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Differential Modulation of Brain Signal Variability During Cognitive Control in Athletes with Different Domains of Expertise

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Abstract—Motor expertise has recently been associated with differences in domain-general cognition. Studies using averaged neurophysiological signals (e.g., event-related potentials) have shown varying degree of expertise-related differences in neural activity. As a result, the precise mechanisms underlying these differences remain to be described. Here we used multiscale entropy analysis (MSE) to investigate whether the complexity of underlying neural systems working in a wide-range time scales can better explain the cognitive characteristics of athletes with different domains of expertise. Behavioral and electroencephalograms (EEG) measures of athletes practicing an interceptive sport (badminton; n = 17) or a static sport (long-distance running; n = 17) were assessed during a flanker task with varying degrees of response conflict. The interceptive sport players showed superior behavioral performance overall on the task relative to the static sport players. Although both groups exhibited greater sample entropy across most time scales in high-conflict relative to low-conflict trials over the parietal site, this effect was only evident at coarser time scales over the midfrontal site for the interceptive sport players. Together, our results suggest that individual differences in motor expertise may be associated with difference in information-processing capacity and information integration during cognitive processing, as demonstrated by differential cognitive modulation of brain signal variability. © 2019 IBRO. Published by Elsevier Ltd. All rights reserved.

Key words: cognitive control, response variability, EEG dynamics, brain signal complexity, sports expertise.

INTRODUCTION

Empirical evidence suggests an association between cognition and success in real-world sports performance (Cona et al., 2015; Vestberg et al., 2012; Vestberg et al., 2017). Further, athletes have been shown to have faster processing speed and better performance on realistic street crossing multitasking than non-athletes (Chaddock et al., 2011), suggesting that superior speed processing in sports may benefit everyday fast-paced multitasking abilities. Indeed, there is ample evidence to indicate that brain and cognitive functioning can be enhanced via long-term sport training, from less complex sensory-perceptual processes to richer cognitive abilities (Nakata et al., 2010; Yarrow et al., 2009). At the cognitive

proficiency on a variety of laboratory-based cognitive measures, including cognitive control (Bianco et al., 2017; Wang et al., 2013a; Wylie et al., 2018), working memory (Moreau 2013), spatial ability (Moreau et al., 2012; Wang et al., 2015), and selective attention (Alves et al., 2013; Hung et al., 2004). Interestingly, individual differences associated with expertise in sports have also been found to modulate some of these effects (Voss et al., 2010), with evidence showing greater cognitive performance in athletes practicing open skill sports that rely on continuous adaptation to changing environments. These types of sports contrast with closed-skill sports, which tap different abilities such as sustained attention on skill execution and invariance over time, in a relatively static environment (Arvinen-Barrow et al., 2007; Jacobson and Matthaeus 2014; Nuri et al., 2013; Wang et al., 2013a). Collectively, these findings corroborate the cognitive transfer hypothesis, a model that describes how sport experience may modulate cognitive performance (Voss et al., 2010). According to this hypothesis, transfer will occur if the specific cognitive challenges of

level, sport expertise has been associated with higher

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sports and the measured cognitive tasks involve overlapping cognitive processes. For example, one major cognitive skill involved in baseball hitting practice, deciding whether or not to swing as quickly as possible, may lead to improved performance in a response inhibition task (a visual go/no-go task) (Kida et al., 2005), as the specific type of task stimuli does not fundamentally alter the underlying cognitive processes involved.

A handful of recent studies have compared electrophysiological measurements (e.g., event-related potentials, ERPs) of athletes practicing different sport types (Bianco et al., 2017; Chueh et al., 2017; Wang et al., 2017; Yamashiro et al., 2015) to characterize the emergence of cognitive transfer. However, the available evidence remains scarce and inconclusive. Within a sample of baseball players and athletic controls from closed skill sports (i.e., track-and-field and swimming), Yamashiro et al. (2015), employing a go/no-go task, investigated the presence of sport-type differences in Nogo-N2, highly relevant to inhibitory control (Folstein and Van Petten 2008). Although there was no group difference in behavioral performance, baseball players were found to exhibit faster and stronger N2 activity than athletic controls. These findings suggest that enhanced inhibitory control processes via a specific athletic training experience do not necessarily translate into behavioral benefits. In contrast with the above findings, Chuehet al. (2017) did not observe any differences in behavior and ERP components associated with visuo-spatial cognitive processing between open-skill athletes (i.e., badminton and tennis) and closed-skill athletes (i.e., track-and-field and swimming). More puzzling perhaps is the absence of neural effects, given the presence of behavioral difference, which was found in Wanget al. (2017). In this study, they measured cognitive control performance and conflict-related N2 during a flanker task in badminton players and closed skill sport athletes. Although badminton players showed superior behavioral performance relative to closed skill sport athletes, comparable conflict-related modulation of N2 was observed. That is, badminton players' advantage in cognitive control that was observed behaviorally was not reflected in the related neural response.

If individual difference in sport expertise modulates domain-general cognition (Jacobson and Matthaeus, 2014; Moreau, 2013; Voss et al., 2010; Wang et al., 2013b), why is this not reflected at the neural level? One possibility is that the unique neurocognitive functioning in athletes is not adequately captured via the sole measurement of mean neural activities (e.g., the ERPs). For example, if sport can be conceptualized as a complex, nonlinear system that operates within neural dynamics, valuable information may be ignored in a linear analysis approach which models neural activity as a static, local entity (Hutka et al., 2013). In this regard, we adopted a novel application of brain signal variability, the moment-to-moment fluctuations in neural dynamics, to address this issue. Typically, the variability in neural time-series is completely ignored or is regarded as background noise resulting from low signal-to-noise ratio in a time-averaging analysis (Garrett et al., 2013b; Hutka

et al., 2013; Hutka et al., 2016). However, it has recently been claimed that the "noise" or variability in brain activity provides meaningful information about network dynamics in the brain (Garrett et al., 2013b). That is, a more variable response may reflect a network with greater number of potential functional configurations or brain states (Deco et al., 2011). Variability in brain signals can thus serve as a proxy into the information-processing capacity of a complex system and of information integration across the network (Garrett et al., 2011; Garrett et al., 2013b; Heisz et al., 2012; Hutka et al., 2016).

Recently, brain signal variability has also proved useful in understanding complex brain systems and their association with task demands, cognitive performance and individual differences (Deco et al., 2011; Garrett et al., 2011; Garrett et al., 2013b). For example, Garrettet al. (2013a) found that variability in blood oxygen level-dependent signal increased with changing cognitive demands, in particular for the younger, faster, and more consistent performers. In relation to this finding, Takahashiet al. (2009) revealed that electroencephalographic (EEG) variability increased in response to photic stimulus in young adults but not in elderly adults, reflecting a age-related difference in functional cortical responses to visual stimulus. In addition, Lianget al. (2014), using a stop-signal task, observed that the EEG activity of successful stop trials was more variable relative to that of failed stop trials, suggesting a greater ability to adapt to environmental changes during successful stopping (i.e., an irregularly-intervening sudden "stop" signal).

There exist several families of statistics for computing temporal variability in neuroimaging signals, such as variance, standard deviation, mean square successive differences, and multiscale entropy (MSE) (Garrett et al., 2013b). Of these, MSE does not capture the overall variance but rather the point-to-point transitions in time series. MSE, in short, is a fractal scaling measure of signal complexity or temporal unpredictability of a physiological signal that calculates sample entropy across multiple time scales, ranging from fine- to coarse-grained sequences (Costa et al., 2002; Costa et al., 2005). Sample entropy was developed to quantify the regularity of time series over time via the identification of reproducible patterns (Costa et al., 2002; Courtiol et al., 2016; Richman and Moorman 2000). A higher entropy value indicates that the signal is less regular and information rich, and is commonly referred to as greater signal complexity, whereas a lower entropy value indicates that the signal is more predictable and less complex (Grundy et al., 2017; Heisz et al., 2012; Liang et al., 2014). Because MSE calculates sample entropy at multiple time scales, it is highly sensible to distinguish meaningful variability from white noise (Costa et al., 2005), and provides more comprehensive indices of brain signal variability than a single timescale (Catarino et al., 2011; Ueno et al., 2014). Specifically, sample entropy at smaller scales capture short-range temporal unpredictability, which reflects local network dynamics. In contrast, sample entropy at larger scales capture long-range temporal irregularity which represents distributed network dynamics (Grundy et al., 2017; Vakorin et al., 2011). Thus, the

assessment of temporal relationship in brain signals via MSE may provide crucial information about the relative contribution of local and global network dynamics underlying cognitive processes.

Recent investigations have demonstrated promising applications of MSE to examining cognitive transfer effects of motor training or lifetime experience (Carpentier et al., 2016; Hutka et al., 2016). One study by Grundyet al. (2017) observed greater MSE values of EEG during task-switching processes in bilinguals than in monolinguals. Because greater signal variability has been linked to the ability to alternate between functional brain states more readily (Beharelle et al., 2012; Grundy et al., 2017), these findings suggest that a second lanquage experience leads to an improved capacity to switch between multiple functional states as a result of practice switching between languages. Further, musical training was also found to increase EEG signal variability when performing untrained music and verbal tasks (Carpentier et al., 2016), suggesting training-induced increases in the diversity of brain network states supporting music skill acquisition and its generalizability to language skills. As such, MSE may have the potential to characterize the type of cognitive transfer elicited from sports training.

This study was designed to explore the potential mechanisms underlying individual differences in sport expertise, by measuring brain signal variability during a cognitive control task. The MSE analysis was applied to the continuous EEG signals recorded during a flanker task from players practicing an interceptive sport (i.e., badminton) which requires coordination between a held implement (e.g., a racket) and an object (e.g., a ball) in the environment, and a static sport (i.e., long distance running) which involves highly consistent, self-paced situations (Voss et al., 2010). The choice of athletes from the two sport types was based on the meta-analysis study showing differences in cognitive superiority in fundamental cognitive tasks (Voss et al., 2010). Further, the flanker task provides an excellent means for testing attentional control (Eriksen and Eriksen 1974) and has been shown relatively higher sensitivity than other attentional paradigms in studies examining the sport-cognition relationship (Voss et al., 2010).

For the behavioral analysis, and in addition to the mean-level dependent variable, this study measured intra-individual variability, an indicator of transient, within-person change in behavioral performance independent of mean reaction times (RTs) (Di Russo et al., 2010; MacDonald et al., 2006; Wu et al., 2011). Response variability is considered to be a valid behavioral index of cognitive control in flanker tasks (Wang et al., 2017; Wu et al., 2011) and is sometimes more sensitive individual differences than mean measures (MacDonald et al., 2006). Importantly, there is increasing evidence showing a negative association between behavioral variability and brain signal variability (Garrett et al., 2013b; McIntosh et al., 2008). Thus, we characterized the relationship between variability in brain activity and behavior, to refine our understanding of the way sport expertise is related to the difference in brain functioning. Notably, because previous work has recommended using

complementary methods when interpreting MSE results (Courtiol et al., 2016; Richman and Moorman 2000), we also analyzed simpler measures of EEG signals associated with flanker interference such as N2d, P3d components as well as midfrontal theta oscillation (Nigbur et al., 2012; Nigbur et al., 2011; Tillman and Wiens 2011).

We hypothesized that if interceptive sport and static sport experience lead to differences in information processing capacity, brain signal variability during cognitive processing measured by MSE would differ between the two groups, providing corroborating evidence to typical findings reporting averaged neural activity. Furthermore, we expected a positive association between MSE values and behavioral performance, assuming that moment-to-moment variability in neural activity is sensitive to processing capacity (McIntosh et al., 2008).

EXPERIMENTAL PROCEDURES

Participants

Seventeen athletes practicing an interceptive sport (badminton, with at least 5 years of training) and 17 athletes from a static sport (long distance running, with at least 7 years of training) participated in this study. Only male athletes were recruited to avoid obscuring the effect of interest with gender-related variability in performance (Voss et al., 2010). All athletes were ranked as Division II in the National Intercollegiate Athletic Games. In addition, all athletes self-reported being active in regular training for at least 3 training sessions per week (at least 2 hours/session for badminton and 2.5 hours/ session for track-and-field). Participants' anthropometric measures are presented in Table 1. All the participants had normal or corrected-to-normal vision and were righthanded. 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 negative emotions that could have affected cognition, as measured by the Beck Depression Inventory II (BDI-II; all scored below 13). Informed consent was obtained from all participants, and the study was approved by the

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

oort Static sport
(n = 17)
20.71 (2.32)
21.28 (1.87)
2.88 (2.32)
14.71 (1.36)
89.12 (14.54)
8.41 (1.18)
55.88 (1.36)

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

Human Research Ethics Committee at National Cheng Kung University.

Measures

Aerobic fitness assessment. In order to control for the potential influence of aerobic fitness on cognitive control and the underlying neural activities (Wang et al., 2019b), participants' aerobic fitness was evaluated using the Progressive Aerobic Cardiovascular Endurance Run (PACER) test, which has been used for examining aerobic fitness in healthy young adults and athletes (Boiarskaia et al., 2011; Wang and Tu, 2017). All participants completed the PACER test during their scheduled training time, under the supervision of university coaches, and the test was administered by the research assistants. After collecting the PACER scores (total laps), we estimated participants' VO2max values by the equation: $41.77 + (PACERlaps * 0.49) - 0.0029 * PACERlaps^2 -$ -(0.62 * BMI) + 0.35 * (age * gender), where gender = 0 for females, 1 for males (Boiarskaia et al., 2011).

Behavioral paradigm. Cognitive and EEG data were collected either prior to physical training sessions or on days during which no training occurred, in order to avoid acute effects of physical training on brain functioning (Moreau and Chou, 2019).

We used an arrow version of the flanker task programmed using E-prime 2.0 (Psychology Software Tools, Inc, Sharpsburg, PA) to measure cognitive control performance (Alves et al., 2013; Wang et al., 2017). In this task, participants were required to respond to a centrally presented target arrow while ignoring flanking arrows. Typically, subjects involuntarily process the flankers despite the fact that they are to be ignored, as evidenced by prolonged responses when processing trials involving incongruent flankers (Bunge et al., 2002; Eriksen and Eriksen 1974).

In the current version of the flanker task, all arrow strings were presented in white against a black background, on a 21-inch cathode-ray tube display. During each trial, a central fixation cross $(0.5^{\circ} \times 0.5^{\circ})$ appeared on screen for 300 ms. The central target arrow, together with all flanking arrows, appeared subsequently. The target arrow pointed either in the same direction as (congruent trial; < < < < < or >>>>>>) as the flanking arrows, or in the opposite direction (incongruent trial; < < > < or >> <> >). The two trial types were equally distributed within each block. The target arrow pointed to in a given direction for 50% of the trials, evenly divided for the congruent and incongruent trials. The arrows were presented on screen until either the participant made a response or until 2 s had elapsed. Each trial was followed by a blank screen of a duration ranging from 1000 to 1500 ms. Participants were instructed to respond by pressing "N" or "M" on the keyboard using their right index and right middle fingers, respectively.

All participants performed the flanker task with concomitant EEG recording. They all received 12 practice trials, to ensure they had understood the task before data collection started. Participants completed 2

blocks of the task, each consisting of 120 trials, for a total of 120 congruent trials and 120 incongruent trials.

EEG recording

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 on an elastic cap (Quik-Cap; Compumedics, Neuroscan Inc.), designed for the International 10-20 System. The left (A1) and right (A2) mastoids [(A1 + A2)/2] were used as the online reference, and a ground electrode was placed on the mid-forehead of the Quik-Cap. 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 $10k\Omega$. EEG data were acquired with an analogue-digital rate of 1000 Hz per channel, filtered with a Butterworth bandpass filter (0.1-70 Hz), a 60-Hz notch filter, and were written continuously to a hard disk for subsequent offline analysis.

Data reduction and statistical analyses

Behavioral data. E-prime 2.0 was used to record behavioral performance in terms of RTs (in milliseconds) and accuracy. RTs were excluded from subsequent analysis if there were (1) non-response trials, (2) error trials, or (3) trials with latencies more than three standard deviations above the mean latency value on correct trials. Variability in behavioral performance was evaluated using the intra-individual coefficient of variation (cvRT: standard deviation/mean RT within each participant). We adopted cvRT to circumvent the fact that the standard deviation often scales with the mean (McIntosh et al., 2008).

A 2 (groups: interceptive sport, static sport) \times 2 (trial type: congruent, incongruent) mixed-design ANOVA with a Bonferroni adjustment for multiple comparisons was conducted to analyze the mean RT and cvRT with the significance level set at $p \le 0.05$. All analyses were carried out using SPSS 18.0.

Event-related potentials. A correction for eye-blinks was first applied to the EEG data, with eye-blink peaks being derived from VEOG by means of regression and correlation and these data used to perform eye movement correction for all electrodes. The ocularcorrected EEG was first segmented into epochs ranging from -100 ms to 800 ms relative to the stimulus onset. The EEG data were then filtered with a digital bandpass of 0.1 and 30 Hz (12 dB/octave) with a FIR filter. The 100 ms pre-target period was used for baseline correction. Data with behavioral errors or artifacts with amplitudes $\pm 100 \,\mu\text{V}$ were discarded. The rest of the resulting artifact-free data was then averaged according to each trial type. This study used the difference waveforms (Gajewski and Falkenstein, 2013), calculated by subtracting the individual ERP average from incongruent-stimulus trials from those from congruentstimulus trials, to assess the effects of flanker on ERP components. Here we examined the N2 and P3 difference

wave forms from electrodes adjacent to midline frontal site (i.e., FCz). Visual inspection of the average ERP waveforms (Fig. 2) indicated that the N2d was most evident in the time window between 300 and 400 ms, while the P3d was most evident in the time window between 450 and 650 ms following stimulus onset. The mean amplitude within these time windows were thus extracted for the analysis of the N2d and P3d. The group difference in the two ERP components were examined using an independent *t*-test in SPSS 18.0.

EEG data preprocessing. The same correction procedure for eye-blinks was also applied to the EEG data which was segmented into epochs ranging from -1500 to 1500 ms relative to the stimulus onset. Trials containing artifacts with amplitudes exceeding $\pm\,150~\mu V$ were discarded (Liang et al., 2014; Wang et al., 2019c). These artifact-free EEG data were used for the subsequent analysis of EEG power and MSE values.

EEG power analysis. The analysis of EEG power was performed using SPM8 for MEG/EEG (Wellcome Department of Cognitive Neurology, London, UK; www.fil.ion.ucl.ac.uk/spm/) and custom (MathWorks) scripts (Hsu et al., 2014). Oscillatory power amplitude was 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. On the basis of previous studies showing evident event-related changes in theta oscillations at midfrontal area when perform a flanker task (Cavanagh et al., 2009; Padrão et al., 2015; Zavala et al., 2013), we thus focus on theta power activity at FCz for the subsequent analysis. A mixed-design ANOVA was conducted to test if the power changed as a function of trial type (congruent, incongruent) or group (interceptive sport, static sport). Values for all time-points, frequencies, and conditions were used in the ANOVA analyses. The significance threshold for all tests was set at q < 0.05 with a false discovery rate (FDR) correction (Benjamini and Yekutieli 2001).

Multiscale entropy analysis. Brain signal variability in different time scales was estimated using multiscale entropy analysis (Costa et al., 2005). EEG data was analyzed using SPM8 and custom MATLAB (Math Works) scripts (Liang et al., 2014; Wang et al., 2014). The algorithm for the MSE analysis is available at http://www.psynetresearch.org/tools.html.

Before computing the MSE, a detrending procedure was employed to the EEG signals from each trial to make brain signals stationary. This detrending procedure was achieved by removing the last mode (i.e. "trend") obtained from empirical mode decomposition (EMD) (Huang et al., 1998). We then calculated MSE

from the detrended EEG signals in two steps and was performed from time scales 1 to 25 in the following time windows: -100 to 500 ms relative to the stimulus onset in the attention condition. First, the algorithm progressively down-sampled the EEG post stimulus time series for each trial in each condition. This down-sampling procedure was defined as a coarse-grained procedure along various time scales in the MSE analysis. For time scale τ , the coarse-grained time series $Y^{(\tau)} = \{y(1), y(2), \dots, y(N^-)\}$ was obtained by averaging data points within non-overlapping windows of length τ . Therefore, each element of a coarse-grained time series, j, was calculated according to:

$$y(j) = \frac{1}{\tau} \sum\nolimits_{i=(j-1)\tau+1}^{j\tau} x_i, \text{ where } 1 \leqslant j \leqslant \tilde{N}^{(\tau)}, \tilde{N}^{(\tau)} = \frac{N}{\tau}$$

Second, the algorithm computed the sample entropy for each coarse-grained time series $\mathbf{Y}^{(\tau)}$. Note that all the superscripts (τ) are omitted in the following to simplify the notation. There are two specified parameters for calculating the sample entropy: pattern length m and tolerance level r for similarity comparisons. Given the coarse-grained time series \mathbf{Y} , the sample entropy was calculated as follows: first, construct

$$Y_m(i): Y_m(i) = \{y(i+k)\}, 0 \le k \le m-1$$

N-m+1vectors

where the distance between two vectors is defined as the absolute maximum difference between the corresponding scalar components

$$d[Y_m(i), Y_m(j)] = \max(|y(i+k) - y(j+k)|), \quad 0 \le k \le m-1.$$

Given r, $n_i^{\prime m}$ is defined as the number of vectors $Y_m(i)$ falling within vector distance r^*s of $Y_m(i)$ without allowing self-matches, where s is the standard deviation of the original time series. Similarly, $n_i^{\prime m+1}$ is defined as the number of vectors $Y_{m+1}(i)$ falling within vector distance r^*s of $Y_{m+1}(i)$. Finally, sample entropy was defined by the negative natural logarithm of the conditional probability that a time series of length N, having repeated itself within a tolerance r^*s (similarity factor) for m points pattern, will also repeat itself for m+1 points pattern

$$S_{E}(m,r,\widetilde{N}) = \ln \frac{\sum_{i=1}^{\widetilde{N}-m} n'_{i}^{m}}{\sum_{i=1}^{\widetilde{N}-m} n'_{i}^{m+1}}$$

Although there are no recommendations regarding the optimum parameters for calculating sample entropy values in EEG studies, some theoretical and clinical applications (Escudero et al., 2006) have suggested setting m=1 or 2 to provide high validity for measuring sample entropy in EEG signals. Thus, in the present study the pattern length, m, was set to 1; that is, one consecutive data point was used for pattern matching. The setting of m higher than 1 (e.g., 2) in the current study is limited by the short data length of the present cognitive task. However, because the aim of applying MSE in the current study is to measure brain signal/state variability rather than the complicated deterministic chaotic patterns, the setting of m equal to 1 could be a relevant choice to

achieve the purpose. In addition, the aforementioned detrending procedure by EMD could also be helpful to improve stability and reliability of the MSE result obtained by m = 1. In terms of r value (i.e., the similarity criterion), because a number of EEG study investigating brainbehavior relationship have applied the r ranging from 0.25 to 0.5 to MSE analysis (Carpentier et al., 2016; Escudero et al., 2006; Grundy et al., 2017; Heisz et al., 2015; Heisz et al., 2012; Liang et al., 2014; Takahashi et al., 2009; Wang et al., 2019c; Wang et al., 2014), here the r was set to 0.35, which means that data points were considered to be indistinguishable if the absolute amplitude difference between them was ≤ 35% of the time series standard deviation. In addition, because previous research has suggested that data lengths of 10^m to 20^m (m: pattern length) should be sufficient to estimate sample entropy (Richman and Moorman 2000), where in estimation of sample entropy in the current coarse-grained EEG data (before the coarse-graining procedure), 600 time points may be sufficient for m = 1 with time scales 1– 25. The time scale indicates the length of each nonoverlapping time bin within which the original data were averaged; for example, time scale 20 refers to averaging within each 20-ms window when the original sampling rate was 1000 Hz.

Based on prior neuroimaging and electrophysiological studies demonstrating that brain activities in the midfrontal and parietal areas are important for processes in flanker tasks (Bunge et al., 2002; Kopp et al., 1996), the electrodes of interest (FCz, Pz) were selected for analysis to test the effect of sport expertise on the EEG complexity during cognitive control process. The Oz electrode was selected to examine whether the effects of interest are due to the changes in basic visual processing. To test the trial type effect (congruent; incongruent) and group effect (interceptive sport players; static sport players) for each electrode, a q < 0.05 with a false discovery rate (FDR) correction (Benjamini and Yekutieli 2001) for multiple comparisons was employed.

Behavior-EEG correlations. Correlations between the behavioral and EEG measures were examined to gain insight into the brain-behavior relationship. Although we mainly focus on MSE for the correlation analysis due to the fact that both groups showed differential patterns of cognitive modulation on MSE values, the other simpler measures of EEG signals (i.e., N2d, P3d and theta power) were also analyzed. Here we examined whether the interference scores of behavioral variables would correlate with those of EEG variables. The correlation analyses were conducted for each group as well as for all participants using the Pearson product-moment correlation with a significance level set at $\alpha=0.05$. We employed an FDR correction approach (Benjamini and Yekutieli 2001) to account for multiple comparisons.

RESULTS

Participant demographics

Demographic variables including age [t(32) = 0.10, p = .919], body mass index (BMI) [t(32) = 0.91, p = .374], BDI scores [t(32) = -0.14, p = .891], years

of education [t(32) = 0.10, p = .919], PACER laps [t(32) = -0.44, p = .662], years of training experience [t(32) = -1.36, p = .182] and estimated VO2max value [t(32) = 0.07, p = .946] did not differ between groups (Table 1).

Behavioral performance

Accuracy. The groups did not differ in terms of task accuracy [t(32) = -1.54, p = .134]. The interceptive sport players performed with 96.97 \pm 2.84 % accuracy, and the athletic controls performed with 98.21 \pm 1.68 % accuracy.

Mean RT. As illustrated in Fig. 1A, the participants had significantly lower RT for congruent trials compared to incongruent ones $[F(1, 32) = 480.20, p = .043, \eta_p^2 = 0.12]$. The main effect of group was also significant $[F(1, 32) = 4.43, p = .015, \eta_p^2 = 0.17]$, with mean RT for interceptive sport players significantly lower than that for static sport players. The trial type by group interaction was not significant $[F(1, 32) = 3.12, p = .087, \eta_p^2 = 0.09]$.

cvRT. As illustrated in Fig. 1B, participants had a significantly smaller cvRT for congruent trials compared to incongruent ones $[F(1, 32) = 13.20, p < .001, \eta_p^2 = 0.29]$. The main effect for group was also significant $[F(1, 32) = 4.65, p = .039, \eta_p^2 = 0.15]$, with the RT variability for badminton players significantly lower than for athletic controls. The trial type by group interaction did not reach significance $[F(1, 32) = 1.87, p = .67, \eta_p^2 = 0.01]$.

Event-related potentials

The amplitudes of N2d and P3d at FCz are illustrated in Fig. 2. Independent *t*-tests revealed that no difference between groups in N2d amplitude [t(32) = 0.09, p = .933] (static sport players: $-2.53 \pm 2.80 \,\mu\text{V}$ vs interceptive sport players: $-2.62 \pm 3.20 \,\mu\text{V}$) or P3d amplitude [t(32) = 0.56, p = .582] (static sport players: $4.80 \pm 2.48 \,\mu\text{V}$ vs interceptive sport players: $5.30 \pm 2.71 \,\mu\text{V}$) was observed.

EEG power analysis

A mixed-design ANOVA revealed a significant main effect of trial type at the theta band (4–7 Hz, around 200 to 550 ms) (all qs < 0.05 FDR corrected). However, no significant effects were observed for group (all qs > 0.05 FDR corrected) and group by trial type interaction (all qs > 0.05 FDR corrected) (Fig. 3), suggesting that both groups exhibited similar level of conflict-related modulation on oscillatory theta power.

Multiscale entropy analysis of EEG

As illustrated in Fig. 4, conflict-induced modulation of MSE values was found for each group at the Pz site, with greater sample entropy being seen for incongruent trials relative to congruent trials at time scales 4–25 in interceptive sport players (all qs < 0.05 FDR corrected) and at time scales 9–13, 14–25 in static sport players (all qs < 0.05 FDR corrected). For the FCz site, the trial

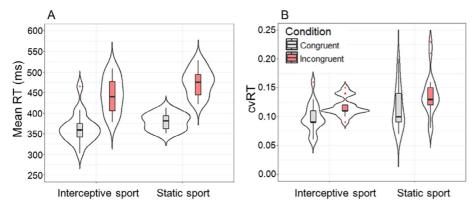


Fig. 1. Mean RT and RT coefficient of variation (cvRT) for each condition, split by group. The plots show the distributions (violin) of mean RT and cvRT together with the median (box central black dot), mean (box central line), first and third quartile (box edges), minimum and maximum (whiskers), and outliers (red dots). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

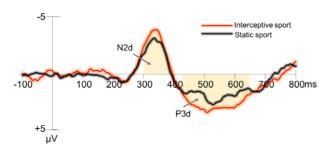


Fig. 2. Grand average ERP waveforms for the N2d and P3d components in both interceptive sport players and static sport players at FCz site. The yellow region indicates the mean amplitudes extracted for analysis. No group-level difference was observed for the mean amplitudes of N2d as well as P3d.

type effect was observed at time scales 15, 17–25 for the interceptive sport players (all qs < 0.05 FDR corrected), whereas such effect was not observed for the static sport players (all qs > 0.05 FDR corrected). No differences across all time scales, electrodes, and trial types were found between groups (all qs > 0.05 FDR corrected). No effects were observed at the Oz site (all qs > 0.05 FDR corrected).

Correlation between behavioral and EEG measures

Mean RT. The correlation analysis revealed that interference score of mean RT was not correlated with N2d (r = -0.23, p = .192), P3d (r = -0.13, p = .471), interference scores of theta power at any time–frequency bins (all qs > 0.05, FDR corrected), and interference scores of MSE at any time scales (all qs > 0.05, FDR corrected). Such effect was similar when examining each group as well as all participants.

cvRT. The correlation analysis revealed that interference score of cvRT was not correlated with N2d (r = 0.276, p = .115), P3d (r = 0.315, p = .070),

interference scores of theta power at any time–frequency bins (all qs > 0.05, FDR corrected), and interference scores of MSE at any time scales (all qs > 0.05, FDR corrected). Such effect was similar when examining each group as well as all participants.

DISCUSSION

In this study, we used a multiscale entropy analysis of EEG to explore the potential neural mechanisms individual differences in performance related to expertise in sports. Behavioral data revealed that, in comparison to static sport players, interceptive sport players exhibited faster response and greater stability. For the EEG data, although the two groups exhibited similar patterns on mean EEG activities during conflict processing, the task-related modulation of the midfrontal sample entropy at coarsergrained time scales was only observed for the interceptive sport players. These findings may help further understand the neural mechanisms underlying individual differences in cognitive ability, especially in the context of motor expertise.

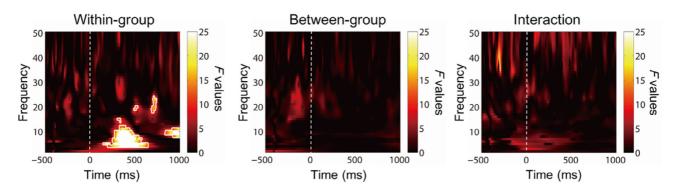


Fig. 3. Time-frequency analysis of the two-way mixed-design analysis of variance (ANOVA) at midfrontal site (FCz). The results revealed that the main effect of the within group factor (congruent vs. incongruent) was most evident around the theta band (4–7 Hz) following the stimulus onset (qs < 0.05, FDR corrected). However, the main effects of between group factor (interceptive sport vs. static sport) and interaction did not reach the significance level (qs > 0.05, FDR corrected), suggesting that both groups exhibited similar levels of conflict-related modulation on midfrontal theta oscillation. Note: the white dotted line denotes the onset of stimuli.

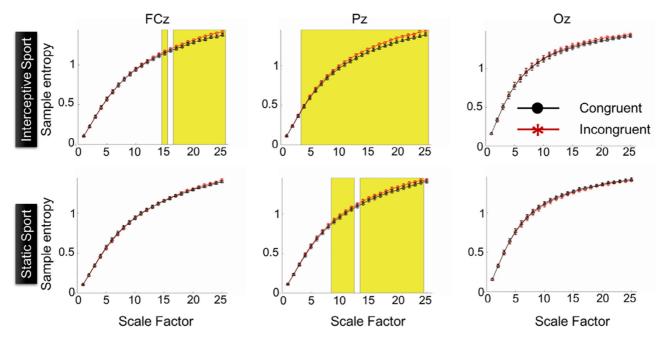


Fig. 4. Conflict-induced differences in EEG-based multiscale entropy (m = 1, r = 0.35) at FCz, Pz, & Oz electrodes for interceptive sport players and static sport players. The yellow region depicts significant effects for contrasts between congruent and incongruent trials (qs < 0.05, FDR corrected). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Behavioral performance. As expected from previous studies using the flanker task (Wang et al., 2017; Wu et al., 2011), both groups exhibited faster and less variable responses in congruent trials than in incongruent trials, which may be attributed to conflict in the form of competition between correct and incorrect responses on the incongruent trials.

The group comparison revealed significantly faster response and smaller trial-to-trial variability for interceptive sport players, in line with numerous prior studies showing superior cognitive performance in athletes practicing open-skill sports than those engaging in close-skill sports (Di Russo et al., 2010; Krenn et al., 2018). Given that these differences were observed in the absence of differences in education, physical fitness, years of training experience, or mental status at the time of this study, our results suggest differences in the cognitive characteristics of motor experts practicing different sport types. More specifically, these findings also shed light on the differences in cognitive requirements between interceptive sports and static sports, which might result in cognitive adaptation to different extends or in different ways, specific to sports demand. Moreover, given the association of intra-individual response variability with the efficiency of top-down processing (Nakata et al., 2012), it is perhaps not surprising to observe greater response stability for interceptive sports players—greater regulation of attentional control may be frequently needed during an externally-paced environment, thus showing better performance in athletes practicing this sport type.

We should note, however, that there is a possibility that innate differences or some combination of innate differences together with practice result in differences between athletes drawn to and participating in different sport types. Although future studies will be necessary to

systematically address this issue, previous research has shown that sport type has the potential to modulate training-induced cognitive benefits (Moreau et al., 2015). In this study, they demonstrated that a complex motor sport exhibited greater cognitive enhancement than aerobic exercise after training for eight weeks, perhaps reflecting the combined benefits of exercise and cognitive challenges to enhance neuroplasticity (Raichlen and Alexander 2017; Wang et al., 2019c).

Taken together, the results of this study confirmed and extended the findings of earlier studies measuring mean level performance (Voss et al., 2010; Wang et al., 2013a; Wang et al., 2013b; Yamashiro et al., 2015) by illustrating differences in behavioral variability between athletes with different domains of expertise.

Brain signal complexity. This study addressed the question of whether there is evidence for functional cortical responses during cognitive processes that could account for the individual differences associated with motor expertise. In order to provide a comprehensive examination of the EEG data, we also analyzed the time-domain averaging and the simpler measure of EEG signals, which helps provide complementary interpretation of MSE results. Our analysis revealed that both groups showed clear midfrontal N2d, P3d and theta oscillation when performing the flanker task. These findings are in line with a number of previous studies showing an association between typical EEG patterns and conflict processing (Liu et al., 2011; Nigbur et al., 2012; Nigbur et al., 2011; Tillman and Wiens 2011). However, individual difference in motor expertise did not modulate these EEG measures. Thus, we speculate that these simpler EEG measures might be less related to the observed group difference in cognitive control.

The analysis of MSE in EEG signal at the parietal site revealed that brain signal variability was higher in the incongruent trials relative to the congruent trials for both groups, with such effect expressed from finer to coarser time scales in interceptive sport players while at coarser time scales in static sport players. This finding suggests that both athletic groups exhibited greater entropy in response to incongruent flankers, and that the neural dynamics around the parietal site supporting conflict processing are both local and distributed for the interceptive sport players, but predominantly distributed for static sport players. This conflict-related modulation of MSE may support the involvement of parietal function in flanker tasks (Bunge et al., 2002; Casey et al., 2000). For example, one functional imaging studv Bungeet al. (2002) found greater parietal activation when the flankers did (i.e., incongruent vs. congruent trials) or did not impact behavioral responses (i.e., congruent vs. neutral trials), suggesting that the functional parietal activity is not specifically linked to selection between competing responses, but rather reflects the sustained activation of a representation of possible responses. In addition, Caseyet al. (2000) has demonstrated that functional brain activity increased in the inferior parietal region but decreased in the superior parietal region during incongruent trials. The authors argued that the former may be more associated with broadening of attention outside the fovea to include the periphery (e.g., flankers), whereas the latter may be more involved in narrowing attentional focus (central target). Together, these complex processes in the parietal area might presumably contribute to the modulation of brain signal variability. Yet, while the incongruent trials manifested overall higher entropy values than the congruent trials over parietal area, such patter of activation was not significantly differentially modulated by motor expertise. A possible implication of this finding is that the expertise-related differences in cognitive functioning may not be particularly associated with automatic or bottom-up control of attention. However, albeit limited, we observed group differences in cognitively modulating sample entropy at some of the finer scales (i.e., time scales 4-8), possibly because local networks in interceptive sport players are more sensitive to perceptually conflicting flankers relative to those of static sport players, though this remains to be confirmed by systematically manipulating the levels of conflicting flankers (i.e., the size or number of flankers).

In contrast, with respect to MSE of EEG at the midfrontal site. we observed unique temporal distributions for each group, when dealing with congruent versus incongruent trials. Interceptive sport players exhibited greater sample entropy when processing incongruent as compared with congruent trials. This difference was primarily expressed at coarser-grained time scales that were previously shown to be associated with distributed information integration, in contrast to the finer time scales representing local information integration (Grundy et al., 2017; Heisz et al., 2012). This finding suggests that interceptive sport players may exhibit greater, distributed information integration for conflict processing. In contrast, static sport players

showed a similar level of MSE between congruent and incongruent trials, reflecting that the processing of conflict in this group was not strong enough to induce changes in brain signal variability. That is to say, it is presumable that players practicing an interceptive sport might rely more on coarser-grained neurophysiological dynamics during conflict processing when compared to those practicing a static sport, and, as a result, showed better cognitive control performance. This is consistent with the idea that open skills typically require global processing for complex feature integration in a dynamically changing environment, in contrast to relatively local processing in the predictable and stable environment that occurs in close-skill sports. Indeed, a number of studies have found differences in cognitive control processes between interceptive sport and static sport athletes (Bianco et al., 2017; Wang et al., 2013a; Yamashiro et al., 2015), which may be honed by long-term participation in open-skill sports requiring greater adaptability and fast decision-making in response to external information in an complex environment (Bianco et al., 2017; Di Russo et al., 2010). Indeed, greater frontal activation has been previously observed in the comparison of incongruent to congruent trials, but not in the comparison of neutral to congruent trials (Bunge et al., 2002), likely reflecting that frontal activity is specifically activated during incongruent trials to select between competing responses (Bunge et al., 2002; Casey et al., 2000). In line with this idea, our results suggest expertise-related differences in top-down attentional processing, and provides complementary evidence with EEG variability measures. It is worth pointing out, however, that the current data showed similar modulation of conflict-related EEG from simpler measures (i.e., theta power oscillations) in both athletic groups. Yet, brain signal variability measured by MSE does not necessarily coincide with EEG power oscillations in response to information processing (Hutka et al., 2016). Collectively, MSE may be a sensitive tool for detecting more subtle individual differences in neural dynamics underlying cognitive functioning.

Moreover, given the association between brain signal variability and efficiency switching between multiple functional brain states (Beharelle et al., 2012; Deco et al., 2011; Grundy et al., 2017), there is another possible interpretation for the data reported here. One recent study has found that bilinguals elicit greater brain signal complexity relative to monolinguals when performing a taskswitching paradigm, suggesting that a lifetime of experience with proficiently switching between two (or more) languages leads to a more efficient alternation between functional brain states when processing a domaingeneral cognitive task. Similarly, athletes in interceptive sports are typically bombarded with information that can either be task-relevant or distracting (e.g., feints). These impact decision-making processes; specifically, when reacting to the feints of an opponent, a player may need to switch rapidly from a planned but inappropriate action to a new, more appropriate response. This process places considerable mental demands on the cognitive control system (Wang et al., 2013a), potentially leading to more efficient switching brain states over time. Arguably, this itself would result in greater brain signal variability when processing incongruent trials, in comparison to congruent trials. Importantly, these novel MSE findings should be considered with caution given that we did not observe any significant correlations between MSE and behavioral observations. Future studies are required to replicate these findings and to explore their generalizability to other cognitive domains or athletic populations.

Finally, we did not observe significant differences in occipital MSE between groups across all time scales. Therefore, our results indicate that the MSE within the occipital region is not related to differential cognitive control processing between groups. In line with this, MSE differences with regard to congruency level were not detectable, which might be due to the fact that the cognitive control task used in this study does not primarily rely on fundamental visual functioning, but rather on top-down and bottom-up attentional control dominated by the frontoparietal network. This suggests that brain signal complexity elicited by basic visual processing does not explain superior cognitive control in athletes practicing an interceptive sport. Nevertheless, it remains possible that future studies using cognitive tasks demanding basic visual processing (Overney et al., 2008) could provide further insight into the modulation on brain signal variability associated with visual processes, in relation to expert behavior in sports.

Our study also has a number of potential limitations. First, the use of a relatively small sample size may limit the generalizability of the present findings. For example, the extent to which the cognitive modulation of MSE seen can be generalized to other types of open-skill sports (e.g., strategy sports such as soccer or volleyball), to different expertise levels, to different training volume, or to female athletes remains to be determined. A larger and broader athletic population is thus warranted to allow extrapolating those claims. Second, the current study was a cross-sectional design, thus limiting any causal interpretation from the behavioral and MSE observations, and hindering our ability to assess the predictive power of MSE with respect to long-term training-induced adaptation. This could be overcome with a longitudinal study to specifically investigate whether sustained participation in a specific sport actually induces changes in brain signal variability inherent in the neural dynamics. In addition, as the temporal dynamics of task performance may reflect sustained attention and cognitive stability over time. However, the present study does not allow for the investigation of whether the individual differences associated with sport expertise is related to lapses in attention. A new specially designed version of the flanker task with a long block lengths design would allow for the study of this relationship in the future. Finally, given the relationship between knowledge representation and brain signal variability (Heisz et al., 2012), it would be of interest to further address the current issue in more ecologically valid conditions using mobile EEG systems (Wang et al., 2019a), which may help understand whether sport-specific knowledge can induce changes in MSE that may be related to real-world sports performance.

In sum, the present study suggests that the cognitive differences related to motor expertise are associated with different information processing capacities supporting cognitive functioning. Specifically, we found that interceptive sport players and static sport players exhibited different patterns of variability in brain signal during conflict processing, suggesting that they may use different networks for processing conflicting stimulus information. This finding further corroborates the idea of experience-dependent plasticity in sports, and is in line with the claim that greater exposure to the type of cognitive challenges involved in sports can transfer outside of sport, and result in improvements on domaingeneral cognitive control (Alves et al., 2013; Wang et al., 2015; Wang et al., 2017; Wylie et al., 2018). The current findings provide additional evidence documenting training-induced cognitive adaptation, by highlighting the role of neural complexity in differentiating cognitive functioning between athletes practicing different domains of expertise. Together with far transfer as postulated in the cognitive skill hypothesis (Alves et al., 2013; Voss et al., 2010), increased brain signal variability may underlie the improved ability to switch between functional brain states. Thus, brain signal variability could represent a proxy into enhanced information processing capacity, a plausible neural mechanism by which cognitive control optimizes behavioral performance in open-skill sport players.

DECLARATION OF COMPETING INTEREST

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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