Visuo-Attentional and Sensorimotor Alpha Rhythms are Related to Visuo-Motor Performance in Athletes

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Abstract: This study tested the two following hypotheses: (i) compared with non-athletes, elite athletes are characterized by a reduced cortical activation during the preparation of precise visuo-motor performance; (ii) in elite athletes, an optimal visuo-motor performance is related to a low cortical activation. To this aim, electroencephalographic (EEG; 56 channels; Be Plus EB-Neuro) data were recorded in 18 right-handed elite air pistol shooters and 10 right-handed non-athletes. All subjects performed 120 shots. The EEG data were spatially enhanced by surface Laplacian estimation. With reference to a baseline period, power decrease/increase of alpha rhythms during the preshot period indexed the cortical activation/deactivation (event-related desynchronization/synchronization, ERD/ERS). Regarding the hypothesis (i), low- (about 8–10 Hz) and high-frequency (about 10–12 Hz) alpha ERD was lower in amplitude in the elite athletes than in the non-athletes over the whole scalp. Regarding the hypothesis (ii), the elite athletes showed high-frequency alpha ERS (about 10–12 Hz) larger in amplitude for high score shots (50%) than for low score shots; this was true in right parietal and left central areas. A control analysis confirmed these results with another indicator of cortical activation (beta ERD, about 20 Hz). The control analysis also showed that the amplitude reduction of alpha ERD for the high compared with low score shots was not observed in the non-athletes. The present findings globally suggest

that in elite athletes (experts), visuo-motor performance is related to a global decrease of cortical activity, as a possible index of spatially selective cortical processes ("neural efficiency"). *Hum Brain Mapp* 30:3527–3540, 2009.   © 2009 Wiley-Liss, Inc.

Key words: EEG; alpha event-related desynchronization/synchronization; elite pistol shooters

INTRODUCTION

"Neural efficiency" hypothesis originates from psychometric tradition [Vernon, 1993] and is considered as a stable, trait-like construct that varies between individuals [Haier et al., 1988; 2004; Rypma et al., 2006]. Previous neuroimaging studies using positron emission tomography (PET), single photon emission computed tomography (SPECT), and functional magnetic resonance imaging (fMRI), have shown that subjects with the highest scores to tests probing intelligent quotient, word fluency, spatial skills, and working memory have weakest fronto-parietal activation during cognitive tasks [Charlot et al., 1992; Haier et al., 1988, 1992, 2004; Parks et al., 1988; Ruff et al., 2003; Rypma and D'Esposito, 1999; Rypma et al., 2002, 2005]. These results support the neural efficiency hypothesis, which postulates a more efficient cortical function in brighter individuals as compared to those with poor performance to test probing cognitive functions. However, the neural efficiency hypothesis has been challenged by other neuroimaging evidence showing that fronto-parietal cortical activation is stronger in subjects with high cognitive performance [Gray et al., 2003; Newman et al., 2003].

To show the physiological mechanism at the basis of the neural efficiency hypothesis, cortical activity has been indexed by an event-related power decrease/increase of resting electroencephalographic (EEG) alpha rhythms in the frequency band 8–12 Hz (alpha event-related desynchronization/synchronization, ERD/ERS). It has been demonstrated that people with high intelligent quotient (IQ) show low-amplitude alpha ERD during several cognitive tasks such as sentence-picture verification test [Neubauer et al., 1995], Posner's letter matching test [Neubauer et al., 1999], forward digit span task [Grabner et al., 2004], attention-switching task [Grabner et al., 2004], working memory task [Grabner et al., 2004], and Stankov's triplet numbers test [Neubauer and Fink, 2003]. The same results were found in subjects highly trained for specific skills ("experts") during the execution of short-term memory tasks: alpha ERD amplitude was lower in experts than in nonexperts [Grabner et al., 2006]. On the whole, these results have indicated a reduced (selective) event-related cortical activation in experts, in line with the neural efficiency hypothesis [Grabner et al., 2004].

In the last years, several lines of evidence have extended the neural efficiency hypothesis to cortical motor systems of experts. Amplitude of fMRI-BOLD activity was lower in professional piano players compared to control subjects during complex finger movements [Krings et al., 2000]. Furthermore, averaged scalp potentials related to the preparation of right voluntary wrist extension (readiness potential, RP) were lower in amplitude over supplementary motor and bilateral sensorimotor areas in elite kendo and gymnastic athletes compared to non-athletes [Kita et al., 2001]. Finally, the RP overlying contralateral sensorimotor area was lower in amplitude in elite rifle and gun shooters compared to amateurs during the preparation of self-paced finger movements [Di Russo et al., 2005; Fattapposta et al., 1996].

Previous evidence have also extended the neural efficiency hypothesis to cortical visual systems of professionals. Compared to amateur rifle shooters, professionals showed a greater increase of occipital alpha power during the period preceding the shooting [Haufler et al., 2000; Janelle et al., 2000]. Furthermore, it has been shown that occipital alpha power increased during the phases preceding the best shots and decreased during the phases preceding the worst shots in expert pistol shooters [Loze et al., 2001].

In the last 15 years, many EEG studies of skilled psycho-motor performance in sport have used the expert-novice paradigm to examine spectral differences and intrasubject variability in the EEG pattern related to performance outcome [for review see Hatfield et al., 2004]. EEG and event-related potential measurements of athletic performers have featured prominently in shaping the concepts of the neuro-cognitive aspects of skilled performance [Hatfield and Hillman, 2001]. Recently, nonlinear analysis was performed in order to characterize visuo-motor expertise and to quantify dimensional complexity of cerebral cortical activity [Hung et al., 2008]. All those findings support the assumption that there is a selective activation of cortical populations during precision visuo-motor performance in experts, which is in agreement with the neural efficiency hypothesis. However, it is still poorly understood whether this is true for both posterior parietal (visuo-attentional) and central (sensorimotor) areas during the preparation of a precise visuo-motor performance. To address this issue, in this present study we tested the hypotheses that (i) compared with non-athletes, elite athletes are characterized by a reduced cortical activation during the preparation of precise visuo-motor performance; (ii) in elite athletes, an optimal visuo-motor performance is related to a low cortical activation. To this aim, EEG data were

recorded in elite athletes (pistol shooters) and non-athletes during the execution of precision shots. EEG data were spatially enhanced by surface Laplacian estimation [Babiloni et al., 1996] and the cortical activation/deactivation was indexed with anticipatory alpha ERD/ERS.

METHODS

Subjects and Ethical Approval

Eighteen (8 women) elite athletes (air pistol shooters) and 10 non-athletes (5 woman) were recruited for this study. The elite air pistol shooters have been regularly competing in national and international tournaments; they also had been practicing pistol shooting for more than 8 years and for at least five times a week. The non-athletes did not ever practice pistol shooting at competitive or amateur level. The mean subjects' age was of 29.2 years (±1.6 standard error, SE; range: 21–45 years) in the elite athletes and 33.1 years (±2.3 SE; range: 22–46 years) in the non-athletes. All subjects were right-handed as measured by Edinburgh Inventory (mean: 71.3% ± 4.8% for the elite athletes and 81.9% ± 5.2% for the non-athletes). Two analyses of variance (ANOVA) using the factor Group (elite athletes, non-athletes) were computed to evaluate the presence or absence of statistically significant differences between the two groups for age and gender. No statistically significant difference was found (age: $P > 0.1$; gender: $P > 0.7$). However, the age and gender values were used as covariates in the subsequent statistical analysis to exclude that small difference in age and gender could influence the subsequent statistical analysis. All subjects gave their informed consent according to the Declaration of Helsinki and were free to withdraw from the study at any time. The procedure was approved by the local Institutional Ethics Committee (I Medical School, University of Rome "Sapienza").

Experimental Procedures

All subjects performed a total of 120 air-pistol shots (intershots interval of about 1 min) in six separate recording blocks (interblocks interval of about 5 min). The subjects were free to relax between two consecutive shots and to shoot when they felt ready. The distance between the shooter and the target was 10 m and the diameter of the target was 6 cm, according to the international shooting competition rule (http://www.issf-shooting.org/rules/english/2006/25_pistol_2005_2nd.html). The shooting score was automatically recorded for each event with Electronic Scoring Targets (EST), and simultaneously with an optical shooting simulator unit (SCATT company, Russia), which permitted to record the trajectories of the pistol on the target during the pointing phases. Furthermore, a device based on acoustic technologies (cardio microphone and powerlab© 16/30, Adinstruments, Australia) was
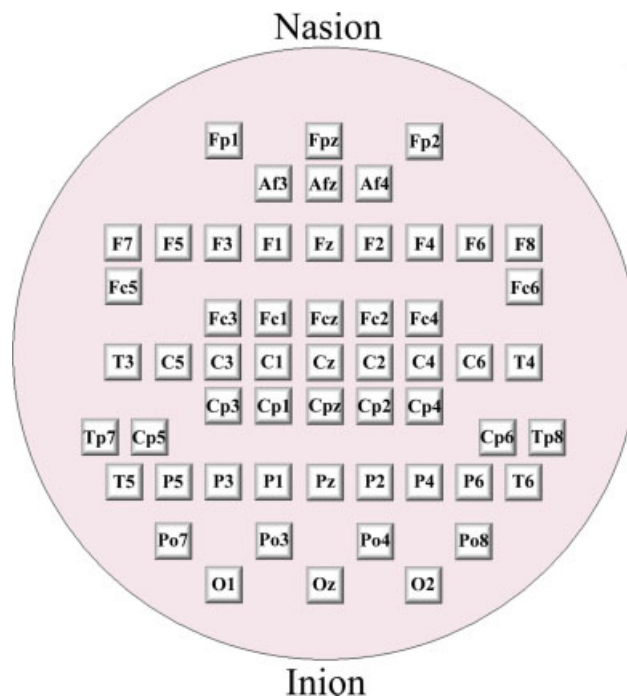

Figure 1.

Electroencephalographic (EEG) electrode montage. [Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.]

used to define the shooting time with a resolution of 1 ms and use it as a reference time for EEG data processing.

EEG Recordings

The EEG data were continuously recorded (bandpass: 0.01–100 Hz, sampling rate: 512 Hz; EB-Neuro Be-plus©, Firenze, Italy) from 56 scalp electrodes (cap) positioned over the whole scalp according to a 10–10 system (see Fig. 1). The electrical reference was located between the AFz and Fz electrodes, and the ground electrode was located between the Pz and Oz electrodes. The electrode impedance was kept below 5 kΩ. Simultaneously, bipolar electro-oculographic data were recorded to monitor blinking and eye movements (EOG; bandpass: 0.1–100 Hz; sampling rate: 512 Hz).

Preliminary Data Analysis

The EEG and EOG data were segmented into single trials of 10 s duration, each trial lasting from −6 s to +4 s with respect to the reference time (i.e. the instant when the shot was released).

Data epochs showing instrumental, ocular, and muscular artifacts were identified and automatically eliminated by a computerized procedure using EEG and EOG signals as input [Moretti et al., 2003]. The EEG data affected by ocular artifacts were corrected with an autoregressive

method [Moretti et al., 2003]. Finally, two expert electroencephalographists (C.D.P. and N.M.) manually confirmed the automatic selection and correction of the EEG single trials, with special attention to residual contaminations of the EEG epochs due to eye movements and blinking. Therefore, only the EEG single trials totally free from artifacts were considered for the subsequent analyses.

The spatial information of the artifact-free EEG epochs was enhanced by surface Laplacian estimation (regularized 3D spline function; Babiloni et al., 1996, 1998]. Indeed, surface Laplacian estimation acts as a spatial filter of EEG potential distribution that reduces head volume conductor effects and eliminates electrode reference influence [Babiloni et al., 1996; Nunez, 1995]. The Laplacian-transformed EEG epochs showing computational artifacts were manually discarded by the mentioned electroencephalographists. On average, the artifact-free Laplacian-transformed EEG data were formed by 93.3 single trials (±3 SE) for the elite athletes and 95.4 single trials (±3 SE) for the non-athletes. Of note, an ANOVA using the factor Group (elite athletes, non-athletes) served to compare the amount of artifact-free EEG single trials between the two groups. No statistically significant difference was found ($P > 0.6$).

For each elite athlete, artifact-free Laplacian-transformed EEG single trials were associated with the corresponding shot scores and were divided in two groups: the "high performance" group included the 50% of the (artifact-free Laplacian-transformed) EEG single trials associated with higher score shots, whereas the "low performance" group included the 50% of the (artifact-free Laplacian-transformed) EEG single trials associated with lower score shots.

Frequency Analysis of Alpha Rhythms

Power spectrum analysis of the artifact-free Laplacian-transformed EEG data was based on FFT approach using Welch technique and Hanning windowing function (1 Hz frequency resolution). To identify the alpha subbands, the individual alpha frequency (IAF) peak was identified according to the literature guidelines [Klimesch 1996, 1999; Klimesch et al., 1998]. The IAF is defined as the frequency that shows the maximum power within the band 6–13 Hz in the EEG spectrum. The alpha subbands of interest were defined with respect to the IAF as follows: the low-frequency alpha band was included between IAF-2 Hz and IAF, whereas the high-frequency alpha band was included between IAF and IAF +2 Hz. The mean IAF value was 9.9 Hz (±0.3 SE) for the elite athletes and 10.5 Hz (±0.3 SE) for the non-athletes. There was no significant intergroup difference in the IAF peak as evaluated by an ANOVA ($P > 0.1$). However, the IAF peak was used as a covariate (together with age and gender) for further statistics on EEG data to control for the effect of IAF on the EEG comparisons.

Event-Related Desynchronization/ Synchronization

To quantify the event-related changes of alpha EEG power, we calculated the alpha ERD/ERS [Pfurtscheller and Aranibar, 1979; Pfurtscheller and Neuper, 1994; Pfurtscheller et al., 1997]. The ERD/ERS of the individual low- and high-frequency alpha bands was computed as follows: Laplacian EEG time series were pass-banded (Bartlett function), squared, averaged across 120 ms periods (8 samples/s), and averaged again across all single trials. The alpha ERD/ERS was defined as the percentage decrement/increment in the instant power density during a given preshot period as compared to the instant power density during the baseline period. The formula was the following:

$$\frac{\text{preshot} - \text{baseline}}{\text{baseline}} \times 100$$

Three preshot periods were considered: T1 is the period from −3 s to −2 s and T2 is the period from −2 s to −1 s, both with respect to the reference time, whereas T3 is the period from −1 s to the reference time. The baseline period is defined as the period from −5 s to −4 s prior to the shot.

For the ERD/ERS analysis, the baseline was defined as the period from −5 s to −4 s prior to the shot, because the time periods preceding −5 s were characterized by body movements including small adjustments of head–trunk and respiration; these movements induced clear EEG artifacts incompatible with a reliable data analysis. Furthermore, three preshot event periods were considered. With respect to the zerotime (shot onset), T1 ranged from −3 s to −2, T2 from −2 s to −1 s, and T3 from −1 s to 0. The event periods were selected before the task shot, to complement and extend previous studies carried out selecting event periods before the performance with rifle, pistol, and archery [Doppelmayr et al., 2008; Hatfield et al., 1984, 2004; Haufler et al., 2000; Hilmann et al., 2000; Janelle et al., 2000; Kerick et al., 2001; Loze et al., 2001]. Another reason was that shot execution period lasts just few milliseconds and is typically followed by large movements of the head, trunk, and arm. This would have provoked a large amount of EEG artifacts.

Topographic Mapping of the Alpha and Beta ERD/ERS Percentage

Topographic maps (256 colors) of the ERD/ERS at the two alpha sub-bands were calculated on a 3D cortical model using a spline interpolating function [Babiloni et al., 1996]. This model is based on the magnetic resonance data of 152 subjects digitized at the Brain Imaging Center of the Montreal Neurological Institute (SPM96, www.mni.mcgill.ca) and is commonly considered an acceptable template for the rendering of group neuroimaging data.
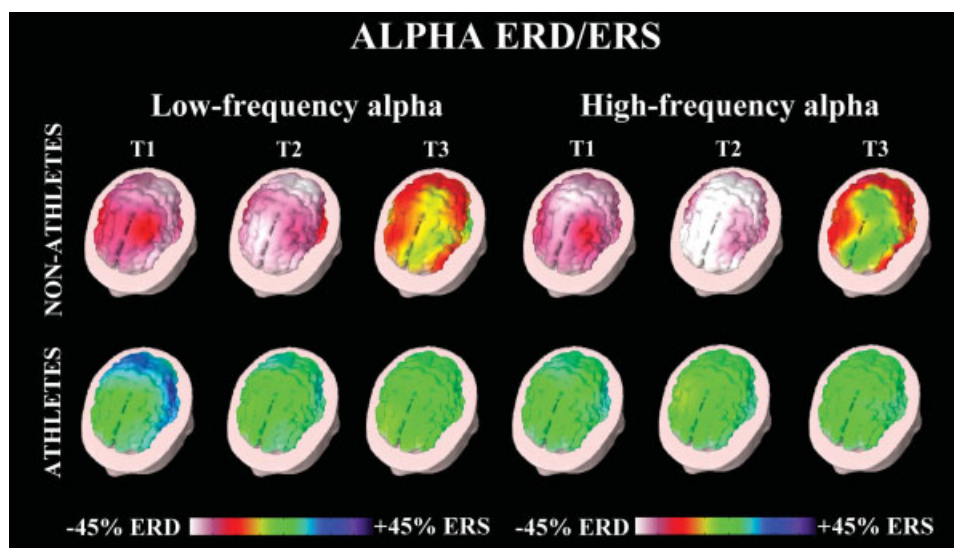
Figure 2.
Topographical distribution of the low- and high-frequency alpha ERD/ERS amplitude in the elite athletes and non-athletes. The alpha ERD/ERS is mapped at three preshot periods: T1 from -3 s to -2 s with respect to zerotime (i.e. zerotime = onset of the shot), T2 from -2 s to -1 s, and T3 from -1 s to zero time. Color scale: maximum ERD and ERS are coded in white and violet, respectively. The maximal (%) value of the ERD/ERS is reported beneath the maps.

Statistical Analysis

Statistical comparisons were performed with ANOVA; Mauchley's test evaluated the sphericity assumption when necessary. Correction of the degrees of freedom was made with the Greenhouse-Geisser procedure, and Duncan's test was used for post-hoc comparisons ($P < 0.05$). In particular, the following three statistical sessions were performed.

In the first session (behavioral data), we tested the control hypothesis that the average shot score of (artifact-free) EEG single trials was higher for the elite athletes compared with the non-athletes. To this aim, we used an ANOVA having the factor Group (elite athletes, non-athletes). Although the shot score differences between the two groups were expected for obvious logical reasons, we performed the statistical analysis to quantify the amount of these differences for illustrative purposes.

In the second session (EEG data), we tested the working hypothesis that the amplitude of alpha ERD (alpha ERS) was lower (higher) in the elite athletes when compared with the non-athletes, in line with the idea of neural efficiency. To this aim, we performed two ANOVA tests (two alpha sub-bands). The ANOVA tests had the amplitude of alpha ERD/ERS as a dependent variable. The ANOVA factors were Group (elite athletes, non-athletes), Time (T1, T2, T3), and Electrode (F3, F4, C3, C4, P3, P4, O1, O2). Subjects' age, gender, and IAF were used as covariates.

In the third session (EEG data), we tested the working hypothesis that in elite athletes, the amplitude of alpha ERD (alpha ERS) was lower (higher) in the high perform-

ance condition than in the low performance condition, in line with the extension of the neural efficiency to the explanation of performance fluctuation in individual experts. To this purpose, we performed two ANOVA tests (two alpha sub-bands). The ANOVA had the amplitude of the alpha ERD/ERS as a dependent variable. The ANOVA factors were Condition (high performance, low performance), Time (T1, T2, T3), and Electrode (F3, F4, C3, C4, P3, P4, O1, O2).

RESULTS

Behavioral Data (Shot Score)

The mean shot score was 9.7 (± 0.1 SE) for the elite athletes and 2.9 (± 0.5 SE) for the non-athletes. As expected, the ANOVA showed a main effect for the factor Group ($F(1,26) = 266.6$; $P < 0.0001$), confirming the control hypothesis of a higher shot score in the elite athletes than in the non-athletes.

Alpha ERD/ERS: Elite Athletes Versus Non-Athletes

For illustrative purpose, Figure 2 shows topographical maps of low- and high-frequency alpha ERD/ERS in the elite athletes and non-athletes during the three preshot periods (T1, T2, T3). The maps of the non-athletes were characterized by an evident alpha ERD over the whole
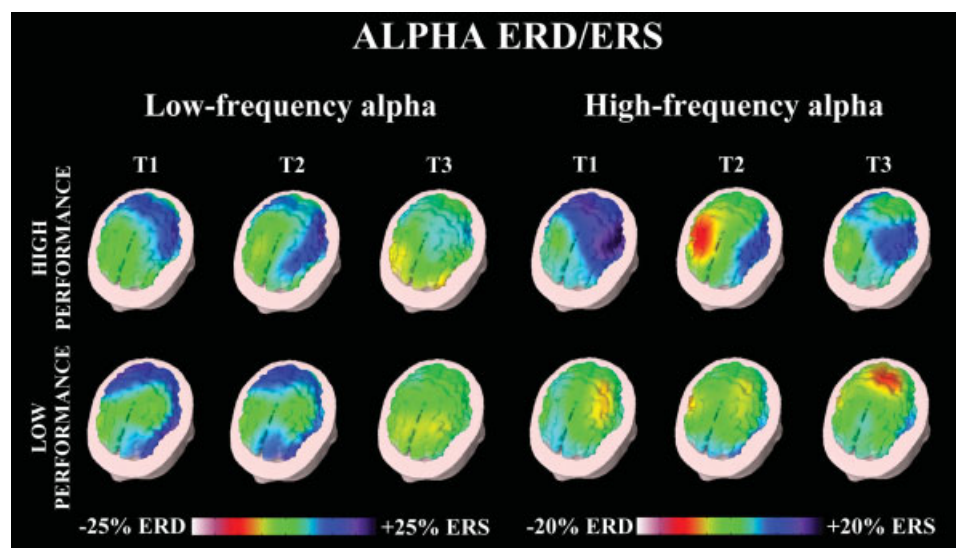
Figure 3.

Topographical distribution of the low- and high-frequency alpha ERD/ERS amplitude for the low performance and high performance conditions in elite athletes. The alpha ERD/ERS are mapped at the three following preshot periods: T1 from −3 s to −2 s with respect to the zerotime (i.e. zerotime = onset of the shot), T2 from −2 s to −1 s, and T3 from −1 s to the zerotime. Color scale: maximum ERD and ERS are coded in white and violet, respectively. The maximal (%) value of the ERD/ERS percentages is reported beneath the maps. [Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.]

scalp. This alpha ERD was stronger during the beginning of the preshot periods (T1, T2) when compared with the last preshot period (T3). Compared with the non-athletes, the elite athletes showed global lower amplitude of the alpha ERD, as a possible index of spatially selective cortical activation (neural efficiency).

The ANOVA of the low- and high-frequency alpha ERD/ERS amplitude showed a main effect for the factor Group (low-frequency: $F(1,23) = 37.6$; $P < 0.0001$; high-frequency: $F(1,23) = 30.3$; $P < 0.0001$), indicating a lower amplitude of the low- and high-frequency alpha ERD for the athletes compared with the non-athletes.

Globally, the present results confirmed the first working hypothesis, namely a lower cortical activation (alpha ERD) in the elite athletes than in the non-athletes, in line with the idea of neural efficiency.

Alpha ERD/ERS: Low-Performance Versus High-Performance

For illustrative purpose, Figure 3 shows the topographical maps of low- and high-frequency alpha ERD/ERS for the high performance and low performance conditions in the elite athletes, during the three preshot periods (T1, T2, T3). For the high performance condition, the low-frequency alpha ERD/ERS pointed to a clear ERS in left frontal (T2), left central (T1, T2), and bilateral parietoccipital areas (time T1, T2), which decreased close to the shot (T3). Furthermore, the maps of high-frequency alpha ERD/ERS

were characterized by a clear ERS in left frontocentral (T1, T2, T3) and bilateral parietoccipital (T1) areas. In parallel, the high-frequency alpha ERD/ERS pointed to a clear ERD in right frontocentral area (T2) and over centroparietal midline (T3). Compared with the maps of the high performance condition, those of the low performance condition showed negligible differences in amplitude of the low-frequency alpha ERD/ERS.

The ANOVA of the low-frequency alpha ERD/ERS amplitude showed no statistically significant difference ($P > 0.1$). Conversely, the ANOVA for the high-frequency alpha ERD/ERS highlighted a statistically significant interaction ($F(7,119) = 3.02$; $P < 0.006$) between the factors Condition (high performance, low performance) and Electrode (F3, F4, C3, C4, P3, P4, O1, O2). Duncan post-hoc testing indicated that when compared with the low performance condition, the high performance condition showed a higher amplitude of the high-frequency alpha ERS at C3 ($P = 0.005$) and P4 ($P = 0.001$) electrodes (see Fig. 4). The present results confirmed the second working hypothesis, namely the hypothesis of a lower cortical activation in the high performance condition than in the low performance condition in the elite athletes.

Table I summarizes the abovementioned results.

Control Analyses

As mentioned earlier, the low- and high-frequency alpha ERD were lower in amplitude in the elite athletes than in
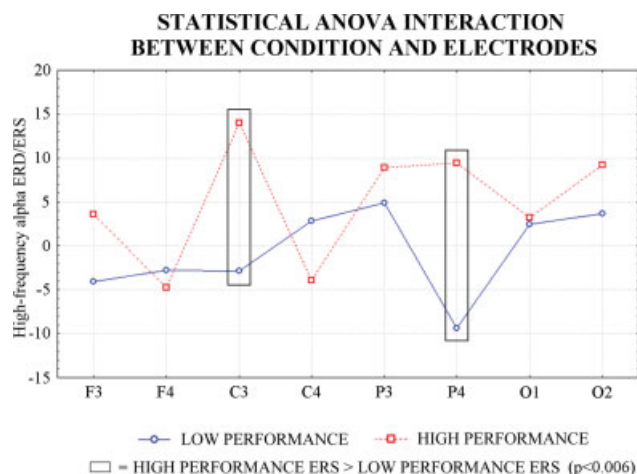
Figure 4.

Mean values of the high-frequency alpha ERD/ERS amplitude illustrating a statistical ANOVA interaction between the factors Condition (low performance, high performance) and Electrode (F3, F4, C3, C4, P3, P4, O1, O2). The rectangles indicate the electrode sites at which alpha ERD/ERS presented statistically significant differences between conditions (Duncan post hoc testing, $P < 0.05$). [Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.]

the non-athletes over the whole scalp. Furthermore, the high-frequency alpha ERS in the elite athletes had larger amplitudes for the high score shots (50%) than for the low score shots at P4 and C3 electrodes. A first control analysis was performed to evaluate whether the amplitude of alpha ERD (alpha ERS) was lower (higher) in the high performance than in the low performance condition in the non-athletes. The control hypothesis was that in the non-

athletes, one cannot observe the reduction of alpha ERD for the high compared with low score shots reported in the athletes. To address this issue, we analyzed the alpha ERD/ERS in high and low performance condition in the non-athletes following the same procedure used in the elite athletes. For illustrative purposes, Figure 5 shows the topographical maps of low- and high-frequency alpha ERD/ERS for the high performance and low performance conditions in the elite athletes, during the three preshot periods (T1, T2, T3). All maps were characterized by an evident alpha ERD over the whole scalp. The maps did not show differences between the high performance and low performance conditions in the athletes. Finally, we performed two ANOVAs, namely one ANOVA for each alpha sub-band. The ANOVAs had the amplitude of the alpha ERD/ERS as a dependent variable. The ANOVA factors were Condition (high performance, low performance), Time (T1, T2, T3), and Electrode (F3, F4, C3, C4, P3, P4, O1, O2). The results showed no statistically significant differences ($P > 0.3$). These results globally indicate that in the non-athletes, the amplitude of alpha ERD was similar between the high score shots and low score shots, thus showing no effect of neural efficiency in the non athletes.

A second control analysis was performed to focus on the difference of high-frequency alpha ERD between the high performance and low performance conditions in occipital areas of the elite athletes, in line with previous evidence [Loze et al., 2001]. To this purpose, we performed a new ANOVA having the alpha ERD/ERS amplitude as a dependent variable. The ANOVA within-factors were Condition (high performance, low performance), Time (T1, T2, T3), and Electrode (O1, O2). The ANOVA highlighted a statistically significant interaction ($F(2,34) = 5.51$; $P < 0.009$) between the factors Condition (high performance, low performance), Time (T1, T2, T3), and Electrode (O1,

TABLE I. Summary of the statistical results

Design	Factors (covariates)	Statistically significant results
Behavioral data: to test the control hypothesis that the average shot score of EEG single trials was higher in the elite athletes than in the non-athletes	*Factors:* Group (elite athletes, non-athletes)	Main effect for the factor Group ($F(1,26) = 266.6$; $P < 0.0001$)
EEG data: to test the working hypothesis that the amplitude of high- and low-frequency alpha ERD (alpha ERS) was lower (higher) in the elite athletes than in the non-athletes, in line with the idea of neural efficiency	*Factors:* Group (elite athletes, non-athletes), Time (T1, T2, T3), and Electrode (F3,F4, C3, C4, P3, P4, O1, O2) *Covariates:* Age, gender, and IAF	*Low-frequency alpha:* main effect for the factor Group ($F(1,23) = 37.6$; $P < 0.0001$) *High-frequency alpha:* main effect for the factor Group ($F(1,23) = 30.3$; p<0.0001)
EEG data: to test the working hypothesis that in elite athletes the amplitude of high-and low-frequency alpha ERD (alpha ERS) was lower (higher) in the high performance than in the low performance	*Factors:* Condition (high performance, low performance), Time (T1, T2, T3), and Electrode (F3, F4, C3, C4, P3, P4, O1, O2)	*Low-frequency alpha:* none *High-frequency alpha:* statistically significant interaction between the factors Condition and Electrode ($F(7,119) = 3.02$; $P < 0.006$)

Statistical comparisons were performed by ANOVA. Mauchley's test evaluated the sphericity assumption when necessary. Correction of the degrees of freedom was made with the Greenhouse-Geisser procedure. Duncan's test was used for post-hoc comparisons ($P < 0.05$).
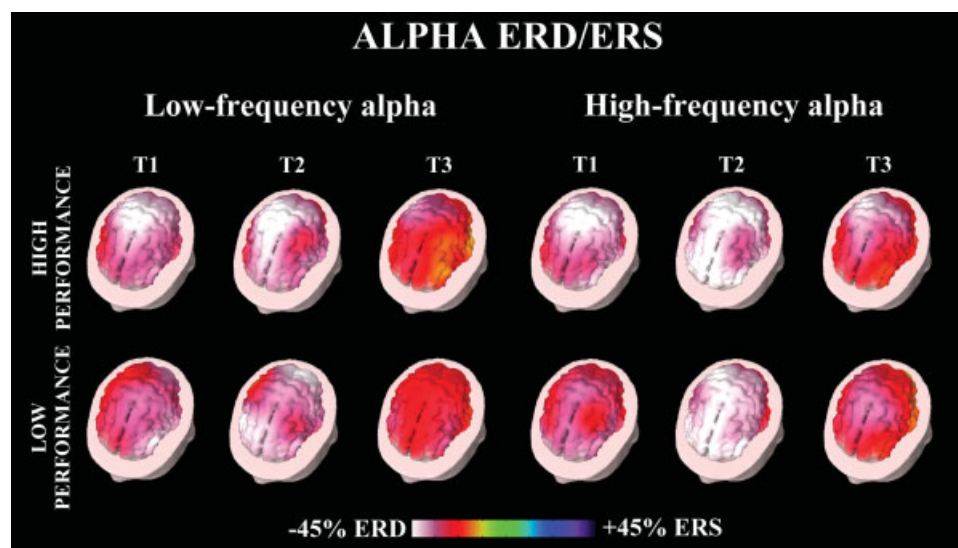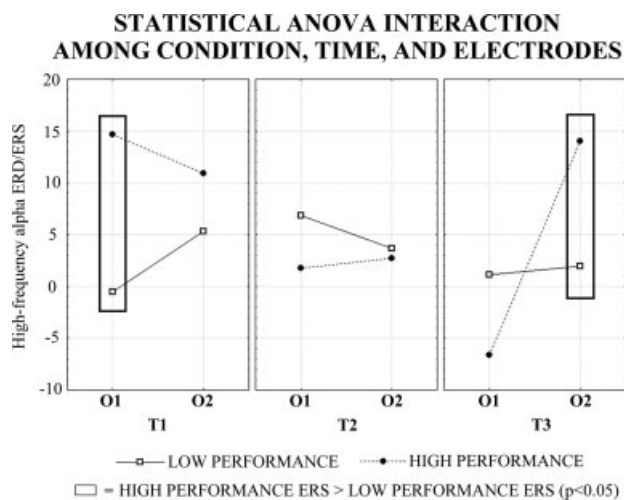
Figure 5.

Topographical distribution of the low- and high-frequency alpha ERD/ERS amplitude for the low performance and high performance conditions in the non-athletes. The alpha ERD/ERS is mapped at the three following preshot periods: T1 from -3 s to -2 s with respect to the zero time (i.e. zero time = onset of the shot), T2 from -2 s to -1 s, and T3 from -1 s to the zerotime. Color scale: maximum ERD and ERS are coded in white and violet, respectively. The maximal (%) value of the ERD/ERS percentages is reported beneath the maps. [Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.]

O2). Duncan post-hoc testing indicated that compared to the low performance condition, the high performance condition showed a larger amplitude in the high-frequency alpha ERS at O1 ($P = 0.005$; T1) and O2 ($P = 0.02$; T3) electrodes (see Fig. 6). These results confirmed the neural efficiency hypothesis in occipital areas, in agreement with previous evidence in shooters [Loze et al., 2001].

A third control analysis was performed to evaluate whether the above mentioned alpha ERD/ERS differences were confirmed using regions of interest (ROIs) instead of single representative electrodes. To this purpose, we considered the following eight ROIs: left frontal (FL; F5, F3 and F1 electrodes), right frontal (FR; F6, F4 and F2 electrodes), left central (CL; C5, C3 and C1 electrodes), right central (CR; C6, C4 and C2 electrodes), left parietal (PL; P5, P3 and P1 electrodes), right parietal (PR; P6, P4 and P2 electrodes), left parieto-occipital (POL; PO3 and O1 electrodes), and right parieto-occipital (POR; PO4, O2). The alpha ERD/ERS amplitude of each ROI was defined as the average of the alpha ERD/ERS across all electrodes included in the ROI. Three ANOVAs were performed. The alpha ERD/ERS amplitude at ROI level was the dependent variable. The first and second ANOVAs tested whether the amplitude of low- and high-frequency alpha ERD was lower in the elite athletes when compared to the non-athletes. The ANOVA within-factors were Group (elite athletes, non-athletes), Time (T1, T2, T3), and ROI (FL, FR,

Figure 6.

Mean values of the high-frequency alpha ERD/ERS amplitude illustrating a statistical ANOVA interaction between the factors Condition (low performance, high performance), Time (T1, T2, T3), and Electrode (O1, O2). The rectangles indicate the electrode sites at which alpha ERD/ERS presented statistically significant differences between conditions (Duncan post hoc testing, $P < 0.05$).

STATISTICAL ANOVA INTERACTION BETWEEN CONDITION AND ROIs
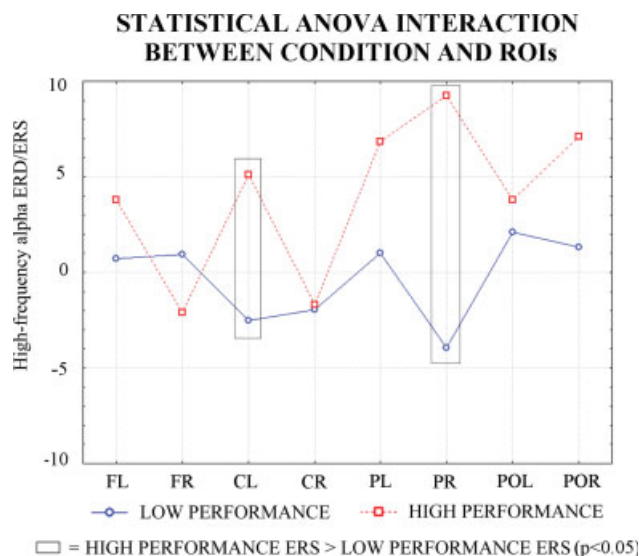
Figure 7.
Mean values of the high-frequency alpha ERD/ERS amplitude illustrating a statistical ANOVA interaction between the factors Condition (low performance, high performance) and ROI (FL, FR, PL, C3, PL, PR, OL, OR). The rectangles indicate the ROIs where alpha ERD/ERS presented statistically significant differences between conditions (Duncan post hoc testing, $P < 0.05$). [Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.]

PL, C3, PL, PR, OL, OR). Subjects' age, gender, and IAF were used as covariates. Both ANOVAs showed a main effect for the factor Group (low-frequency alpha: $F(1,23) = 40.7$; $P < 0.0001$; high-frequency alpha: $F(1,23) = 41.6$; $P < 0.0001$), indicating a lower amplitude of the low- and high-frequency alpha ERD in the athletes than in the non-athletes. The third ANOVA tested whether the amplitude of high-frequency alpha ERD in the elite athletes was lower in the high performance condition than in the low performance condition. The ANOVA within-factors were Condition (high performance, low performance), Time (T1, T2, T3), and ROI (FL, FR, PL, C3, PL, PR, OL, OR). The ANOVA highlighted a statistically significant interaction ($F(7,119) = 2.29$; $P < 0.03$) between the factors Condition and ROI. Duncan post-hoc testing indicated that compared to the low performance condition, the high performance condition showed a higher amplitude of the high-frequency alpha ERS at CL ($P = 0.05$) and PR ($P = 0.006$; Fig. 7). Therefore, the present results confirmed those obtained with single representative electrodes.

A fourth control analysis evaluated alpha ERD/ERS values averaged across all 56 electrodes, as a global index of cortical activity. To this purpose, three ANOVAs were performed. The first and second ANOVAs tested whether the amplitude of global low- and high-frequency alpha ERD was lower in the elite athletes when compared to the non-athletes. The ANOVA within-factors were Group (elite

athletes, non-athletes) and Time (T1, T2, T3). Subjects' age, gender, and IAF were used as covariates. Both ANOVAs showed a main effect for the factor Group (low-frequency alpha: $F(1,23) = 36.7$; $P < 0.0001$; high-frequency alpha: $F(1,23) = 39.1$; $P < 0.0001$), indicating a lower amplitude of the global low- and high-frequency alpha ERD in the athletes than in the non-athletes. The third ANOVA tested whether the amplitude of global high-frequency alpha ERD in the elite athletes was lower in the high performance condition than in the low performance condition. The ANOVA within-factors were Condition (high performance, low performance) and Time (T1, T2, T3). The ANOVA showed no statistically significant difference ($P > 0.1$). These results support the idea of a lower global cortical activity in the elite athletes when compared to non-athletes, in line with the neural efficiency hypothesis.

Because sensorimotor cortical activity is revealed not only by alpha ERD but also by beta ERD, one might argue that the present results should be confirmed by a parallel analysis of beta ERD. In this line, a fifth control analysis was performed to evaluate whether the amplitude of beta ERD was lower in the elite athletes when compared to the non-athletes. For each subject, we identified the individual beta frequency peak (IBF). The IBF is defined as the frequency showing the maximum power density within 14–30 Hz of EEG spectrum. The beta subbands of interest were defined with respect to the IBF as follows: the low-frequency beta band ranged between IBF-2 Hz and IBF, whereas the high-frequency beta band ranged between IBF and IBF +2 Hz. Specifically, the mean IBF value was 20.3 Hz (± 0.6 SE) for the elite athletes and 19.8 Hz (± 0.9 SE) for the non-athletes. We analyzed beta ERD/ERS with the same procedure followed for the analysis of alpha ERD/ERS. For illustrative purpose, Figure 8 shows topographical maps of low- and high-frequency beta ERD/ERS for the elite athletes and non-athletes during the three preshot periods of interest (T1, T2, T3). The maps of the non-athletes were characterized by an evident beta ERD over the whole scalp. Such beta ERD was stronger during the beginning of the preshot periods (T1, T2) compared to the last preshot period (T3). Compared to the non-athletes, the elite athletes globally showed lower amplitude of the beta ERD, as a possible index of spatially selective cortical activation (neural efficiency). Finally, we performed two ANOVAs (low- and high-frequency beta sub-bands). The ANOVAs had the amplitude of beta ERD/ERS as a dependent variable. The ANOVA factors were Group (elite athletes, non-athletes), Time (T1, T2, T3), and Electrode (F3, F4, C3, C4, P3, P4, O1, O2). Subjects' age, gender, and IBF were used as covariates. The ANOVA of the low- and high-frequency beta ERD/ERS amplitude showed a main effect for the factor Group (low-frequency: $F(1,23) = 14.7$; $P < 0.0008$; high-frequency: $F(1,23) = 19.9$; $P < 0.0002$), indicating a lower amplitude of the low- and high-frequency beta ERD in the athletes than in the non-athletes over the whole scalp. The present results on beta ERD globally confirmed those of the main analysis on alpha ERD.
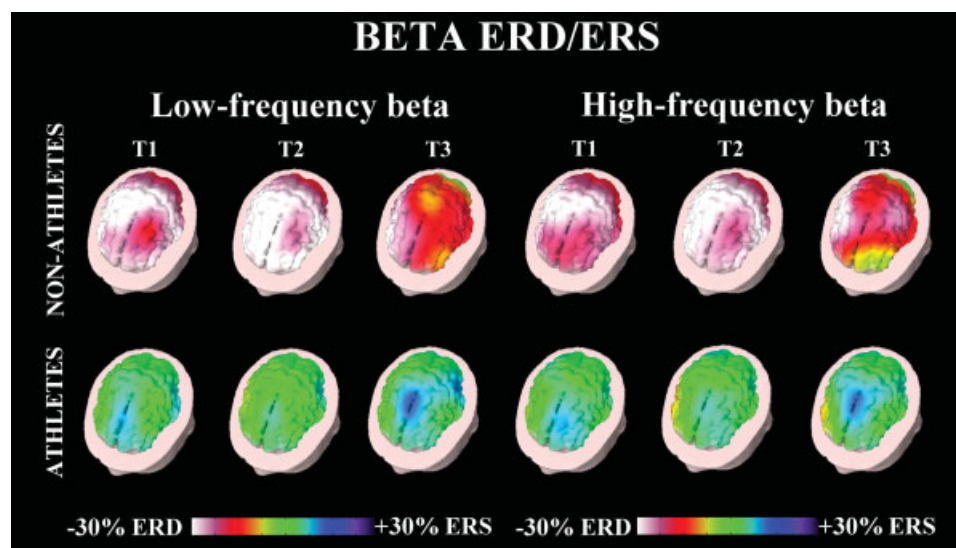
Figure 8.

Topographical distribution of the low- and high-frequency beta ERD/ERS amplitude in the elite athletes and non-athletes. The beta ERD/ERS is mapped at the three preshot periods of interest: T1 from −3 s to −2 s with respect to zero time (i.e. zero time = onset of the shot), T2 from −2 s to −1 s, and T3 from −1 s to zero time. Color scale: maximum ERD and ERS are coded in white and violet, respectively. The maximal (%) value of ERD/ERS is reported beneath the maps. [Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.]

DISCUSSION

Methodological Remarks

In this study, cortical alpha rhythms were modeled by surface Laplacian estimation of highly sampled scalp potentials (i.e., 56 channels), to partially overcome the two main limitations of EEG. The first limitation is that different conductivities of cortex, dura mater, skull, and scalp artificially enhance the low spatial components of scalp EEG distribution, the so called spatial blurring of scalp potentials [Gevins, 1989; Nunez, 1990]. The second limitation is that electrical reference affects the voltage of scalp EEG distribution [Nunez, 1981]. Surface Laplacian acts as a spatial filter that removes both the low spatial components of potential distribution and the influence of electrode reference [Babiloni et al., 1996]. Practically, it results in a sort of "spatial deblurring" of scalp potential distribution. Compared to more advanced techniques for EEG source estimation (i.e. equivalent current dipole, linear inverse estimation, beamformers), surface Laplacian requires neither a priori assumptions on EEG sources (shape, number, extension, etc.) nor hypotheses on the linear versus nonlinear relationship between these sources and scalp potentials. In previous EEG studies, surface Laplacian estimation has been useful to investigate cortical alpha rhythms related to somatosensory, motor, and cognitive events [Babiloni et al., 2002, 2003, 2004, 2006, 2008; Del Percio et al., 2006, 2007, 2008]. As an important limitation, surface Laplacian estimation cannot resolve fine details of event-related cortical activity when compared to PET or fMRI. Indeed, surface Laplacian estimation roughly determines topographical details of cortical sources of EEG data [Babiloni et al., 1996]. For example, surface Laplacian estimates at C3 electrode overlie left hand region of primary sensorimotor cortex but might be partially affected by EEG activity generated from left premotor cortex. Finally, it should be remarked that the present EEG spatial sampling (56 electrodes) was higher than all previous field studies [Doppelmayr et al., 2008; Hatfield et al., 1984, 2004; Haufler et al., 2000; Hilmann et al., 2000; Janelle et al., 2000; Kerick et al., 2001; Loze et al., 2001].

Alpha ERD/ERS Fits the Neural Efficiency Hypothesis

In line with the neural efficiency hypothesis in experts, we tested the hypothesis that compared with non-athletes, elite athletes (air pistol shooters) are characterized by a reduced cortical activation (alpha ERD) during the preparation of a precise visuo-motor performance (pistol shot). Furthermore, we predicted that in elite athletes, an optimal visuo-motor performance is related to a low cortical activation. The event-related reduction of cortical activation was indexed by surface Laplacian estimation of EEG data, namely the decrease of alpha ERD and/or the increase of alpha ERS. Of note, it is worth mentioning that we did not include a comparison of alpha ERD/ERS in elite pistol shooters versus control subjects engaged in simple generic

finger movements, because the neural efficiency hypothesis in those conditions has been thoroughly confirmed in previous studies [Del Percio et al., 2008; Di Russo et al., 2005; Fattapposta et al., 1996; Kita et al., 2001].

Concerning the first working hypothesis, we showed that the amplitude of low- (about 8–10 Hz) and high-frequency (about 10–12 Hz) alpha ERD was lower in the elite athletes than in the non-athletes over the whole scalp. These results suggest that the preparation of visuo-motor performance is related to a lower alpha ERD in elite athletes than non-athletes, as a possible index of spatially selective cortical activation (neural efficiency). This conclusion was corroborated by a control analysis showing that the alpha ERD/ERS results were confirmed by another well known index of sensorimotor cortical activation, namely the beta ERD/ERS.

The present results indicate that alpha (beta) rhythms might represent one of the physiological mechanisms at the basis of neural efficiency during the preparation of visuo-motor performance. These rhythms reflect the functional modes of thalamo-cortical and cortico-cortical loops that facilitate/inhibit the transmission and retrieval of both sensorimotor and cognitive information into the brain [Brunia, 1999; Deeny et al., 2003; Pfurtscheller and Lopes da Silva, 1999; Steriade and Llinas, 1988]. The functional meaning of low- and high-frequency alpha rhythms is supposed to be different. On one hand, low-frequency alpha rhythms would subserve subject's global attentive readiness. On the other hand, high-frequency alpha rhythms would reflect the task-related oscillation of specific neural systems for the elaboration of sensorimotor or semantic information [Klimesch, 1996, 1999; Klimesch et al., 1998]. In this sense, the present results hint that compared with the brain of non-athletes, the brain of elite athletes requires a quite selective engagement of thalamo-cortical and cortico-cortical loops for an optimal visuo-motor performance. It can be speculated that such modulation of alpha rhythms might support both global attentional (low-frequency alpha rhythms) and task specific (high-frequency alpha rhythms) processes [Klimesch, 1996, 1999; Klimesch et al., 1998]. This might be the same mechanism at the basis of a well known phenomenon observable in healthy subjects: the progressive reduction of event-related cortical activity along learning phases. In this vein, it has been shown that training induces a decrease of activity in motor cortex from pre- to post-training phase during motor tasks [Haufler et al., 2000; Jäncke et al., 2006; Koeneke et al., 2006]. Furthermore, trained motor tasks have been found to be performed with a suppression of cognitive processes [Kerick et al., 2001, 2004].

The present results complement previous EEG findings showing that the amplitude of sensorimotor cortical activity was lower in elite athletes (kendoists, gymnasts, shooters) than in non-athletes performing voluntary right finger movements [Del Percio et al., 2008; Di Russo et al., 2005; Kita et al., 2001]. Furthermore, the present results are in agreement with previous EEG evidence of a reduced amplitude cortical activity in brighter people engaged in cognitive tasks such as stimulus encoding, working memory, and memory retrieval processes [Grabner et al., 2004, 2006; Neubauer and Fink, 2003; Neubauer et al., 1995, 1999].

Concerning the second working hypothesis, athletes' high-frequency anticipatory alpha ERS (about 10–12 Hz) had larger amplitude for high performance than for low performance shots at right posterior parietal (P4) and left central (C3) electrodes. On the contrary, the amplitude of alpha ERD was similar between the high and low score shots in the non-athletes. These results suggest that a sort of neural efficiency in right posterior parietal and left central areas may explain, at least in part, the fluctuation of high and low visuo-motor performances in athletes engaged in task repetition. According to previous evidence [Klimesch, 1996, 1999; Klimesch et al., 1998], it can be speculated that the present high-frequency alpha ERD/ERS reflects task-specific processes in right posterior parietal cortex, which is a crucial region for upright standing, visuo-spatial information processing, and spatial attention to visual targets [Corbetta et al., 2005; Del Percio et al., 2007; Driver and Vuilleumier, 2001; Vallar et al., 1988]. The same may be true for high-frequency alpha ERD/ERS in the hand region of left sensorimotor central cortex, which is dominant for fine and skillful sensorimotor control of right hand in right-handed subjects [Stancàk et al., 2000; Wheaton et al., 2008].

The present results also extend previous evidence supporting the occurrence of greater occipital alpha power before successful shot performance as an indication of neural efficiency [Hatfield and Hilman, 2001; Hatfield et al., 1984, 2004; Haufler et al., 2000; Janelle et al., 2000; Loze et al., 2001].

At the present stage of this research, we cannot predict how much the observed high-frequency alpha ERS is associated with an interaction of excitatory and inhibitory cortical processes. In previous studies, it has been reported an oculo-motor model of alpha rhythms posing that amplitude of alpha oscillations increases during intentional visual behavior, in line with reports of enhanced alpha power in the few seconds prior to a skilled sporting actions or visual tasks [Loze et al., 1999, 2001; Palva and Palva, 2007; Shaw, 1993, 1996; Wertheim, 1974, 1981]. Furthermore, it has been reported that motor behavior learning depends on a context-dependent interaction of both excitatory and inhibitory processes relative to learned motor programs [Hummel et al., 2002]. The suppression of learned motor programs has been associated with an increase of high-frequency alpha power in sensorimotor areas in healthy subjects [Hummel et al., 2002]. In contrast, dystonic patients with deficits of the inhibitory motor control did not show any increase of alpha power during the suppression of learned motor programs [Hummel et al., 2002]. It might be speculated that the increment of alpha power observed in the results of this study might be

representative of a mechanism similar to the one explaining the gradual reduction of event-related cortical activity during learning phases. Specifically, it has been shown that training for a given motor task induces a decreased activity in the motor cortex from pre- to post-training phase [Haufler et al., 2000; Jäncke et al., 2006; Koeneke et al., 2006].

The outcomes of this study show that the high score shots were not related to a modulation of low-frequency alpha ERD/ERS. In general, low-frequency alpha rhythms are supposed to be associated with global brain arousal/subject's attentive readiness and effort. Therefore, the results suggest that these features did not characterize winning shot performances in elite pistol shooters.

In conclusion, the present results showed that that low- and high-frequency alpha ERD was lower in amplitude in the elite athletes than in the non-athletes during the preparation of visuo-motor performance. Furthermore, it was found that in the elite athletes, high-frequency alpha ERS was higher in amplitude with the shots characterized by a high score than those characterized by a low score. This was true in right posterior parietal and left central areas. These results suggest that a good visuo-motor performance is related to relatively low (high) amplitude of alpha ERD (ERS), as a possible index of spatially selective cortical activation. In future studies, cortical alpha rhythms may be trained to produce a low ERD (strong ERS) during the execution of shots, with the aim of improving motor control in subjects suffering from motor deficits. Such training could be performed by alpha neuro-feedback [Hanslmayr et al., 2005] during computer simulation of motor performances (i.e. videogame, virtual reality). After the training, alpha rhythms and motor performance could be measured again.

ACKNOWLEDGMENTS

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