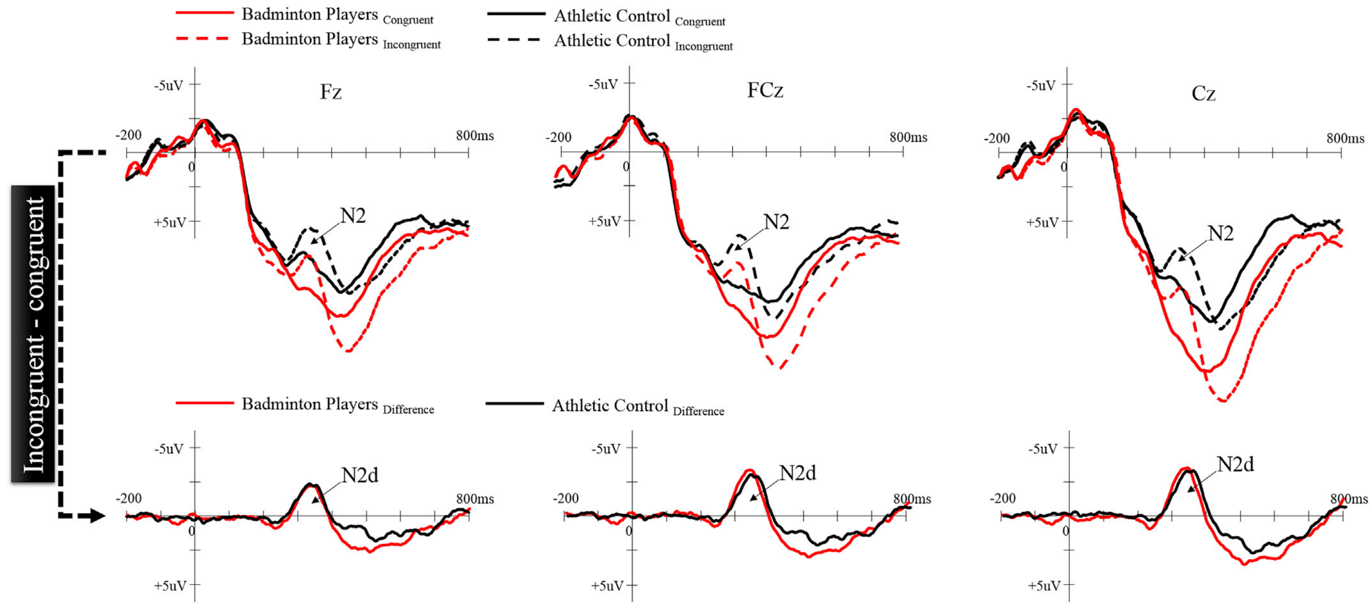

Fig. 3. Grand average ERP waveforms for congruent and incongruent trials (upper panel), and difference waveforms (lower panel) for badminton players and athletic controls at Fz, FCz, and Cz electrodes. No group-level difference was found for the peak latency or mean amplitude of N2d.

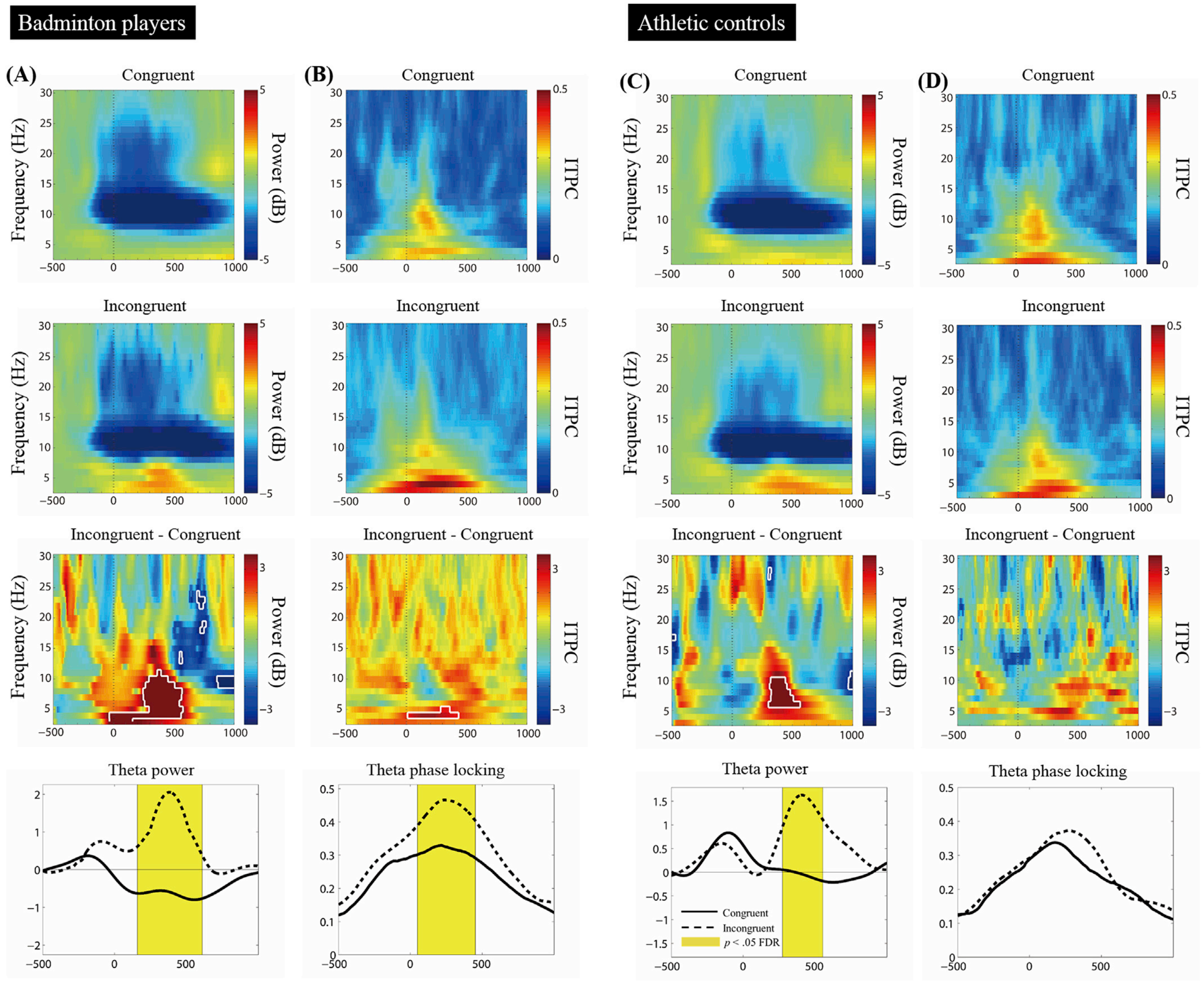

Fig. 4. Time-frequency decomposition with Morlet wavelets in the midfrontal regions (Fz, FCz, Cz). (A) Cue-locked rescaled oscillatory power averaged across midfrontal regions ($n = 18$, stimulus presented at $t = 0$) in badminton players. (B) Cue-locked ITPC averaged across midfrontal regions ($n = 18$, stimulus presented at $t = 0$) in badminton players. (C) Cue-locked rescaled oscillatory power averaged across midfrontal regions ($n = 18$, stimulus presented at $t = 0$) in athletic controls. (D) Cue-locked ITPC averaged across midfrontal regions ($n = 18$, stimulus presented at $t = 0$) in athletic controls. Congruent trials are shown on the top, incongruent trials are shown in the middle, and the average differences between the two (masked at $p < .05$ FDR correction) are shown on the bottom, with the yellow shadows representing temporal clusters that reach significance level when comparing incongruent and congruent trials ($p < .05$ FDR correction). Averaged power over 4–7 Hz was significantly higher during incongruent trials relative to congruent trials in both groups. Averaged ITPC over 4–5 Hz was significantly greater during incongruent trials relative to congruent trials in the badminton players ($p < .05$ FDR correction), whereas such effect did not reach significance level in the athletic controls.

3.4.2. *Theta phase coherence over the midfrontal area*

When analyzing EEG ITPC (Fig. 4b and d), we found that badminton players showed greater theta phase consistency for incongruent trials compared to that seen for congruent trials after target onset (0–500 ms, 4 Hz; 300–400 ms, 5 Hz) ($q < .05$, FDR). However, such an effect was not seen for the athletic controls (all $qs > .05$, FDR corrected).

3.5. *Behavior-EEG correlations*

3.5.1. *Mean RTs*

The correlation analysis revealed that flanker effect on mean RTs were not correlated with any of conflict-related EEG measurements (see Fig. 5a) (all $ps > .05$).

3.5.2. *Trial-to-trial RT variability*

The flanker effect on RT variability was positively correlated with conflict-related ITPC in the theta band (Fig. 5b, $r = -.36$, $p = 0.032$). However, no such significant correlations were found for other variables (i.e., N2d and theta power).

4. Discussion

The aim of the present study was to elucidate the characteristics of changes in cognitive task performance as a result of sporting participation by exploring the temporal dynamics of both behavior and in neural activity during cognitive control in athletes. Our behavioral results revealed that badminton players showed faster mean RTs and lower RT variability than athletic controls. This suggests that practicing an interceptive sport (i.e., badminton) induces alterations in cognition that lead to improved performance in a cognitive control task. Importantly, the fact that this difference is seen between two groups with high and matched levels of fitness is consistent with the effect being independent of the enhanced fitness levels associated with sports training, a potential confound that has often not been adequately controlled in previous

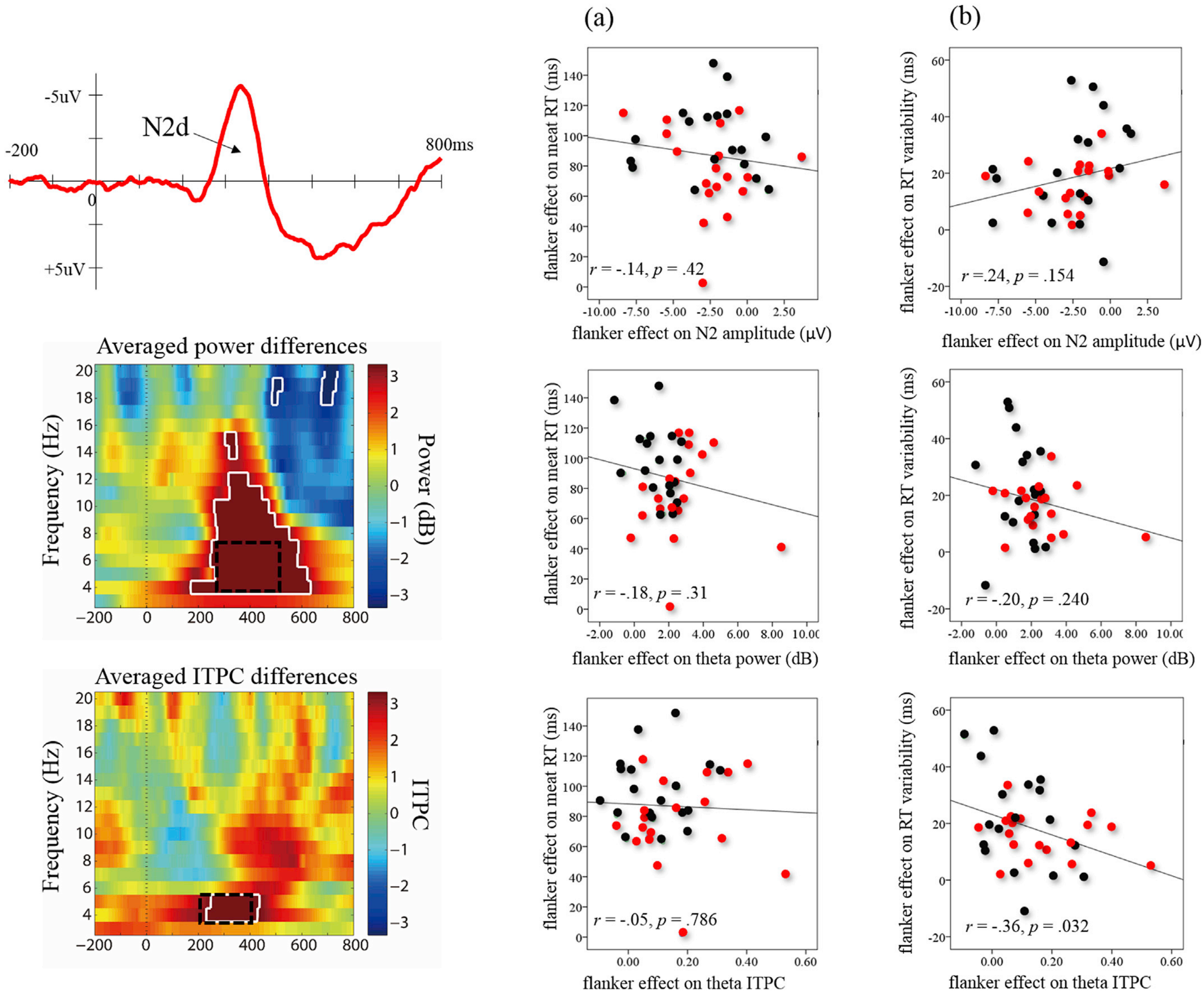

Fig. 5. The behavior-EEG correlations in terms of (a) mean RTs and (b) RT variability. The left panel shows the flanker effect on N2 component (N2d), theta power and theta ITPC across midfrontal areas (Fz, FCz, Cz). The area enclosed by white line in the time-frequency representation denotes the area that reached statistical significance ($p < .05$, FDR correction), suggesting the significant flanker interference effect. The flanker effect on theta power (4–7 Hz, 300–500 ms) and theta ITPC (4–5 Hz, 200–400 ms) enclosed by black dashed line were averaged for further correlation analysis. The results revealed that only the Flanker effect on RT variability significantly correlated with conflicted-related change in theta ITPC ($r = -.36$, $p = 0.032$). Other conflicted-related behavior-EEG correlations did not reach significance level. Note: The red dots represent the badminton players, while the the black dots represent the athletic controls.

studies. Neural data showed significant conflict-related theta ITPC modulation for badminton players but not for athletic controls, despite the absence of group difference in conflict-related N2 and oscillatory theta power. Moreover, such modulation of theta ITPC was significantly correlated with the flanker effect on RT variability while the mean-level difference could not account for this effect, suggesting that smaller conflict-related increased response variability in badminton players may be mostly attributable to greater modulation in theta phase consistency. The present study is the first to convincingly document the neural variability associated with enhanced performance in motor experts, while controlling for extraneous factors.

Taken together, these findings are consistent with the idea that training in a sport which requires the use of complex cognitive skills can improve neurocognitive functions (Nakata et al., 2010), as evidenced by the temporal dynamics of behavioral and neural measures. This study thus supports the idea that laboratory tests of cognition can shed light on the cognitive and neural correlates of motor training (Voss et al., 2010), and our findings further extend this view in several ways detailed hereafter.

4.1. *Motor expertise rather than aerobic fitness affects mean task performance*

Previous studies have reported that athletes showed better cognitive abilities on a range of task relative to non-athletes, yet these have failed to control for the influence of physical fitness (Alves et al., 2013; Chaddock et al., 2011; Di Russo et al., 2006; Hung et al., 2004). This leaves the possibility that increased fitness levels in athletes can explain any differences in cognitive performance seen, given the close relationship between aerobic fitness and domain-general cognition (Colcombe et al., 2004; Hillman et al., 2008; Tsai et al., 2014; Wang et al., 2015a), rather than being a result in the skill-training aspect of the sport under investigation. Thus, this study used groups matched for (or at least, not significantly differing in) physical fitness levels to minimize potential confounding factors associated with the benefits of exercise (Moreau et al., 2012).

Results demonstrated that badminton players responded faster than athletic controls, with a larger effect for high-conflict trials. Because such a group effect was observed in the absence of any effects on accuracy, this RT difference likely be attributed to specific sport expertise, rather than to a speed-accuracy trade-off. This finding is in line with research showing that baseball players outperformed athletes practicing track-and-field or swimming in a go/no-go task (Yamashiro et al., 2015). Moreover, a related go/no-go study also reported that high-fitness fencers made less commission errors than did fitness-matched non-fencers (Chan et al., 2011). Taken together, our results suggest that interceptive sports may elicit cognitive improvements in conflict-related processing, and, importantly, that this advantage may be found irrespective of aerobic fitness indices.

As mentioned previously, the investigation of expert behavior via a comparison of athletes across various sport types has shown inconsistent findings, with some studies observing better performance in cognitively or motorically complex sports (Moreau et al., 2012; Overney et al., 2008; Yamashiro et al., 2013) while some did not (Chang et al., 2015; Memmert et al., 2009). In light of the present findings, we believe two related points might help to interpret this seemingly contradictory evidence.

First, different open-skill sport types (e.g. interceptive, strategic sports) may result in different cognitive benefits, both in terms of range and extent. A meta-analysis by Voss et al. (2010) revealed that athletes in interceptive sports (e.g., racket sports, fencing, or baseball) showed larger expertise effects on cognitive performance than those in more strategy-related sports (e.g., volleyball, basketball, or soccer) in a variety of attention or speeded tasks. This could explain why, relative to close-skill athletes, open-skill athletes involved in certain sports, such as tennis or baseball, displayed better performance in some studies (Overney et al., 2008; Yamashiro et al., 2013), while open-skill athletes such as handball players did not (Memmert et al., 2009). Within our own work, this argument may also explain discrepancies between this study, involving interceptive sport players, and a previous one with strategy sport players (i.e., volleyball) (Alves et al., 2013), despite similar methodological paradigms.

Second, the specific experimental tasks are almost certainly important when investigating a motor expert's advantage. For example, motorically complex sports (e.g., wrestling or Wushu), which involve complex mental representation, may mostly benefit spatial ability (e.g., mental rotation) (Moreau et al., 2012, 2015; Schmidt et al., 2016) rather than other non-spatial abilities (e.g., neuropsychological assessments) (Chang et al., 2015). In addition, racket sports such as tennis, where players need to react under strong time constraints, have been associated with superiority in certain time-related visual perceptual tasks (e.g., speed discrimination) but not tasks which seem unrelated to the demands of tennis (e.g., pattern detection task) (Overney et al., 2008). According to this idea, it is plausible that the higher cognitive control of badminton players observed in our study is due to the inherent importance of misdirection in badminton (e.g., feints) (Fuchs et al., 2014), a feature that may extensively involve selective attention and conflicting resolution mechanisms. Nevertheless, future research should aim to determine the specific connections between skill-specific training and changes in domain-general cognition.

4.2. Motor-induced cognitive features can be reflected in trial-to-trial RT variability

Novel to the current study was the assessment of response variability, which allows probing of the underlying components of cognitive performance independent of central tendency parameters such as mean RTs (MacDonald et al., 2006; Wu et al., 2011) and prevents erroneous inference that can arise when solely considering mean-level performance (MacDonald et al., 2009).

Replicating the findings of previous research (West et al., 2002; Wu et al., 2011), both groups tested in the current study exhibited increased RT variability in the task condition requiring a greater amount of cognitive control compared to the less cognitively demanding condition. Importantly, we found significantly lower RT variability in badminton players compared with athletic controls regardless of levels of response conflict. This is consistent with previous research by Di Russo et al. (2010) showing the benefits of wheelchair basketball, an open-skill sport, on response variability. Di Russo et al. (2010) found that players demonstrated lower response variability than did disabled swimmers in both simple RT and choice RT tasks. The authors suggested that participating in sports involving complex cognitive skills might partially compensate for inconsistency in repeated assessment of visuo-motor responses. Following this rationale, the present data suggests that engaging in a sport involving high cognitive demands may result in more response consistency. This is interesting because within-individual performance variability has been linked to information processing efficiency related to top-down regulation of attention control (Nakata et al., 2012; West et al., 2002). Specifically, it has been suggested that increased variability during an inhibition task allows maintaining task performance, and thus reflects greater demand for cognitive control (Bellgrove et al., 2004). Accordingly, our data suggests that long-term participation in interceptive sports could have beneficial effects on individuals by efficiently regulating attentional control during conflict-related processing, as evidenced by greater processing consistency.

Despite these promising findings, future studies are necessary to determine whether different open-skill sports (e.g., interceptive vs. strategy) could elicit benefits of different extent on response variability, even in the absence of mean difference. Given that the two measures are sometimes independent of each other (MacDonald et al., 2006; Wu et al., 2011), it is also informative to use both measures to further characterize motor experts.

4.3. Conflict-related N2 component may not reflect cognitive features in athletes

N2 is known to be an electrophysiological index of cognitive control associated with conflict monitoring or attentional control processes in flanker tasks (Bartholow et al., 2005; Hsieh and Lin, 2014; Tillman and Wiens, 2011). In line with previous research (Folstein and Van Petten, 2008; Tillman and Wiens, 2011), we observed an evident fronto-central N2 amplitude (N2d, Fig. 3) by using a subtraction method (i.e., incongruent minus congruent) (Gajewski and Falkenstein, 2013), indicative of higher activity of the cognitive control system during high-conflict trials. However, such conflict-related N2 in terms of amplitude and latency did not differ between groups. Moreover, correlation analyses revealed that neither the flanker effect on mean RT nor on RT variability related to the N2 effect. This is consistent with another go/no-go study in which no difference in the no-go N2 amplitude between baseball players and athletic controls (i.e., track-and-field or gymnastic athletes) was observed (Nakamoto and Mori, 2008). Additionally, Smith et al. (2006) found that faster responders did not exhibit an augmented no-go N2 compared to slower responders. Accordingly, we speculate that the modulation of N2 might reflect some other control processes required for the task rather than the same cognitive processes as behavioral performance (Folstein and Van Petten, 2008; Tillman and Wiens, 2011), thus failing to detect group differences.

Notably, this finding contrasts with previous go/no-go research showing the N2 modulation of cognitive-motor expertise in athletes. For example, Di Russo et al. (2006) investigated the neural correlates related to fencers' flexible behavior and observed that the N2 was stronger and shorter in fencers than in non-athletes. A more recent go/no-go study revealed a stronger and faster no-go N2 in baseball players relative to athletic controls (i.e., track-and field athletes) who presumably received much less sensorimotor skill training (Yamashiro et al., 2015). Although it is difficult to interpret these discrepancies across studies, it is possible that differences in the specific tasks used could explain these disparate findings. Despite the anterior N2 seeming to be generally sensitive to cognitive control (Folstein and Van Petten, 2008), this component might reflect different mechanisms across different cognitive tasks. For example, the N2 in go/no-go task is driven by inhibition of an intended response (Di Russo et al., 2006; Folstein and Van Petten, 2008), whereas the N2 in flanker tasks is induced by conflict or higher attentional control processes (Bartholow et al., 2005; Hsieh and Lin, 2014; Tillman and Wiens, 2011). Thus, it seems that the generalization of cognitive-motor expertise effects on the N2 component might greatly depend on the cognitive processes being examined and should be interpreted cautiously. Future studies are encourage to address this issue by examining sport expertise in a variety of tasks involving cognitive control.

4.4. Neural oscillations in theta power and inter-trial phase coherence during conflict

Another novel contribution of this study is the use of time-frequency analysis of EEG, which allows investigation of brain dynamics during cognitive processing that cannot be observed in time-averaging approaches such as ERPs (Cohen, 2011). Thus, certain effects of interest may not be seen in the previous N2 research given that recent studies using single trial analysis have revealed that this may not reflect the same neurocognitive processes as non-phase-locked neural activity like theta power (Cohen and Donner, 2013).

Consistent with previous studies (Nigbur et al., 2012; Zavala et al., 2015), we found that both groups showed greater theta oscillatory power for incongruent trials compared to congruent trials. An increase in theta power has been linked to cognitive control demands in conflict situations (Cavanagh et al., 2009; Nigbur et al., 2012) and such enhancement of theta activity following incongruent flanker trials has been found to be evident around medial frontal regions that are important for cognitive control (Cohen and Cavanagh, 2011; Nigbur et al., 2011, 2012). Thus, our finding are consistent with the notion that midfrontal theta relates to the need for top-down control in the presence of stimulus-response conflict (Cavanagh and Frank, 2014; Cohen and Donner, 2013; Nigbur et al., 2011; Zavala et al., 2015).

However, no significant differences in theta power oscillations were seen for badminton players in comparison to athletic controls, and also the conflict-related theta differences had no observable correlation with behavioral performance. This may suggest that modulation of theta power associated with conflict-related processes may not be the leading mechanism for the superior behavior in badminton players. Although this seems inconsistent with our previous investigation that showed theta power enhancement during visuo-spatial processing was higher for badminton players relative to sedentary controls (Wang et al., 2015c), this could mean that the changes seen in this previous study were a consequence of effects of aerobic fitness on oscillatory theta power (Wang et al., 2015a), an effect that would be present in both groups in the current study. Consequently, expert-novice differences in cognitively modulated theta power might be attenuated when controlling for aerobic fitness. A more definitive answer to this would need systematic assessment of different levels of expertise and aerobic fitness.

In addition to theta power, we also analyzed time-varying changes in the theta phase angle (i.e., theta ITPC). Previous studies have suggested that conflict processing may preferentially modulate theta power amplitude rather than theta phase consistency (Cavanagh et al., 2009), indicating that the theta ITPC might not essentially reflect transfer of conflict-related information (Cavanagh and Frank, 2014; Cohen and Donner, 2013). Rather, it has recently been proposed that the theta phase-locked dynamics around midfrontal areas may be a neurophysiologic correlate underlying the integration of choice-relevant information during goal-directed behavior, such as when subjects need to select one response over another (Cavanagh and Frank, 2014; Womelsdorf et al., 2010). This type of response selection processing is particularly relevant in incongruent trials, in which the flanking stimulus points in the opposite direction from the central target. Our results indicate that theta ITPC was greater for incongruent trials than for congruent trails selectively for the badminton players. Such an effect, however, was not significant for the athletic controls. Interestingly, we found that the greater the demand-related enhancement in theta ITPC, the smaller the differences in RT variability between conflict types. A recent lifespan study, using a go/no-go task, found that theta ITPC during highly cognitively demanding trials increased with maturation but decreased with age, and that such lifespan differences are mirrored by RT variability measures (Papenberg et al., 2013). This is presumably due to the association between response variability and information processing efficiency (Bellgrove et al., 2004). Therefore, data here might reflect more stable control processes in the midfrontal cortex during conflict-related decision-making, contributing to less variability in response latencies in badminton players. Taken together, these findings suggest that the selection underlying conflicting information sources for a response might be particularly effective for badminton players, with this shown by greater midfrontal theta reorganization and resulting in lower response variability.

Despite theta ITPC modulation seeming to be less related to RT results, our understanding of the differences in cognitive requirements between athletes from different sport types may motivate another possible explanation for the findings reported here. Zavala et al. (2013), recording subthalamic nucleus local field potential during the flanker task, found that the stimulus-locked theta ITPC was significantly lower for slow-incongruent trials than for fast-incongruent trials. They speculated that when subject's attention failed to ignore the flanking stimulus, competing neural activity associated with task-irrelevant information might serve to diminish theta phase reorganization, thus slowing responses. Applying such a rationale to the current study, this may explain why only badminton players showed significant conflict-related modulation of theta ITPC along with relatively faster responses during incongruent trials. This group may be better able to efficiently attend to the central target while inhibiting response activations from the flanking stimulus. In contrast, the athletic controls may fail (relatively) to effectively ignore the flanking stimulus, which would then lead to attenuation of theta ITPC and thus delay responses. This argument is supported by the behavioral observation that the group difference was significant for the incongruent trials while being only marginal for the congruent trials, suggesting that badminton players experienced less interference from flanking stimuli. Indeed, athletes trained in a sport requiring distinguishable level of cognitive skills have shown better selective attention or cognitive control relative to those trained in a more stable situation (Wang et al., 2013a; Yamashiro et al., 2015). Moreover, a recent study reveals that the cognitive components in sports training can be reflected in spontaneous brain oscillations (Di et al., 2012; Ermutlu et al., 2015). Hence, the differences in behavior and neural oscillations during conflict observed in badminton players may be related to their ability to effectively focus on task-relevant information and to flexibly regulate selective attention. Longitudinal designs or training studies may be required, however, to further investigate any such causal relationship between sports training and neurocognitive modulation.

4.5. Limitations of the present study

There are potential limitations to the present study that might influence interpretation of our findings. First, because all participants were male athletes, our findings may not be generalizable to female athletes. Future studies designed to test the effects of expertise on temporal dynamics of cognitive control will ideally also need to cautiously examine the impact of gender-sport interactions (Voss et al., 2010). Second, this study only employed one type of open-skill sport, badminton, and thus it is possible that the current findings may be limited to this particular interceptive sport, or at least to sports with shared features. To better understand the nature of motor expertise in sports, future investigations should systematically address this issue by employing diverse sports types (e.g., interceptive sports, strategy sports, motorically complex sports, static sports). Third, a note of caution is needed regarding the sample size of the present study, since a small sample size would presumably reduce the likelihood of detecting a true effect. For example, and despite the relatively large partial eta-squared reported for the behavioral findings (Cohen, 1973; Pallant, 2007) at both between-group and within-group levels, the group differences in modulating conflict-related N2 and theta power were not observed. To provide more definitive answers, replications employing a larger sample size are thus warranted. Fourth, it would be worth examining whether the sports expertise effect on inter-trial phase coherence is preferentially at theta band or, alternatively, is task-dependent. Thereby, the current work needs to be extended to other cognitive domains, such as working memory or visuospatial attention, which typically induce changes in other frequency bands such as alpha rhythm (Sauseng et al., 2005; Wang et al., 2017; Zanto et al., 2011). Doing so would expand the generalizability of the reported expertise effect to different domain of cognitive tasks. Finally, the present study does not allow the claim that any difference observed is a definite consequence of the different natures of sporting expertise in the groups investigated, as a cross-sectional design was employed (for example, it could be that the differences are a reflection of personality differences between individuals who play badminton to a high standard versus those who prefer track-and-field or dragon boat racing). Therefore, the notion that badminton training elicited cognitive and neural changes is an extrapolation of our findings and can only be confirmed with direct experimental manipulation by means of a training study with random assignment of participants to different groups. Despite these limitations, we believe this study adds valuable findings to the currently available literature on motor expertise.

5. Conclusions

This study investigated the behavioral and neural basis of cognitive expertise in athletes. Results reveal that, compared to athletic controls, badminton players exhibit faster and more stable responses in a cognitive control task. Because these findings were independent from aerobic fitness levels, it is argued that such differences are likely due to training-induced adaptations, consistent with the idea of specific transfer from cognitive components involved in sport training to domain-general cognition (Alves et al., 2013; Moreau et al., 2012; Voss et al., 2010). Although no expertise-related effect was present in either the N2 or theta power oscillations, a significant demand-induced difference in midfrontal theta ITPC for badminton players was seen, with this oscillatory activity related to the flanker effect on RT variability. This suggests that temporal synchrony of theta phase during action selection facilitates integration of neural processing to support efficient goal-directed behavior in badminton players. By exploring expertise-related differences in modulating midfrontal theta ITPC during conflict processing, these findings offer an interesting window for future studies to improve our understanding of neuroplasticity in response to training experience.

Given the utility of temporal dynamics of cognitive and brain processes in the investigation of motor expertise in athletes, further research would be desirable to investigate the relationship between sport training and cognitive enhancement using brain dynamics. For example, is there a dose-response relationship between sport practice and neurocognitive variability? Knowing whether the dynamics of brain function and behavior in athletes varies as a function of expertise level would provide crucial information for those interested in talent identification in sport. In addition, given the well-documented benefits of physical exercise on brain function, how do combinations of physical and cognitive demands alter temporal dynamics of brain function and cognition more generally? Answering these questions seems likely to advance our understanding of the interactions between sport and physical activity and neural systems, and potentially allowing use of specific sports as a potential intervention in individuals with difficulties in specific cognitive processes.

Conflicts of interest

No.

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