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Neural efficiency in basketball players is associated with bidirectional reductions in cortical activation and deactivation during multiple-object tracking task performance

Fanghui Qiu[a,1], Yanling Pi[b,1], Ke Liu[b], Hua Zhu[a], Xuepei Li[a], Jian Zhang[a], Yin Wu[c,*]

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This article shows that **MOT performance is correlated to the basketball player level**. Brain recordings indicate a **higher efficiency in specific areas in Elite players** (First Ligue, China) compared to beginners.

At **high attentional workload** (4 targets at MOT), **Elite players** show **higher performance** (**54% ±15%** of positive hits) compared to beginners (**39% ±11%** positive hits).

Neurofy allows high workload training of spatial attention in a fully immersive 3D-MOT environment.

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ABSTRACT

Although sports expertise has been shown to have transferable cognitive benefits, it is unclear how motor expertise influences brain activity during perceptual-cognitive tasks. The aim of the present study was to investigate whether improved perceptual-cognitive behavioral task performance in individuals with well-developed motor skills is associated with characteristic cortical activation and deactivation. Blood oxygenation-level dependent (BOLD) functional MRI (fMRI) was conducted in 23 athletes and 24 age- and education-matched non-athletes performing a multiple object tracking (MOT) task with graded levels of attentional load (two, three, or four targets). Compared to non-athletes, athletes had better performance in the three- and four-target conditions of the MOT task. Less activation of the left frontal eye field (FEF) and bilateral anterior intraparietal sulcus (aIPS) and less deactivation in the bilateral medial superior frontal gyrus (mSFG) were observed in athletes compared to non-athletes. Importantly, as the attentional load was increased, differences in deactivation of the left middle temporal gyrus (MTG) between athletes and non-athletes became larger. Behavioral performance in the high attentional load condition correlated negatively with activation in the left FEF and right aIPS, and correlated positively with that in the mSFG and left MTG. Better performance in elite athletes may transfer from the sport domain to a general cognitive domain owing to higher neural efficiency, which may be represented by a bidirectional reduction phenomenon encompassing both reduced activation of areas associated with task execution and reduced deactivation of areas associated with irrelevant information processing.

1. Introduction

Motor skill learning is associated with neuroplastic changes in the brain (Dayan & Cohen, 2011; Debarnot et al., 2014; Doyon & Benali, 2005). Several studies have demonstrated functional changes, including increased activation in brain areas, in motor skill experts (Calvo-Merino et al., 2005; Wei & Luo, 2010; Wright et al., 2010). These studies suggest that, through long-term training, motor skill experts gain the ability to generate preferential activation of brain areas involved in action planning and action comprehension (Yang, 2015). However, findings of decreased activation in certain brain areas have also been observed in motor skill experts (Guo et al., 2017; Jäncke et al., 2000; Krings et al., 2000; Naito & Hirose, 2014; Percio et al., 2009; Percio et al., 2008). Although long-term physical training has been shown to improve cognitive processing (Alves et al., 2013; Voss et al., 2010), it has not been clarified how motor expertise influences brain activity during perceptual-cognitive task performance.

Behavioral studies showing that athletes perform better than non-athletes in perceptual-cognitive tasks have suggested that athletic training can transfer positive effects to a general cognitive domain (Alves et al., 2013; Voss et al., 2010). Training-induced behavioral changes are accompanied by neural activity changes (Karbach & Schubert, 2013). It remains to be resolved how the development of motor expertise may alter brain activity during perceptual-cognitive task performance. In a study investigating brain activation during visuospatial cognitive task performance, Guo et al. (2017) found that athletes exhibited lower cortical activation than non-athletes in task-relevant brain areas. They concluded that long-term training in athletes may have led to the development of a focused and efficient organization of task-related neural networks that enabled cognitive skills developed

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in athletic training to be transferred to similar processes in other domains. Decreased cortical activation in experts has been postulated to reflect greater neural efficiency (Gobel et al., 2011; Guo et al., 2017; Krings et al., 2000; Milton et al., 2007; Nakata et al., 2010), and has been associated with better performance in expertise-related tasks (Boe et al., 2012; Guo et al., 2017; Haufler et al., 2000). The neural efficiency model of expertise has been supported by electroencephalography studies reporting reduced cortical activation (less pronounced alpha-frequency event-related desynchronization) in elite athletes, compared to non-athletes, during the performance of visuo-motor tasks related to the athletes' expertise (Babiloni et al., 2010; Percio et al., 2009; Percio et al., 2008). It has been supposed that decreased cortical activation may reflect a sharpening of network activity such that, with practice, fewer neurons fire strongly during task performance (Kelly & Garavan, 2005; Poldrack, 2000).

In addition to activity changes in regions supporting task execution, deactivations were observed in regions involved in resting-state processing (Fox et al., 2005; Kelly & Garavan, 2005; Ossandón et al., 2011; Raichle, 2015; Raichle et al., 2001), such as the default mode network (DMN), whose activity is thought to reflect suppression of irrelevant information processing (Fox et al., 2005; Kelly & Garavan, 2005; Petersson et al., 1999). Training-induced automaticity may decrease the need for such suppression (Kelly & Garavan, 2005; Meshulam et al., 2017; Patel et al., 2013). Thus, we posited that neural efficiency may be associated with reduced activity in areas associated with task execution as well as reduced activity in areas associated with suppression of irrelevant information processing.

The multiple object tracking (MOT) task (Pylyshyn & Storm, 1988) is a well-established paradigm for investigating goal-driven attention in dynamic environments. While performing the MOT task, subjects must allocate cognitive resources to multiple targets while inhibiting identical-looking distractors (Dørum et al., 2016). Neuroimaging studies of subjects performing the MOT task have shown activations along the dorsal attention network (DAN)—including in the frontal eye fields (FEFs), the superior parietal lobe, the anterior intraparietal sulcus (aIPS), and the posterior intraparietal sulcus—and deactivation within the DMN—including the medial prefrontal cortex (mPFC) and the temporal cortex (Alnaes et al., 2015; Culham et al., 1998; Culham et al., 2001; Dørum et al., 2016; Jovicich et al., 2001). The DAN, which is involved in goal-driven (top-down) selection and responses, supports selective and sustained visuospatial attention (Corbetta et al., 2008; Corbetta & Shulman, 2002; Fox et al., 2006). The DMN, which exhibits high metabolic activity at rest and during relatively simple tasks, is deactivated during the performance of cognitively demanding tasks (Gusnard & Raichle, 2001; Raichle, 2015; Raichle et al., 2001). Using the MOT task to compare differences in brain activation between experts and novices provides a means of investigating the relationship between behavioral performance and changes in brain activation, and thus is useful for assessing the characteristics of neural efficiency.

The MOT paradigm replicates the demands of team sport play well (Faubert, 2013; Faubert & Sidebottom, 2012; Mangine et al., 2014; Memmert et al., 2009; Scholl, 2009). For example, basketball players must monitor the movements and positions of their teammates while inhibiting irrelevant information on the court. Indeed, behavioral studies have shown that, relative to sport novices, basketball and soccer players exhibit better multiple-object tracking performance (Faubert, 2013; Mangine et al., 2014), and supports the notion that a MOT task is an appropriate model with which to investigate training effects on brain activity.

In this study, we compared cortical activation and deactivation between basketball players and non-athletes in a MOT-paradigm perceptual-cognitive task at three attentional load levels (two, three, and four targets). Based on prior evidence suggesting that long-term athletic training may improve neural efficiency (Gobel et al., 2011; Guo et al., 2017; Krings et al., 2000; Milton et al., 2007; Percio et al., 2008) and studies suggesting that brain activation differences between athletes and novices may only be detected during the performance of challenging tasks (Aglioti et al., 2008; Wu et al., 2013), we hypothesized that, relative to non-athletes, athletes would exhibit better MOT performance at a high attentional load while showing less activation in DAN core areas and less deactivation in DMN core areas.

2. Materials and methods

2.1. Participants

Twenty-six basketball players and 26 non-athletes participated in the study. Three basketball players and 2 non-athletes were excluded due to excessive head motion in the scanner (see fMRI preprocessing). Thus, the final analysis included 23 basketball players (mean age: 20.43 ± 1.56 years, range: 19–26 years) and 24 age- and education-matched non-athletes (mean age: 20.71 ± 2.03 years, range: 18–25 years). All participants were right-handed men. The basketball players were first- and second-level national athletes recruited from Shanghai University of Sport's basketball team. The athletes had trained an average of 14.35 ± 2.29 h per week (range: 10–20 h) for 6.48 ± 1.47 years (range: 5–10 years). The non-athletes were university students without training experience in competitive basketball or any other sports. All participants reported normal or corrected-to-normal vision. The experimental protocol was approved by the regional ethics committee of the Shanghai University of Sport. All participants provided written informed consent for participation prior to the start of the experiment.

2.2. Stimuli and procedure

Visual stimuli were created in MATLAB and presented on a screen situated outside of and nearby the scanner. The participants viewed the stimuli via a small mirror located inside the scanner. As depicted in Fig. 1, for each trial, a white fixation point was presented on a grey background (visual field, $20^{\circ} \times 15^{\circ}$), followed by 10 blue objects (diameter 1.33°) for 0.5 s. During active tracking conditions, a subset of the objects (two, three, or four) were highlighted in red for 2 s to designate them as tracking targets. The target objects were turned back to blue so that no cue remained to distinguish them from the non-tracking items. After 1.5 s, all 10 objects started to move in random directions at a constant speed (10°/s) for 8 s. Finally, at the end of the tracking period, the objects stopped moving before a subset of the objects (the same number as that of the highlighted targets in the same trial) turned green (probe; Fig. 1). The participants were instructed to press a number key (0, 1, 2, 3, or 4) to indicate the number of probe items that matched the targets. During the passive viewing condition, all objects remained blue throughout the moving period. The participants were instructed to passively watch the whole display without paying attention to any particular objects and to press the 0 button. Participants were instructed to fixate on the white fixation point throughout the trial. Initial object positions were generated randomly from trial to trial. Circles made random changes per second to make object movements unpredictable. To avoid collision or overlap, objects were programmed to change movement directions when they approached each other or touched the screen border.

The experiment contained 96 trials divided into 24 cycles of four trials each (passive viewing, two targets, three targets, and four targets). The trial sequence order within the cycles was random. Participants had 15 s rest (fixation condition) between blocks. Participants were familiarized with the task prior to performing it in the scanner. Response accuracy data were recorded. To optimize accuracy, we did not ask participants to respond quickly (Jovicich et al., 2001; Pylyshyn & Annan, 2006).

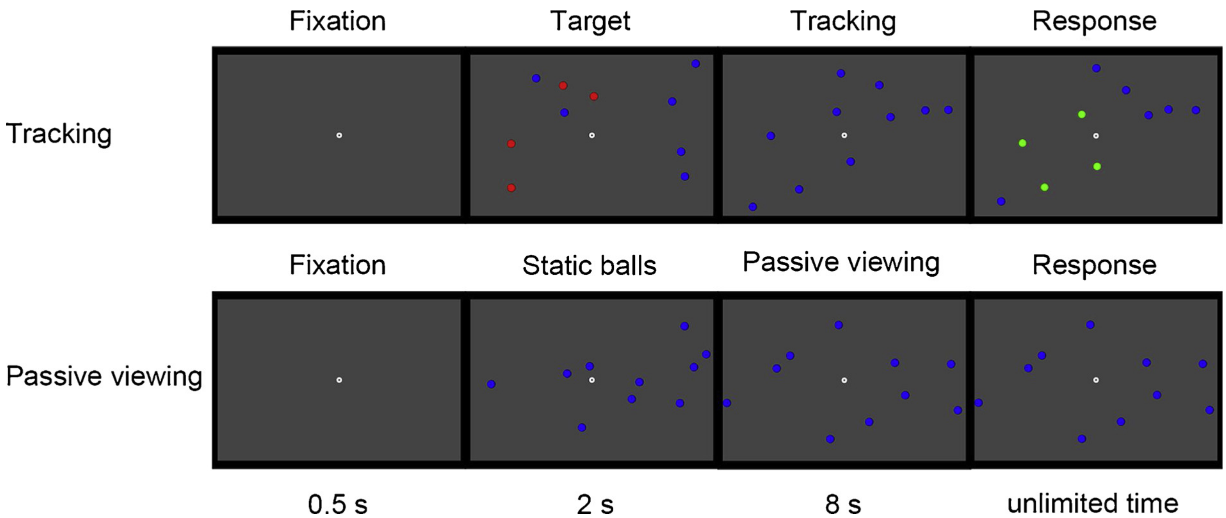

Fig. 1. Schematic diagram of visual stimuli in the MOT task. Participants were instructed to fixate on a central white dot throughout the trial. During attentional tracking conditions, 10 blue objects were presented and two, three, or four of them were highlighted red for 2 s before turning back to blue. Then all 10 objects moved 10°/second for an 8-second tracking period. When the objects stopped moving, participants indicated the number of probe items that matched the target items (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

2.3. fMRI data acquisition

Functional images were collected with a 3-T Siemens scanner at the Center for Functional Magnetic Resonance Imaging at East China Normal University. A standard head coil was used with foam padding to restrict head motion. Functional images were obtained via a gradient echo-planar imaging (EPI) sequence with the following parameters: repetition time (TR) = 2000 ms, one shot per repetition, echo time (TE) = 30 ms, flip angle (FA) = 90°, and field of view (FOV) = 210 × 210 mm^2, slice thickness = 4 mm). Thirty-three contiguous axial slices covering the entire brain were acquired with 3.3 × 3.3 × 4 mm^3 voxels.

At the same slice locations as the functional images, T1 anatomical images were acquired with a magnetization-prepared rapid gradient echo (MPRAGE) sequence: 192 slices, TR = 2530 ms, TE = 2.34 ms, slice thickness = 1 mm, voxel size = 1 × 1 × 1 mm^3, FA = 7°, and FOV = 256 × 256 mm^2.

2.4. Data analysis

2.4.1. Behavioral data

Means are reported with standard deviants. Accuracy data were analyzed with a two-way analysis of variance (ANOVA) with group (athletes vs. non-athletes) as a between-subject factor and attentional load (two, three, and four targets) as a within-subject factor. The statistical analyses were conducted in SPSS® for Windows version 22.0.

2.4.2. Functional magnetic resonance imaging

We conducted functional and anatomical data preprocessing using a Data Processing & Analysis for Brain Imaging toolbox (DPABI version 2.3, http://rfmri.org/dpabi) (Yan et al., 2016), based on the Statistical Parametric Mapping package (SPM8, http://www.fil.ion.ucl.ac.uk/spm) implemented in MATLAB 8.1 (The MathWorks Inc., Natick, MA). Preprocessing included slice-timing correction, head motion correction, segmentation of structural T1-weighted images into grey matter, white matter, and cerebrospinal fluid, and co-registration of mean functional images with each subject's own T1-weighted images. Co-registration was done using the diffeomorphic registration algorithm DARTEL, which creates an average structural brain template from all of the subjects' T1 images (Ashburner, 2007). Images were then normalized into standard Montreal Neurological Institute (MNI) space (3 × 3 × 3 mm voxel size) and smoothed with a 6-mm full-width half-maximum (FWHM) isotropic Gaussian kernel for the group analysis. Functional runs were excluded from further analysis if translational movements exceeded 3 mm or rotational movements exceeded 3°.

Additional analyses were performed in SPM8, including first-level (within-subject) analysis computed via an event-related approach in the context of a general linear model. We created *t*-statistic maps by contrasting each tracking condition (two, three, or four targets) against the passive viewing condition. Contrast images were subsequently used for group statistics calculated as random effects analyses at the second level. To test whether possible inter-group differences varied with attentional load, we specified a SPM8 full factorial model via a 2 × 3 repeated measure ANOVA, with group (athletes, non-athletes) as the between-subject factor and attentional load (two, three, four targets) as the within-subject factor. We focused on a main effect of group to evaluate attention effect differences between the two groups, and whether there was a significant group × attentional load interaction.

Mean contrast values were calculated and compared across groups and tracking conditions. The regions were defined based on the automated anatomical labeling (AAL) atlas (Tzourio-Mazoyer et al., 2002) that parcellates the brain into 116 regions and the Brodmann areas (BA) atlas in the DPABI toolbox. Corrections for multiple comparisons were carried out at the cluster level. Cluster size was determined based in Gaussian random field (GRF) theory (Worsley et al., 1996). For the main effect of group, we considered cortical regions with a cluster forming threshold of $z > 3.09$ and a cluster significance of $p < .05$, GRF-corrected, to be significant. For interactions, we considered cortical regions with a cluster forming threshold of $z > 2.3$ and a cluster significance of $p < .05$, GRF-corrected, to be significant.

2.4.3. Correlation analyses

Contrast values for significant clusters were extracted from each individual's dataset under the three attentional conditions. We calculated Pearson correlation coefficients between behavioral (accuracy rates for each MOT condition) and functional (Mean contrast values in each significant cluster for each condition) measures.

3. Results

3.1. Behavioral results

Group tracking accuracies are shown as a function of target number in Fig. 2. Overall, the subjects' mean tracking accuracy was

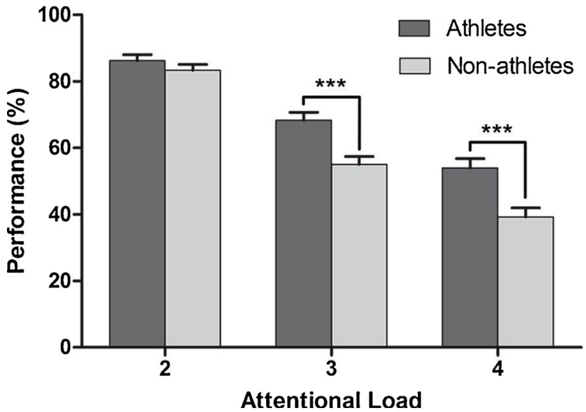

Fig. 2. Mean MOT task performance. Performance data were collected during fMRI, as a function of the attentional load (number of balls tracked). Error bars represent ± 1 standard error (SE); ***$p < .001$.

84.75 ± 8.70% for two targets, 61.52 ± 13.24% for three targets, and 46.45 ± 15.17% for four targets. A two-way repeated-measures ANOVA revealed a significant main effect of attentional load on accuracy ($F_{2,\ 44} = 192.57$, $p < .001$, $\eta^2 = 0.90$), indicating that tracking accuracy declined as tracking load was increased. Similarly, a significant main effect of group on accuracy ($F_{1,\ 45} = 17.16$, $p < .001$, $\eta^2 = 0.28$) was revealed with a significant interaction between group and attentional load ($F_{2,\ 44} = 5.76$, $p = .006$, $\eta^2 = 0.21$). Post hoc analyses revealed that accuracy scores were higher for athletes than for non-athletes tracking three targets (athletes: 68.30 ± 12.67%; non-athletes: 55.03 ± 10.35%; $F_{1,\ 45} = 15.50$, $p < .001$, $\eta^2 = 0.26$) and four targets (athletes: 53.99 ± 15.26%; non-athletes: 39.24 ± 11.25%; $F_{1,\ 45} = 14.31$, $p < .001$, $\eta^2 = 0.24$), but not in tracking two targets (athletes: 86.23 ± 7.69%; non-athletes: 83.33 ± 9.52%; $F_{1,\ 45} = 1.31$, $p = .258$).

3.2. fMRI results

3.2.1. Group differences in attention

A 2 (group: athletes, non-athletes) × 3 (attentional load: two, three, four) ANOVA revealed a main effect of group. As expected, between-group analyses revealed significant differences in cortical activation between athletes and non-athletes. The non-athlete group had greater cortical activation than athletes in several brain areas including the left FEF and bilateral aIPS, which are core areas of the DAN. Greater activation was seen in the athlete group than in the non-athlete group in the medial superior frontal gyrus (mSFG), an important part of the DMN. These areas are displayed in Table 1 and Fig. 3. The mean contrast values obtained for each group in each of the three tracking conditions are shown with their standard errors in Fig. 3.

3.2.2. Group differences in attentional load

An ANOVA also revealed a significant group × attentional load interaction. Voxel-by-voxel comparisons unveiled a complex activation pattern showing that differences in tracking multiple objects between athletes and non-athletes was modulated by the number of tracking objects. This effect manifested in the left middle temporal gyrus (MTG), a component of the DMN, which exhibited more differences between athletes and non-athletes when subjects were tracking more targets (Fig. 4; Table 1).

3.3. Correlation analysis

We found negative correlations between behavioral scores and activity in the left FEF (r = -0.3, p = 0.042) and right aIPS (r = -0.25, p = 0.087, trend), and positive correlations between behavioral scores and activity in the mSFG (r = 0.32, p = 0.026) and left MTG (r = 0.36, p = 0.012) in the high attentional load condition (Fig. 5). No significant correlations were found for the two-target or three-target conditions.

4. Discussion

The present study investigating the relationship between motor expertise and brain activity in a perceptual-cognitive task showed that athletes performed better in the MOT task than non-athletes. This behavioral difference was associated with decreased cortical activation in the left FEF and bilateral aIPS and decreased deactivation in the mSFG of the athlete group. Decreased deactivation in left MTG was observed in athletes, relative to non-athletes, specifically in the high attentional load condition.

4.1. Differences in MOT behavioral performance

The MOT task shares similarities with the dynamic attention scene characteristic of open confrontational sports situations. It is widely believed that skill transfer can occur if the trained and transfer tasks engage overlapping cognitive processes and brain regions (Alves et al., 2013; Dahlin et al., 2008; Jonides, 2004). We found that athletes performed better than non-athletes when tracking three and four targets, supporting the notion that team sports training may enhance visual attention ability. This finding is consistent with previous studies in which team sports players were required to track four targets in a MOT task (Faubert, 2013; Mangine et al., 2014). The lack of a perceptual-cognitive advantage in athletes under a low attentional load condition suggests that the trained-athlete advantage emerges only when a task is sufficiently difficult to challenge subjects' cognitive resources.

4.2. Expertise-related decreased activation

Analyses of differences in cortical activation between athletes and

Table 1
Brain regions with significant main effects of group and group × attentional load interactions identified by a two-way ANOVA.

Brain region	BA	F_{max}	Cluster size	MNI coordinates		
				x	y	z
Attention effect differences: Athletes > Non-athletes						
Left mSFG / right mSFG	32/8	21.97	46	0	36	39
Attention effect differences: Non-athletes > Athletes						
Left FEF	6	18.44	33	−45	−9	54
Left aIPS	40	23.13	23	−24	−42	54
Right aIPS	7/40	19.72	26	18	−48	57
Interaction effect of Group by Attentional load						
Left MTG	21	7.72	49	−48	−27	−12

Note: Regions are specified by anatomical labels and associated Brodmann area (BA), cluster size, local peak effect (F value and MNI coordinates). Multiple comparisons were corrected with Gaussian random field (GRF) approach (for main effect of group: $z > 3.09$, cluster significance $p < .05$; for interaction effect: $z > 2.3$, cluster significance $p > .05$). mSFG: medial superior frontal gyrus; FEF: frontal eye field; aIPS: anterior intraparietal sulcus; MTG: middle temporal gyrus.

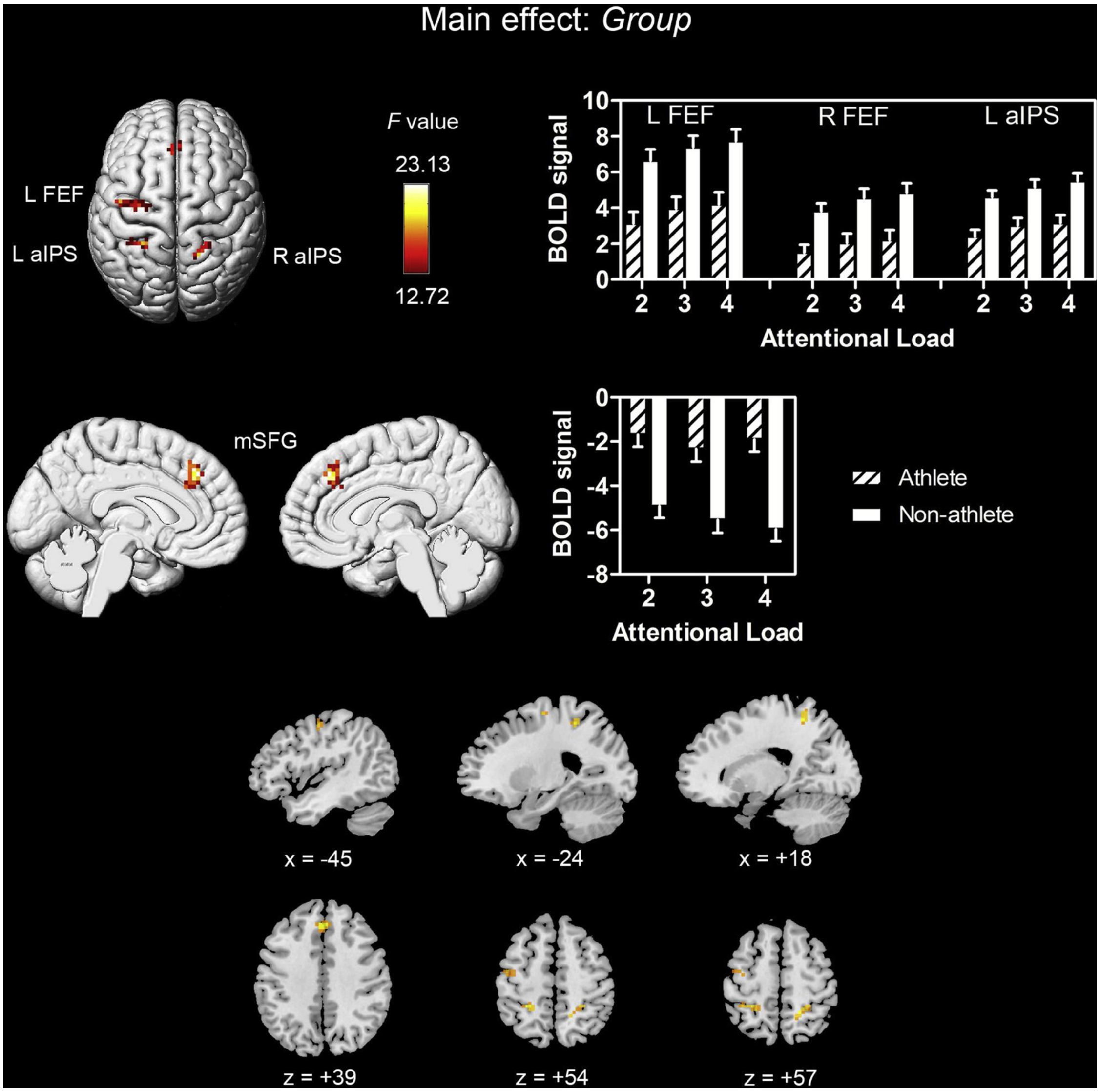

Fig. 3. Significant activation clusters of group differences in cortical activation during MOT task performance. Multiple comparisons were corrected with Gaussian random field (GRF) approach (z > 3.09, cluster significance: $p < .05$). Surface-rendered maps of significant group differences in cortical activation (left) and mean BOLD signal are shown for each cluster and each group (means ± SEs) (right) are shown above, and significant clusters are displayed in sagittal (x) and transverse (z) views below. FEF: frontal eye field; aIPS: anterior intraparietal sulcus; mSFG: medial superior frontal gyrus.

non-athletes showed decreased activation in athletes in the left FEF and bilateral aIPS during the MOT task. Previous studies have highlighted the importance of parietal and frontal cortices in attention-related processing (Corbetta & Shulman, 2002). The FEF is responsible for covert and overt shifts in attention (Corbetta et al., 1998; Schall, 2004) and eye movements (Culham et al., 1998; Culham et al., 2001; Howe et al., 2009). The aIPS processes information about target locations (Xu & Chun, 2006) and mediates active tracking of objects, a function beyond simply attending to them (Howe et al., 2009). MOT performance was shown to be impaired by inhibition of the aIPS with low-frequency transcranial magnetic stimulation (TMS) (Battelli et al., 2009) and improved when the aIPS was facilitated by transcranial direct current stimulation (tDCS) (Blumberg et al., 2015). It is noteworthy that areas exhibiting less activity in athletes than in non-athletes during MOT task performance are core parts of the DAN, which subserves spatial attention, spatial working memory, and visuomotor behavioral functions (Corbetta & Shulman, 2002; Ptak, 2012).

Decreased cortical activation in experts is a common finding among studies examining training or practice (Gobel et al., 2011; Guo et al., 2017; Kelly & Garavan, 2005; Krings et al., 2000; Milton et al., 2007; Tomasi et al., 2004). The primary mechanism proposed to underlie these decreases is increased neural efficiency, implying a task-specific economization of brain function (Ludyga et al., 2016; Neubauer & Fink, 2009). It has been supposed that athletes may be able to perform training-related tasks in a relatively automated, energy-efficient processing mode developed through extensive training rather than in a controlled, effortful processing mode (Callan & Naito, 2014; Neubauer & Fink, 2009). The differences between experts and non-experts are thus thought to reflect increased fluidity of neural processing (i.e., facilitation) in experts (Gobel et al., 2011; Percio et al., 2008). Reduced activation in core areas of the DAN in athletes may reflect a higher neural efficiency of attention systems. Our finding of an inverse correlation of MOT task performance with brain activity in the left FEF and right aIPS in the high attentional load condition is consistent with the view that high neural efficiency is represented by good performance and supports the notion that cortical activation in regions positively associated with task performance may become more functionally efficient with training (Kelly & Garavan, 2005; Percio et al., 2008).

On the other hand, inconsistent with the current study, some studies have demonstrated functional changes in motor experts characterized

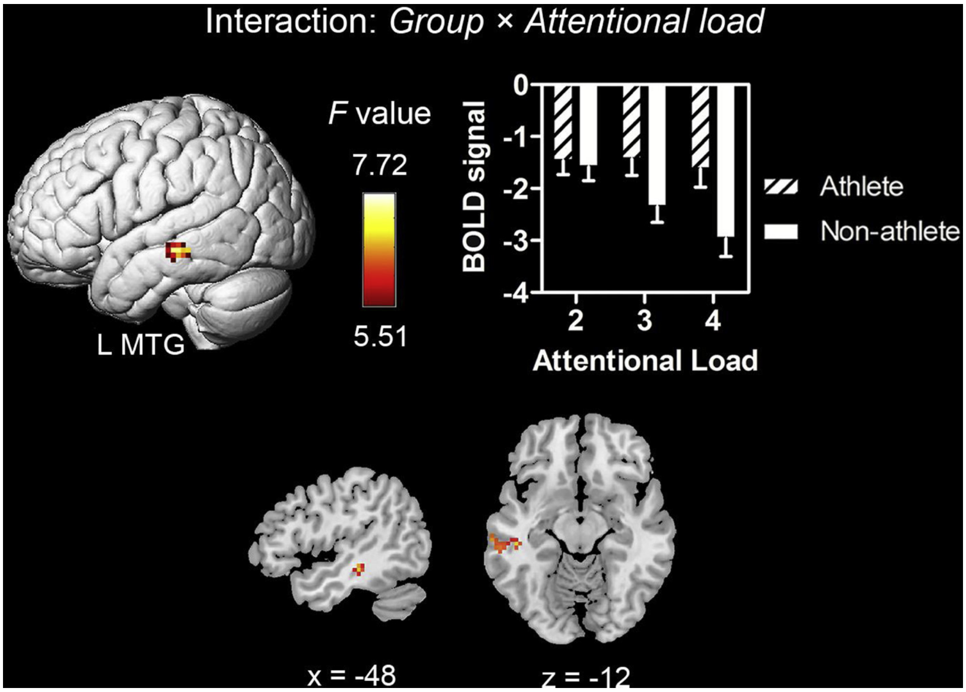

Fig. 4. Significant activation cluster of the interaction effect. Multiple comparisons were corrected with Gaussian random field (GRF) approach (z > 2.3, cluster significance: $p < .05$). A surface rendered map showing the location of the significant interaction effect is shown above with a graph of the mean BOLD signals (± SE) for the cluster obtained for each group. Sagittal (x) and transverse (z) views of the same region are shown below. MTG: middle temporal gyrus.

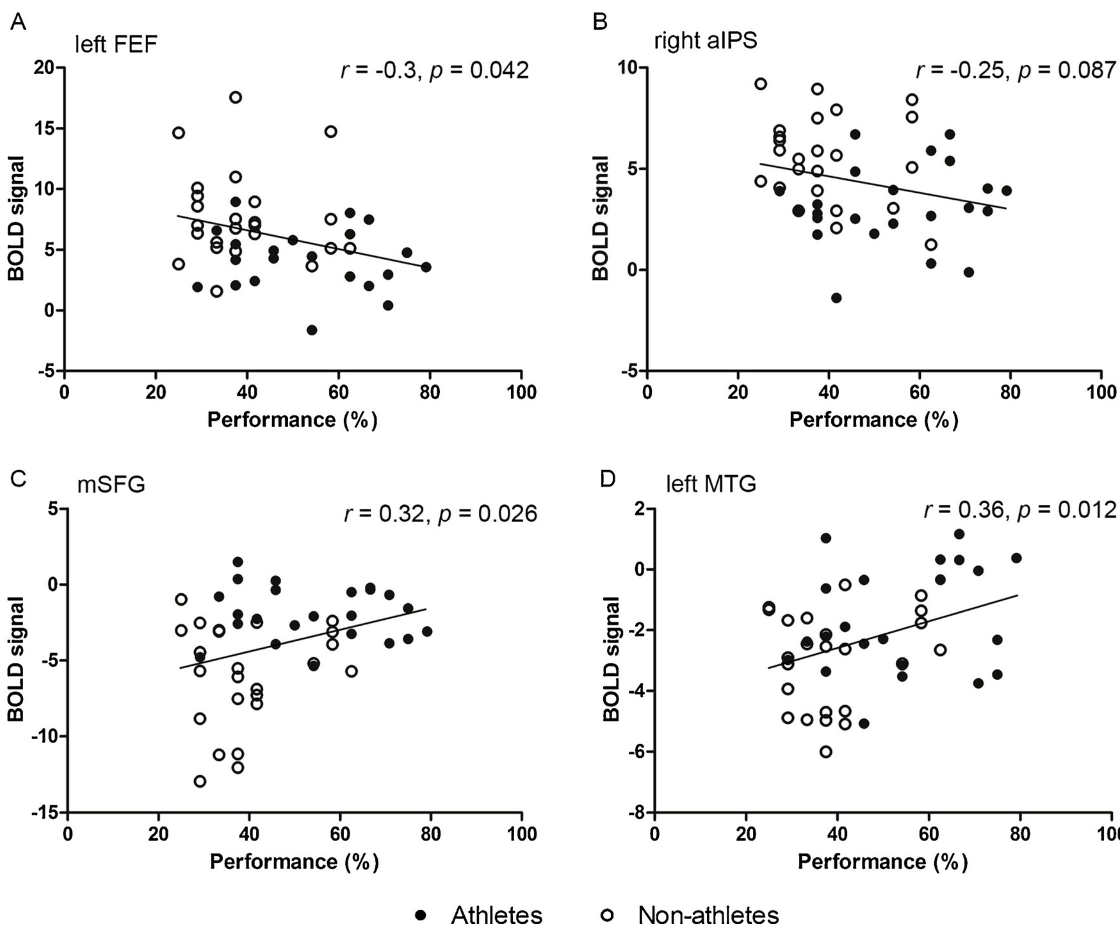

Fig. 5. Relationship between behavioral and functional measures. The abscissa shows the behavioral performance in the high attentional load (four target tracking) condition. The ordinate shows fMRI BOLD signal intensity. BOLD signal data are shown for one cluster. Significant correlations were found in the (A) left FEF, (B) right aIPS, (C) mSFG, and (D) left MTG.

by increased activation in brain areas (Calvo-Merino et al., 2005; Wei & Luo, 2010; Wright et al., 2010). It may be that such increases reflect augmented cortical activity in a sport-specific context, such as motor imagery (Wei & Luo, 2010), action observation (Calvo-Merino et al., 2005), and sport-related anticipation (Wright et al., 2010). Meanwhile, in the present study, we assessed the relationship between basic cognitive skills and athletic expertise (Alves et al., 2013). A recent meta-analysis showed that brain areas with motor expertise-related increases in activity were involved in action planning and action comprehension (Yang, 2015). MOT task performance involves attentional processing, rather than motor-related processing. It requires several attention and mental skills, including selective, dynamic, distributed, and sustained attention skills (Faubert, 2013).

4.3. Expertise-related decreased deactivation

In addition to requiring continual updating of spatiotemporal information about targets, the MOT task also requires inhibition of attending to target-similar distractors (Dørum et al., 2016). Deactivations may represent suppression of irrelevant information processing (Kelly & Garavan, 2005; Kerick et al., 2004; Kerick et al., 2001; Ludyga et al., 2015; Petersson et al., 1999). It is possible that mSFG and left MTG deactivations reflect activity in the DMN (Fox et al., 2005; Raichle et al., 2001) given that these areas are putative key hubs of the DMN. Training-induced increases in automaticity may lead to decreases in the need for attentional suppression of irrelevant information processing, thereby decreasing the magnitude of deactivation in these areas (Kelly & Garavan, 2005; Meshulam et al., 2017; Patel et al., 2013). Thus, the decreased mSFG and MTG deactivations observed in our athlete group may reflect a lesser need to suppress irrelevant information processing.

The present findings are consistent with the results of several studies showing that practice or training can reduce cortical deactivation in regions supporting task-irrelevant information processing (Gobel et al., 2011; Kelly & Garavan, 2005; Mason et al., 2007; Meshulam et al., 2017; Patel et al., 2013; Petersson et al., 1999; Simpson, Drevets et al., 2001; Simpson, Snyder et al., 2001; Tomasi et al., 2004). For example, a positron-emission tomography (PET) study of subjects performing verbal tasks showed greater deactivation in the mPFC during “Novel” trials compared to “Practiced” trials (Simpson, Drevets, et al., 2001; Simpson, Snyder, et al., 2001). It is possible that this decreased activation after practice might reflect habituation to the environment and experimental conditions (Tomasi et al., 2004). More recently, a prior fMRI study showed that learned, automated processing in the rule application phase of a behavioral paradigm was associated with greater activation (i.e., less deactivation) in the DMN than that in controlled, effortful processing in the rule acquisition phase (Vatansever et al., 2017). In this context, our present finding of a positive correlation of MOT performance with brain activity in the mSFG and left MTG in the high attentional load condition suggests that the observed greater deactivation in these regions in non-athletes may be related to their need to exert more effortful focused attention to the task. The decreased deactivation in core DMN areas in athletes may account for an improved ability to suppress irrelevant information processing, thereby enabling better performance on the MOT task.

4.4. Attentional load-modulated deactivation

Our finding of a significant group × attentional load interaction indicated that increasing attentional load leads to greater deactivation in the left MTG in non-athletes than in athletes. As discussed above, if decreased deactivation reflects an improved ability to suppress irrelevant information processing, then greater deactivation may indicate a need to devote more energy to the task. Hence, with increasing attentional load, greater deactivation in the left MTG in non-athletes may reflect a greater need for focused attention towards more difficult task.

Consistent findings have indicated that skilled marksmen exhibit greater alpha power (8–13 Hz) in the left temporal region while preparing to shoot that is suggestive of a reduction in self-talk or constrained analytical thinking during superior performance (Haufler et al., 2000; Janelle et al., 2000; Kerick et al., 2004; Kerick et al., 2001). Based on these findings, one would have expected athletes to have lesser left temporal activation than non-athletes, which is inconsistent with the present findings. This inconsistency may be due to different functions of brain areas across different tasks. The left temporal area, known for its involvement in verbal-analytic and semantic processing (Vandenberghe et al., 1996), is involved in explicit monitoring of task requirements and associated covert verbalizations or instructional self-talk (Gibson & Foster, 2007). Dependency on self-talk is thought to reflect early-stage skill development, before the automaticity associated with expert performance has developed. Thus, lesser left temporal activation in experts, relative to non-experts, during the performance of motor-related tasks as well as following skill acquisition is consistent with moving beyond a dependency on self-talk as skill proficiency reaches the automaticity associated with expert performance.

During MOT task performance, areas associated with attention are activated and areas associated with irrelevant cognitive processes (e.g. verbal-analytical processing) are suppressed, resulting in less interference with essential attentional process (Hatfield & Kerick, 2007). Although athletes showed greater left MTG activation than non-athletes in the present study, both groups showed deactivation suggestive of left MTG suppression during tracking. Inhibition of task-irrelevant processes may reduce interference in task-relevant processing (Kelly & Garavan, 2005; Kerick et al., 2004; Kerick et al., 2001; Ludyga et al., 2015; Petersson et al., 1999). Greater deactivation in non-athletes suggests they exert more effort to suppress task-irrelevant processing, while lesser MTG deactivation in athletes may account for an improved ability to suppress irrelevant information processing, thereby enabling better MOT task performance.

4.5. Bidirectional reduction in neural efficiency

The neural efficiency hypothesis postulates that expertise is characterized by more efficient cortical function such that better cognitive performance is associated with less energy consumption (Neubauer & Fink, 2009; Percio et al., 2008). The present findings of MOT performance correlating negatively with left FEF and right aIPS activation, while correlating positively with mSFG and left MTG activation during high attentional load trials may reflect more efficient brain use during better task performance. These findings are consistent with the notion that neural efficiency may be represented by a bidirectional reduction encompassing reduced activation in regions supporting task execution as well as reduced deactivation in regions associated with irrelevant information processing.

4.6. Transfer to motor performance domain

Given that a perceptual-cognitive task was used in this study rather than a motor task, it is of interest to explore how neural efficiency in the cognitive domain may transfer to the motor performance domain. One possibility is that there may be psychomotor efficiency (Deeny et al., 2003; Hatfield & Kerick, 2007) such that neural efficiency in the cognitive domain reduces nonessential connectivity between essential motor and non-motor processes. That is, neural efficiency of cognitive processes may reduce neuromotor noise, thereby allowing intended motor actions to proceed without interference from non-essential neural activity affecting the motor planning region (van Gemmert et al., 1997). The reduction of such interference would prevent unintended movements that could be disruptive of the kinematic qualities of one’s envisioned actions, thereby enabling efficient fluid movement.

4.7. Strengths and limitations

This study contributes to our understanding of the neural correlates underlying the transfer of enhanced abilities across domains. This work is the first study to propose that neural efficiency may be represented by bidirectional alterations encompassing activation of task-relevant brain regions in conjunction with deactivation of other regions to suppress distraction.

This study had two noteworthy limitations. First, we did not conduct objective assessments of the participants' basketball abilities (Mangine et al., 2014; Romeas et al., 2016). However, other researchers have reported that laboratory MOT-task training improved athletic performance (Junyent et al., 2015; Romeas et al., 2016). In addition, MOT task performance has been reported to be related to a basketball player's ability to observe and respond appropriately to various simultaneous stimuli (Mangine et al., 2014), which suggests that enhanced tracking capability is a discerning measure for evaluating athletic performance. In light of previously reported psychomotor efficiency studies (Deeny et al., 2003; Hatfield & Kerick, 2007), the current results suggest that neural efficiency in the cognitive domain may reduce interference from non-essential neural activity to ensure the kinematic qualities of intended motor actions. Secondly, although our results were interpreted in terms of networks (DAN and DMN), no measurements of network properties were undertaken. Independent component analysis studies examining whether there are expertise-related alterations in correlations between DAN and DMN components during attentional processing should be conducted to test the validity of these interpretations.

Declaration of interest

The authors declare no conflict of interest.

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References

Aglioti, S. M., Cesari, P., Romani, M., & Urgesi, C. (2008). Action anticipation and motor resonance in elite basketball players. *Nature Neuroscience, 11*(9), 1109–1116.

Alnaes, D., Sneve, M. H., Richard, G., Skatun, K. C., Kaufmann, T., Nordvik, J. E., ... Westlye, L. T. (2015). Functional connectivity indicates differential roles for the intraparietal sulcus and the superior parietal lobule in multiple object tracking. *Neuroimage, 123*, 129–137. https://doi.org/10.1016/j.neuroimage.2015.08.029.

Alves, H., Voss, M. W., Boot, W. R., Deslandes, A., Cossich, V., Salles, J. I., & Kramer, A. F. (2013). Perceptual-cognitive expertise in elite volleyball players. *Frontiers in Psychology, 4*. https://doi.org/10.3389/fpsyg.2013.00036 Artical 36.

Ashburner, J. (2007). A fast diffeomorphic image registration algorithm. *Neuroimage, 38*(1), 95–113.

Babiloni, C., Marzano, N., Infarinato, F., Iacoboni, M., Rizza, G., Aschieri, P., ... Del Percio, C. (2010). "Neural efficiency" of experts' brain during judgment of actions: A high-resolution EEG study in elite and amateur karate athletes. *Behavioural Brain Research, 207*(2), 466–475.

Battelli, L., Alvarez, G. A., Carlson, T., & Pascual-Leone, A. (2009). The role of the parietal lobe in visual extinction studied with transcranial magnetic stimulation. *Journal of Cognitive Neuroscience, 21*(10), 1946–1955.

Blumberg, E. J., Peterson, M. S., & Parasuraman, R. (2015). Enhancing multiple object tracking performance with noninvasive brain stimulation: A causal role for the anterior intraparietal sulcus. *Frontiers in Systems Neuroscience, 9*, 3. https://doi.org/10.3389/fnsys.2015.00003.

Boe, S. G., Cassidy, R. J., Mcilroy, W. E., & Graham, S. J. (2012). Single session motor learning demonstrated using a visuomotor task: Evidence from fMRI and behavioural analysis. *Journal of Neuroscience Methods, 209*(2), 308–319. https://doi.org/10.1016/j.jneumeth.2012.06.016.

Callan, D. E., & Naito, E. (2014). Neural processes distinguishing elite from expert and novice athletes. *Cognitive and Behavioral Neurology: Official Journal of the Society for Behavioral and Cognitive Neurology, 27*(4), 183–188. https://doi.org/10.1097/WNN.0000000000000043.

Calvo-Merino, B., Glaser, D. E., Grèzes, J., Passingham, R. E., & Haggard, P. (2005). Action observation and acquired motor skills: An FMRI study with expert dancers. *Cereb Cortex, 15*(8), 1243–1249.

Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews Neuroscience, 3*(3), 201–215. https://doi.org/10.1038/nrn755.

Corbetta, M., Akbudak, E., Conturo, T. E., Snyder, A. Z., Ollinger, J. M., Drury, H. A., ... Van Essen, D. C. (1998). A common network of functional areas for attention and eye movements. *Neuron, 21*(4), 761–773.

Corbetta, M., Patel, G., & Shulman, G. L. (2008). The reorienting system of the human brain: From environment to theory of mind. *Neuron, 58*(3), 306–324. https://doi.org/10.1016/j.neuron.2008.04.017.

Culham, J. C., Brandt, S. A., Cavanagh, P., Kanwisher, N. G., Dale, A. M., & Tootell, R. B. (1998). Cortical fMRI activation produced by attentive tracking of moving targets. *Journal of Neurophysiology, 80*(5), 2657–2670.

Culham, J. C., Cavanagh, P., & Kanwisher, N. G. (2001). Attention response functions: Characterizing brain areas using fMRI activation during parametric variations of attentional load. *Neuron, 32*(4), 737–745. https://doi.org/10.1016/S0896-6273(01)00499-8.

Dahlin, E., Neely, A. S., Larsson, A., Bäckman, L., & Nyberg, L. (2008). Transfer of learning after updating training mediated by the striatum. *Science, 320*(5882), 1510–1512. https://doi.org/10.1126/science.1155466.

Dayan, E., & Cohen, L. G. (2011). Neuroplasticity subserving motor skill learning. *Neuron, 72*(3), 443–454. https://doi.org/10.1016/j.neuron.2011.10.008.

Debarnot, U., Sperduti, M., Rienzo, F. D., & Guillot, A. (2014). Experts bodies, experts minds: How physical and mental training shape the brain. *Frontiers in Human Neuroscience, 8*, 280. https://doi.org/10.3389/fnhum.2014.00280.

Deeny, S. P., Hillman, C. H., Janelle, C. M., & Hatfield, B. D. (2003). Cortico-cortical communication and superior performance in skilled marksmen: An EEG coherence analysis. *Journal of Sport & Exercise Psychology, 25*(2), 188–204. https://doi.org/10.1123/jsep.25.2.188.

Dørum, E. S., Alnæs, D., Kaufmann, T., Richard, G., Lund, M. J., Tønnesen, S., ... Gjertsen, Ø. (2016). Age-related differences in brain network activation and co-activation during multiple object tracking. *Brain and Behavior, 6*(11), e00533.

Doyon, J., & Benali, H. (2005). Reorganization and plasticity in the adult brain during learning of motor skills. *Current Opinion in Neurobiology, 15*(2), 161–167. https://doi.org/10.1016/j.conb.2005.03.004.

Faubert, J. (2013). Professional athletes have extraordinary skills for rapidly learning complex and neutral dynamic visual scenes. *Scientific Reports, 3*, 1154. https://doi.org/10.1038/srep01154.

Faubert, J., & Sidebottom, L. (2012). Perceptual-cognitive training of athletes. *Journal of Clinical Sport Psychology, 6*(1), 85–102. https://doi.org/10.1123/jcsp.6.1.85.

Fox, M. D., Corbetta, M., Snyder, A. Z., Vincent, J. L., & Raichle, M. E. (2006). Spontaneous neuronal activity distinguishes human dorsal and ventral attention systems. *Proceedings of the National Academy of Sciences of the United States of America, 103*(26), 10046–10051.

Fox, M. D., Snyder, A. Z., Vincent, J. L., Corbetta, M., Van Essen, D. C., & Raichle, M. E. (2005). The human brain is intrinsically organized into dynamic, anticorrelated functional networks. *Proceedings of the National Academy of Sciences of the United States of America, 102*(27), 9673–9678. https://doi.org/10.1073/pnas.0504136102.

Gibson, A. S. C., & Foster, C. (2007). The role of self-talk in the awareness of physiological state and physical performance. *Sports Medicine, 37*(12), 1029–1044. https://doi.org/10.2165/00007256-200737120-00003.

Gobel, E. W., Parrish, T. B., & Reber, P. J. (2011). Neural correlates of skill acquisition: Decreased cortical activity during a serial interception sequence learning task. *Neuroimage, 58*(4), 1150–1157. https://doi.org/10.1016/j.neuroimage.2011.06.090.

Guo, Z., Li, A., & Lin, Y. (2017). "Neural efficiency" of athletes' brain during visuo-spatial task: An fMRI study on table tennis players. *Frontiers in Behavioral Neuroscience, 11*, 72. https://doi.org/10.3389/fnbeh.2017.00072.

Gusnard, D. A., & Raichle, M. E. (2001). Searching for a baseline: Functional imaging and the resting human brain. *Nature Reviews Neuroscience, 2*(10), 685–694.

Hatfield, B. D., & Kerick, S. E. (2007). The psychology of superior sport performance: A cognitive and affective neuroscience perspective. In G. Tenenbaum, & R. C. Eklund (Eds.). *Handbook of sport psychology* (pp. 84–109). Hoboken, New Jersey: John Wiley & Sons, Inc.

Haufler, A. J., Spalding, T. W., Maria, D. L. S., & Hatfield, B. D. (2000). Neuro-cognitive activity during a self-paced visuospatial task: Comparative EEG profiles in marksmen and novice shooters. *Biological Psychology, 53*(2), 131–160. https://doi.org/10.1016/S0301-0511(00)00047-8.

Howe, P. D., Horowitz, T. S., Morocz, I. A., Wolfe, J., & Livingstone, M. S. (2009). Using fMRI to distinguish components of the multiple object tracking task. *Journal of Vision, 9*(4), https://doi.org/10.1167/9.4.10 Article 10: 11-11.

Jäncke, L., Shah, N. J., & Peters, M. (2000). Cortical activations in primary and secondary motor areas for complex bimanual movements in professional pianists. *Cognitive Brain Research, 10*, 177–183.

Janelle, C. M., Hillman, C. H., Apparies, R. J., Murray, N. P., Meili, L., Fallon, E. A., & Hatfield, B. D. (2000). Expertise differences in cortical activation and gaze behavior during rifle shooting. *Journal of Sport & Exercise Psychology, 22*(2), 167–182. https://doi.org/10.1123/jsep.22.2.167.

Jonides, J. (2004). How does practice makes perfect? *Nature Neuroscience, 7*(1), 10–11. https://doi.org/10.1038/nn0104-10.

Jovicich, J., Peters, R. J., Koch, C., Braun, J., Chang, L., & Ernst, T. (2001). Brain areas specific for attentional load in a motion-tracking task. *Journal of Cognitive*

Neuroscience, 13(8), 1048–1058. https://doi.org/10.1162/089892901753294347.
Junyent, L. Q., Blázquez, A. P., Fortó, J. S. I., & Torradeflot, G. C. (2015). Perceptual-cognitive training with the neurotracker 3D-MOT to improve performance in three different sports. *Apunts EducaciÃ³n FÃsica Y Deportes, 119*(1), 97–108. https://doi.org/10.5672/apunts.2014-0983.es.(2015/1).119.07.
Karbach, J., & Schubert, T. (2013). Training-induced cognitive and neural plasticity. *Frontiers in Human Neuroscience, 7*. https://doi.org/10.3389/fnhum.2013.00048 Article 48.
Kelly, A. M., & Garavan, H. (2005). Human functional neuroimaging of brain changes associated with practice. *Cereb Cortex, 15*(8), 1089–1102. https://doi.org/10.1093/cercor/bhi005.
Kerick, S. E., Douglass, L. W., & Hatfield, B. D. (2004). Cerebral cortical adaptations associated with visuomotor practice. *Medicine and Science in Sports and Exercise, 36*(1), 118–129.
Kerick, S. E., Mcdowell, K., Hung, T. M., Santa Maria, D. L., Spalding, T. W., & Hatfield, B. D. (2001). The role of the left temporal region under the cognitive motor demands of shooting in skilled marksmen. *Biological Psychology, 58*(3), 263–277.
Krings, T., Töpper, R., Foltys, H., Erberich, S., Sparing, R., Willmes, K., & Thron, A. (2000). Cortical activation patterns during complex motor tasks in piano players and control subjects. A functional magnetic resonance imaging study. *Neuroscience Letters, 278*(3), 189–193. https://doi.org/10.1016/S0304-3940(99)00930-1.
Ludyga, S., Gronwald, T., & Hottenrott, K. (2015). The athlete's brain: Cross-sectional evidence for neural efficiency during cycling exercise. *Neural Plasticity, 2016*(2), 1–7. https://doi.org/10.1155/2016/4583674.
Ludyga, S., Gronwald, T., & Hottenrott, K. (2016). Effects of high vs. Low cadence training on cyclists' brain cortical activity during exercise. *Journal of Science and Medicine in Sport, 19*(4), 342–347.
Mangine, G. T., Hoffman, J. R., Wells, A. J., Gonzalez, A. M., Rogowski, J. P., Townsend, J. R., ... Pruna, G. J. (2014). Visual tracking speed is related to basketball-specific measures of performance in NBA players. *Journal of Strength and Conditioning Research, 28*(9), 2406–2414. https://doi.org/10.1519/JSC.0000000000000550.
Mason, M. F., Norton, M. I., Horn, J. D. V., Wegner, D. M., Grafton, S. T., & Macrae, C. N. (2007). Wandering minds: The default network and stimulus-independent thought. *Science, 315*(5810), 393–395.
Memmert, D., Simons, D. J., & Grimme, T. (2009). The relationship between visual attention and expertise in sports. *Psychology of Sport and Exercise, 10*(1), 146–151. https://doi.org/10.1016/j.psychsport.2008.06.002.
Meshulam, M., Golan, T., Harel, M., Groppe, D., Keller, C., Megevand, P., ... Malach, R. (2017). Repeated performance in problem-solving tasks attenuates human cortical responses. *bioRxiv*. https://doi.org/10.1101/189217.
Milton, J., Solodkin, A., Hluštík, P., & Small, S. L. (2007). The mind of expert motor performance is cool and focused. *Neuroimage, 35*(2), 804–813. https://doi.org/10.1016/j.neuroimage.2007.01.003.
Naito, E., & Hirose, S. (2014). Efficient foot motor control by Neymar's brain. *Frontiers in Human Neuroscience, 8*. https://doi.org/10.3389/fnhum.2014.00594 Article 594.
Nakata, H., Yoshie, M., Miura, A., & Kudo, K. (2010). Characteristics of the athletes' brain: Evidence from neurophysiology and neuroimaging. *Brain Research Reviews, 62*(2), 197–211. https://doi.org/10.1016/j.brainresrev.2009.11.006.
Neubauer, A. C., & Fink, A. (2009). Intelligence and neural efficiency. *Neuroscience and Biobehavioral Reviews, 33*(7), 1004–1023. https://doi.org/10.1016/j.neubiorev.2009.04.001.
Ossandón, T., Jerbi, K., Vidal, J. R., Bayle, D. J., Henaff, M. A., Jung, J., ... Lachaux, J. P. (2011). Transient suppression of broadband gamma power in the default-mode network is correlated with task complexity and subject performance. *Journal of Neuroscience, 31*(41), 14521–14530. https://doi.org/10.1523/JNEUROSCI.2483-11.2011.
Patel, R., Spreng, R. N., & Turner, G. R. (2013). Functional brain changes following cognitive and motor skills training: A quantitative meta-analysis. *Neurorehabilitation and Neural Repair, 27*(3), 187–199.
Percio, C. D., Babiloni, C., Marzano, N., Iacoboni, M., Infarinato, F., Vecchio, F., ... Toran, G. (2009). "Neural efficiency" of athletes' brain for upright standing: A high-resolution EEG study. *Brain Research Bulletin, 79*, 193–200. https://doi.org/10.1016/j.brainresbull.2009.02.001.
Percio, C. D., Rossini, P. M., Marzano, N., Iacoboni, M., Infarinato, F., Aschieri, P., ... Babiloni, C. (2008). Is there a "neural efficiency" in athletes? A high-resolution EEG study. *Neuroimage, 42*(4), 1544–1553. https://doi.org/10.1016/j.neuroimage.2008.05.061.
Petersson, K. M., Elfgren, C., & Ingvar, M. (1999). Dynamic changes in the functional anatomy of the human brain during recall of abstract designs related to practice. *Neuropsychologia, 37*(5), 567–587.
Poldrack, R. A. (2000). Imaging brain plasticity: conceptual and methodological issues—a theoretical review. *Neuroimage, 12*(1), 1–13.
Ptak, R. (2012). The frontoparietal attention network of the human brain: Action, saliency, and a priority map of the environment. *Neuroscientist, 18*(5), 502–515. https://doi.org/10.1177/1073858411409051.
Pylyshyn, Z. W., & Annan, V. (2006). Dynamics of target selection in multiple object tracking (MOT). *Spatial Vision, 19*(6), 485–504. https://doi.org/10.1163/156856806779194017.
Pylyshyn, Z. W., & Storm, R. W. (1988). Tracking multiple independent targets: Evidence for a parallel tracking mechanism. *Spatial Vision, 3*(3), 179–197. https://doi.org/10.1163/156856888X00122.
Raichle, M. E. (2015). The brain's default mode network. *Annual Review of Neuroscience, 38*(1), 413–427. https://doi.org/10.1146/annurev-neuro-071013-014030.
Raichle, M. E., Macleod, A. M., Snyder, A. Z., Powers, W. J., Gusnard, D. A., & Shulman, G. L. (2001). A default mode of brain function. *Proceedings of the National Academy of Sciences of the United States of America, 98*(2), 676–682.
Romeas, T., Guldner, A., & Faubert, J. (2016). 3D-Multiple Object tracking training task improves passing decision-making accuracy in soccer players. *Psychology of Sport and Exercise, 22*, 1–9. https://doi.org/10.1016/j.psychsport.2015.06.002.
Schall, J. D. (2004). On the role of frontal eye field in guiding attention and saccades. *Vision Research, 44*(12), 1453–1467.
Scholl, B. J. (2009). What have we learned about attention from multiple-object tracking (and vice versa)? In D. Dedrick, & L. Trick (Eds.). *Computation, cognition and pylyshyn* (pp. 49–77). Cambridge, MA: MIT Press.
Simpson, J. R., Drevets, W. C., Snyder, A. Z., Gusnard, D. A., & Raichle, M. E. (2001). Emotion-induced changes in human medial prefrontal cortex: II. During anticipatory anxiety. *Proceedings of the National Academy of Sciences of the United States of America, 98*(2), 688–693.
Simpson, J. R., Snyder, A. Z., Gusnard, D. A., & Raichle, M. E. (2001). Emotion-induced changes in human medial prefrontal cortex: I. During cognitive task performance. *Proceedings of the National Academy of Sciences of the United States of America, 98*(2), 683–687.
Tomasi, D., Ernst, T., Caparelli, E. C., & Chang, L. (2004). Practice-induced changes of brain function during visual attention: A parametric fMRI study at 4 Tesla. *Neuroimage, 23*(4), 1414–1421. https://doi.org/10.1016/j.neuroimage.2004.07.065.
Tzourio-Mazoyer, N., Landeau, B., Papathanassiou, D., Crivello, F., Etard, O., Delcroix, N., ... Joliot, M. (2002). Automated anatomical labeling of activations in SPM using a macroscopic anatomical parcellation of the MNI MRI single-subject brain. *Neuroimage, 15*(1), 273–289. https://doi.org/10.1006/nimg.2001.0978.
Vandenberghe, R., Price, C., Wise, R., Josephs, O., & Frackowiak, R. S. J. (1996). Functional anatomy of a common semantic system for words and pictures. *Nature, 383*(6597), 254–256. https://doi.org/10.1038/383254a0.
Vatansever, D., Menon, D. K., & Stamatakis, E. A. (2017). Default mode contributions to automated information processing. *Proceedings of the National Academy of Sciences of the United States of America, 114*(48), 1–6.
Voss, M. W., Kramer, A. F., Basak, C., Prakash, R. S., & Roberts, B. (2010). Are expert athletes 'expert' in the cognitive laboratory? A meta-analytic review of cognition and sport expertise. *Applied Cognitive Psychology, 24*(6), 812–826. https://doi.org/10.1002/acp.1588.
Wei, G., & Luo, J. (2010). Sport expert's motor imagery: Functional imaging of professional motor skills and simple motor skills. *Brain Research, 1341*, 52–62. https://doi.org/10.1016/j.brainres.2009.08.014.
Worsley, K. J., Marrett, S., Neelin, P., Vandal, A. C., Friston, K. J., & Evans, A. C. (1996). A unified statistical approach for determining significant signals in location and scale space images of cerebral activation. *Human Brain Mapping, 4*(1), 58–73. https://doi.org/10.1002/(SICI)1097-0193(1996)4:1<58::AID-HBM4>3.0.CO;2-O.
Wright, M. J., Bishop, D. T., Jackson, R. C., & Abernethy, B. (2010). Functional MRI reveals expert-novice differences during sport-related anticipation. *NeuroReport, 21*(2), 94–98. https://doi.org/10.1097/WNR.0b013e328333dff2.
Wu, Y., Zeng, Y., Zhang, L., Wang, S., Wang, D., Tan, X., ... Zhang, J. (2013). The role of visual perception in action anticipation in basketball athletes. *Neuroscience, 237*(5), 29–41.
Xu, Y., & Chun, M. M. (2006). Dissociable neural mechanisms supporting visual short-term memory for objects. *Nature, 440*(7080), 91–95. https://doi.org/10.1038/nature04262.
Yan, C. G., Wang, X. D., Zuo, X. N., & Zang, Y. F. (2016). DPABI: Data processing & analysis for (resting-state) brain imaging. *Neuroinformatics, 14*(3), 339–351.
Yang, J. (2015). The influence of motor expertise on the brain activity of motor task performance: A meta-analysis of functional magnetic resonance imaging studies. *Cognitive, Affective & Behavioral Neuroscience, 15*(2), 381–394. https://doi.org/10.3758/s13415-014-0329-0.