Differential modulation of motor cortex plasticity in skill- and endurance-trained athletes

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Abstract

Purpose Extensive evidence exists that regular physical exercise offers neuroplastic benefits to the brain. In this study, exercise-specific effects on motor cortex plasticity were compared between 15 skilled and 15 endurance trained athletes and 8 controls.

Methods Plasticity was tested with a paired associative stimulation (PAS) protocol. PAS is a non-invasive stimulation method developed to induce bidirectional changes in the excitability of the cortical projections to the target muscles. Motor cortex excitability was assessed by motor-evoked potentials (MEPs) in the task-relevant soleus muscle, elicited with transcranial magnetic stimulation, before and following PAS. To test for changes at the spinal level, soleus short latency stretch reflexes (SLSR) were elicited before and after PAS.

Results PAS induced a significant (76 ± 83 %) increase in MEP amplitude in the skill group, without significant changes in the endurance (-7 ± 35 %) or control groups (21 ± 30 %). Baseline MEP/post MEP ratio was significantly different between the skill and endurance groups. SLSR remained unchanged after the PAS intervention.

Conclusion The possible reason for differential motor cortex plasticity in skill and endurance groups is likely related to the different training-induced adaptations. The findings of the current study suggest that long-term skill training by skill group induced preferable adaptations in the task-related areas of the motor cortex because increased plasticity is known to enhance motor learning.

Keywords Physical activity · Training adaptation · Motor cortex · Brain plasticity · Paired associative stimulation

Abbreviations

EMG	Electromyography
LTP	Long-term potentiation
MEP	Motor-evoked potential
MVC	Maximal voluntary contraction
PAS	Paired associative stimulation
RMT	Resting motor threshold
SLSR	Short latency stretch reflex
TMS	Transcranial magnetic stimulation

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Introduction

Regular, mainly endurance type of training has been shown to enhance cognitive and neural plasticity in several brain regions including the cerebellum, hippocampus and cerebral cortex (Kramer and Erickson 2007; Thomas et al. 2012). More recent studies also demonstrate that dance training induces structural and functional benefits to the brain (Coubard et al. 2011; Katiuscia et al. 2009; Kattenstroth et al. 2013). The effect of sport type on motor cortex

plasticity remains unknown. Plasticity in the primary motor cortex might be of special importance, as it is known that this structure is highly involved in the learning of new motor skills (Sanes and Donoghue 2000). Based on training studies that show exercise-specific adaptations of the corticospinal system (Adkins et al. 2006), it is reasonable to hypothesize long-term sports-specific neuroplasticity. For example, following skill training synaptogenesis and reorganization of movement representations within the motor cortex have been reported (Karni et al. 1995; Kleim et al. 1996; Nudo et al. 1996) whereas after endurance training angiogenesis in the motor cortex has been observed without changes in the number of synapses (Kleim et al. 2002). Expansion of movement presentations has been shown to parallel with motor learning (Monfils et al. 2005). Furthermore, there was a high inter-individual variability (standard deviation of ± 105 %) in the motor cortex plasticity of the leg area in our previous study (Kumpulainen et al. 2012), where the subjects represented variety of sport back grounds as well as non-athletes. Therefore, the present study was designed to test if primary motor cortex plasticity is different between skill and endurance-trained athletes. Skill training is defined as the acquisition and subsequent refinement of novel movement sequences such as those in dance, gymnastics, and figure skating (Adkins et al. 2006). Conversely, endurance training repeats the same movement sequences aiming to increase the capacity for continued motor output such as in cross-country skiing, running and orienteering (Adkins et al. 2006). Both sport groups involve a high fitness level and the main separating factor is the way lower limb muscles are used; skill athletes learn new coordination patterns continuously and progressively while the coordination pattern of endurance athletes does not change considerably throughout the training years.

Motor cortex plasticity can be tested with paired associative stimulation (PAS), which is a non-invasive stimulation method based on Hebb's law of coincident summation (Ziemann et al. 2008). PAS combines repeatedly electrical stimulation of a peripheral nerve innervating the target muscle followed by transcranial magnetic stimulation (TMS) over the contralateral motor cortex. Depending on the order of these two stimuli, PAS can produce either long-term potentiation (LTP)—or long-term depression—like plasticity in the target synapse. As in animal preparations at cellular level, PAS shows LTP plasticity properties such as rapid onset, associativity, duration, specificity, and NMDA-receptor dependence (Cooke and Bliss 2006; Ziemann et al. 2008). These animal experiments strongly suggest that LTP is one important mechanism of memory and learning (Cooke and Bliss 2006). PAS-induced LTP-like plasticity occurs within the motor cortex (Di Lazzaro et al. 2009). PAS and motor training have been shown to share common neural mechanisms, which suggests that PAS tests functionally relevant neuronal circuits (Jung and Ziemann 2009; Rosenkranz et al. 2007a; Stefan et al. 2006; Ziemann et al. 2004). In addition, association between motor skill learning and PAS-induced LTP-like plasticity has been demonstrated by Frantseva et al. (2008).

In the current study, the PAS intervention was applied to induce LTP-like plasticity in the cortical projections to the soleus muscle as this muscle is a major contributor to force production during the ground contact phase of walking, running and jumping (Ishikawa et al. 2005) and hence a training-relevant muscle for both athlete groups. Motor evoked potentials (MEPs) recorded from soleus muscle before and after PAS was used as an indicator of the possible excitability changes in the cortical projections to soleus muscle. To identify potential changes at the spinal level, soleus short latency stretch reflexes (SLSR) were mechanically elicited and compared between the groups using imposed ankle joint rotations. It was hypothesized that due to the increased synapse number induced by skill training, skill athletes will show a higher degree of plastic changes in the motor cortex when compared to endurance athletes.

Methods

Ethical approval and subjects

Fifteen skill athletes; 12 females and 3 males, 23 ± 4 years, 60 ± 10 kg, 166 ± 7 cm (mean $\pm$ standard deviation) and fifteen endurance athletes; 10 females and 5 males, 26 ± 4 years, 62 ± 8 kg, 172 ± 8 cm, participated in the study. Detailed training background information up to the date of measurements was collected with a specific questionnaire. The skill group had trained skill sports on average 14 ± 4 years, 5 ± 1 times and 8 ± 2 h per week up to the date of measurements. Eleven participants practiced dancing, two gymnastics and two figure skating. The dancers represented a variety of different genres including ballet, jazz and modern dance. Participants in the endurance group had trained endurance sports on average 12 ± 4 years, 7 ± 2 times and 10 ± 2 h per week up to the date of measurements. Eight participants practiced cross-country skiing, four orienteering and three long-distance running. All subjects in the endurance group and ten in the skill group trained for competitions. None of the subjects had any history of neuromuscular or orthopedic diseases and all subjects were naïve to the experiments. Before testing, subjects were informed about the procedures and gave written informed consent. The study was approved by the ethics board from the University and was performed in conformity with the declaration of Helsinki. The participants were asked not to perform any physical activities on measurement day to avoid any possible interference

Fig. 1 a Picture of the measurement setup in the ankle dynamometer. **b** Anterior view of the recording and stimulation electrodes. **c** Posterior view of the recording and stimulation electrodes

with the PAS protocol (Ziemann et al. 2004). In addition, non-athletes from our previous study (Kumpulainen et al. 2012) were treated as a control group in the analysis. From the total of 24 subjects, only non-active were selected; 8 females, 21 ± 1 years, 73 ± 13 kg, 171 ± 8 cm. Members of the control group did not attend any formal training and did physical exercise less than 3 h per week.

Experimental design

During the whole experiment, participants were positioned on a custom-built ankle dynamometer (University of Jyväskylä, Finland) with the hip at 110°, the knee in an extended position at 180°, the ankle at 90° and the right foot resting on a pedal (Fig. 1a). A seat belt restricted movement of the upper body and straps secured the right leg and foot. Hands were resting in the lap during all measurements. After the positioning procedure, the participants performed three maximal isometric plantar flexion actions with a 3 min rest interval between trials. The highest force value was considered as the maximal voluntary contraction (MVC). Transcranial magnetic stimulation (TMS) was used to measure changes in the motor evoked potentials (MEPs) of soleus muscle before and 5 min after the PAS intervention. To test for changes at the spinal level, soleus SLSRs were elicited before the first TMS measurement and right after the last TMS measurement.

Recordings

For electromyography (EMG) measurements pseudomonopolar electrodes (Blue Sensor N, Ag/AgCl, 28 mm^2, Ambu A/S, Ballerup, Denmark) were placed on the right soleus muscle with a reference on the bony surface of the tibia (Fig. 1b, c). Bipolar electrodes (Blue Sensor N, Ag/

AgCl, 28 mm^2, Ambu A/S, Ballerup, Denmark) were also placed on the soleus muscle and a ground electrode (Unilect, Ag/AgCl, Unomedical Ltd., Redditch, UK) was placed on the head of the tibia (Fig. 1b, c). The pseudomonopolar electrode configuration was chosen for MEP recordings as this montage allows larger signals to be recorded (Kumpulainen et al. 2012). The bipolar configuration was chosen for SLSR recordings to minimize the noise generated by the perturbations of the ankle dynamometer. The skin under the electrodes was shaved, abraded and cleaned with alcohol to reduce the resistance below 5 kΩ. EMG signals were amplified (100× for pseudomonopolar and 1,000× for bipolar configuration), band-pass filtered (10–1,000 Hz) and sampled at 5 kHz (Neural Systems NL 900D and NL 844, Digitimer Ltd., Hertfordshire, UK). The EMG activities and the reaction forces from the pedal were collected with Spike2 software (CED, Cambridge, UK) via 16-bit AD converter (CED power 1401, Cambridge Electronics Design Limited, UK) and stored for later analysis. Spike2 was used for all offline analyses.

Procedures

An electrical rectangular pulse with duration of 1 ms was delivered to the posterior tibial nerve using a constant-current stimulator (DS7AH, Digitimer Ltd., Hertfordshire, UK). The optimal site for stimulation was located, where the highest M-wave amplitude at submaximal current was elicited in the soleus muscle. A circular cathode with a pickup area of 77 mm^2 (Unilect short-term ECG Electrodes, Ag/AgCl, Unomedical Ltd., UK) was placed over the tibial nerveon the popliteal fossa and an oval shaped, 5.08 × 10.16 cm, anode (V-trodesneurostimulation electrodes, Mattler Electronics corp., USA) was placed above the patella (Fig. 1b, c).

The latency of the somatosensory-evoked potential elicited from the tibial nervestimuli was measured with conventional electroencephalography needle electrodes inserted into the skin 2 cm behind and 5 cm in front of the vertex. The signals were amplified (100 000), filtered (1–500 Hz) and averaged using the electrical stimulation as a trigger (Neuropack Four Mini, MEB-5304 K, Nihon Kohden, Tokyo Japan). The intensity of the electrical stimulus was set to motor threshold, where minimal intensity induced a visually observable muscle twitch in the soleus-muscle. 200 sweeps were averaged and the occurrence of the first negative peak P32 was quantified.

TMS was delivered using a mono-pulse Magstim 2002 stimulator with a 9-cm double batwing coil (Magstim, Whitland, UK). The optimal stimulus site for soleus muscle was located on average 1-cm lateral and 1-cm posterior to the vertex on the left hemisphere. A custom made coil holder and rubber straps were used to fix the coil firmly on the head. The coil was not removed until the last TMS measurement was performed. The position of the coil was marked on a closely fitted cap worn by the subjects. The cap also protected hair from cold spray (PRF101, Taerosol, Kangasala, Finland), which was used to cool down the coil during the measurements if needed. Resting motor threshold (RMT) was defined as the lowest stimulus intensity to elicit a MEP with a peak-to-peak amplitude of 50 µV in three out of five consecutive trials. Stimulus intensity was set to 120 % of RMT and this intensity was used throughout the experiment. Ten MEPs were elicited in the resting soleus muscle before (baseline) and after PAS (post). During these passive measurements the subjects were asked to perform an attention task, which consisted of silently counting backwards from 200. Before baseline and post MEP recordings, subjects were sitting still for one minute and complete muscle relaxation was continuously monitored with EMG displayed on the screen. In the offline analysis, the root mean square of a 1 s window prior each TMS was calculated to quantify baseline EMG; trials with any activity were excluded and the rest were averaged. Peak-to-peak amplitudes of the resting soleus MEPs were determined and averaged.

PAS consisted of a single electrical stimulation delivered to the tibial nerve at 150 % of motor threshold and a single TMS pulse at 120 % of RMT with an interstimulus interval, that was calculated from the individually determined latencies of somatosensory-evoked potentialplus 18 ms. The optimal interstimulus interval to induce LTP-like plasticity in the soleus muscle has been determined in a previous study (Kumpulainen et al. 2012). A total of 200 pairs of stimuli were applied at a rate of 0.2 Hz. To optimize the PAS effect, subjects were required to perform an attention task consisting of counting the peripheral stimuli applied to the tibial nerve and to produce a slight plantar flexion force

after every 20 stimuli between the sequential stimuli (Stefan et al. 2004).

Soleus SLSRs were elicited with ten perturbations induced by the ankle dynamometer before (baseline) setting the coil on the head and after (post) the last TMS measurement to avoid possible coil movements. Subjects were asked to maintain 20 % of their maximal plantar flexion force while a 6 deg dorsiflexion perturbation was delivered every 4–7 s with a velocity of 120 deg/s. The onset of the SLSR was visually determined from ten ensemble-averaged and rectified EMG traces. Root mean square of a 20 ms window from the SLSR onset was calculated. This value was normalized to the root mean square (100 ms window) of the MVC and then used as an indication of the size of SLSR. The background EMG level during 20 % of MVC was defined as the root mean square in a window placed from 120 to 20 ms prior to the perturbations.

Statistical analysis

Statistical analysis was conducted using IBM SPSS 19.0 (SPSS, Chicago, USA). All variables were found to be normally distributed by Shapiro-Wilk's W tests. Differences between the subject groups for training years, MVC, RMT and baseline MEPs were tested by unpaired t tests. The averaged soleus MEPs were compared with a two-way repeated measures ANOVA with within—subjects factor PAS of two levels (before PAS/after PAS) and between—subjects factor group of three levels (skill/endurance/control). To compare MEP changes between the groups, the post-MEPs were normalized to baseline MEPs and one-way ANOVA with main factor group of three levels (skill/endurance/control) was performed. SLSR responses were analyzed with a two-way repeated measure ANOVA with within-subjects factor PAS of two levels (before PAS/after PAS) and between- subjects factor group of two levels (skill/endurance). Differences in baseline EMG and background EMG before and after PAS were compared with a paired t test. The significance level was set at $P = 0.05$. All data are given as mean ± standard deviation.

Results

There were no differences ($P > 0.05$) between the groups in RMT (skill, 51 ± 10 % stimulator output; endurance, 54 ± 4 % stimulator output; control, 57 ± 11 % stimulator output) or baseline MEPs (skill, 0.47 ± 0.36 mV; endurance, 0.50 ± 0.29 mV; control, 0.36 ± 0.18 mV). There were no differences between the skill and endurance groups in training years (skill, 14 ± 4 years; endurance, 12 ± 4 years) or MVC (skill, 1,250 ± 430 N; endurance, 1,150 ± 280 N).
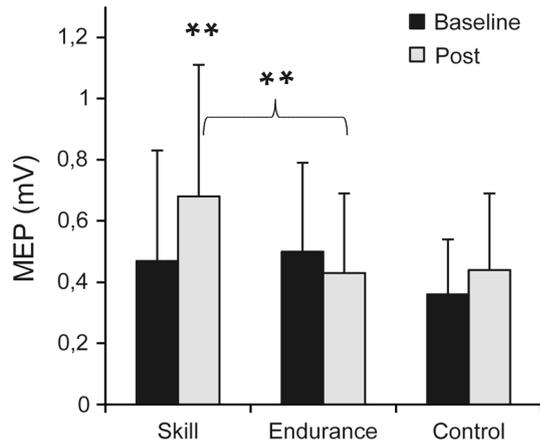
Fig. 2 Mean MEP amplitudes in skill, endurance and control groups before (baseline) and 5 min following PAS (post). The average soleus MEP amplitude increased significantly by 76 % (**$P < 0.01$) in the skill group. The ratio of baseline and post MEPs differed significantly between the skill and endurance groups (**$P < 0.01$)
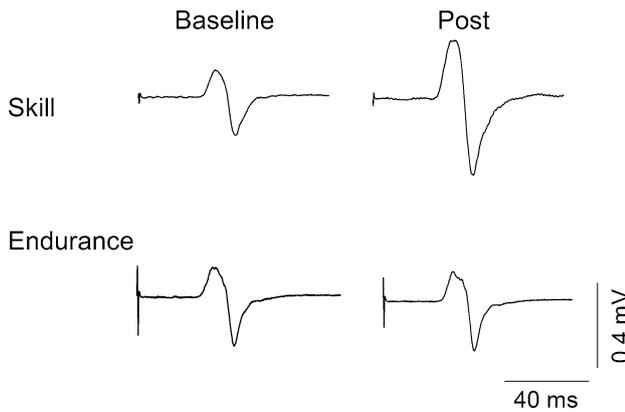

Fig. 3 Traces for one representative skill and endurance subject before (baseline) and after (post) the PAS. Each trace is an average of 10 trials
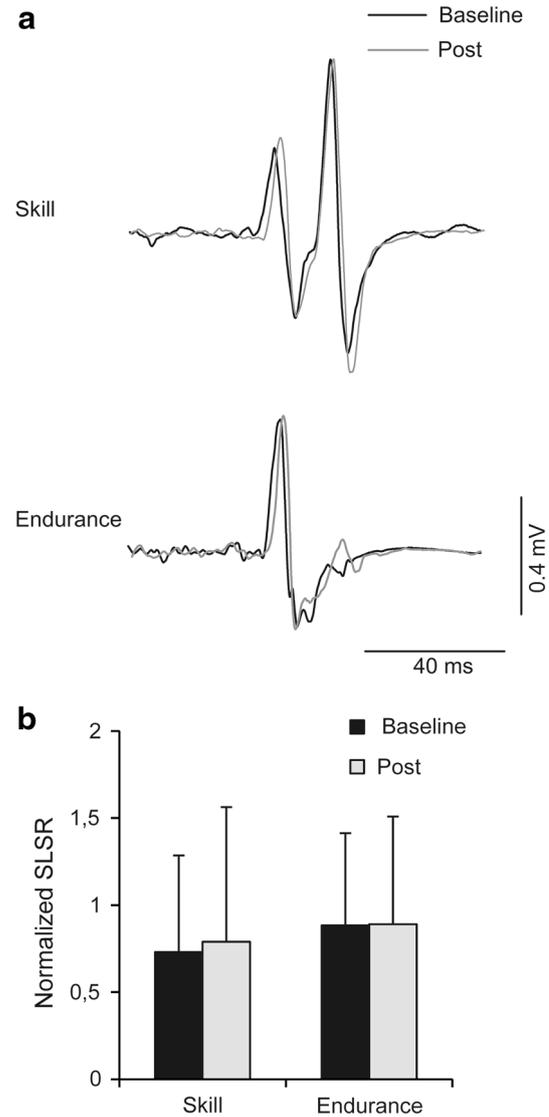

Fig. 4 Effect of the PAS intervention on short latency stretch reflex responses. **a** Raw EMG traces for one representative skill and endurance subject before (*black line*) and after (*gray line*) the PAS. Each trace is an average of 10 trials. **b** The group SLSRs (root mean square window of 20 ms) before (*black bars*) and after (*gray bars*) the PAS are normalized to root mean square(window of 100 ms) of MVC

Across all subjects the post-intervention soleus MEPs size was 0.68 ± 0.43 mV in the skill group 0.43 ± 0.26 mV in the endurance group and 0.44 ± 0.25 mV in the control group. The group mean results before and 5 min following PAS are presented in Fig. 2. There was no difference in the baseline EMG before and after PAS ($P > 0.05$). Figure 3 depicts original MEP recordings from one representative skill and endurance trained athlete before PAS and 5 min following PAS. A two-way repeated measures of ANOVA revealed a significant effect of PAS ($F_{(1,35)} = 5.25$, $P < 0.05$) and interaction of PAS and group ($F_{(2,70)} = 9.08$, $P = 0.001$) for the MEPs. Post hoc analysis using a two-tailed paired t test revealed that MEP amplitude increased significantly by 76 ± 83 % in the skill group ($P = 0.001$) and decreased by 7 ± 35 % in the endurance

group ($P = 0.44$) and increased by 21 ± 30 % in the control group ($P = 0.07$). One-way ANOVA for normalized MEPs revealed significant effect of group ($F_{(2,35)} = 7.68$, $P < 0.05$). Post hoc analysis using Bonferroni test revealed significant difference between the skill and endurance groups ($P = 0.001$), and non-significant difference between the control and skill ($P = 0.84$) and the control and endurance ($P = 0.12$) groups.

SLSR responses were not affected by PAS ($F_{(1,28)} = 0.317$, $P = 0.58$), group ($F_{(1,28)} = 0.33$, $P = 0.57$) nor their interaction ($F_{(1,28)} = 0.206$, $P = 0.65$). Figure 4

shows SLSR recordings from one representative skill and endurance athlete before and following PAS and the group mean results. Normalized pre-intervention values were 73 ± 55 % in the skill group and 88 ± 53 % in the endurance group. There was no difference in the level of background EMG between the baseline and post-measurements ($P > 0.05$).

Discussion

The aim of this study was to measure changes in the excitability of the cortical projections to soleus muscle in skill-trained, endurance-trained and control subjects following PAS. Significant LTP-like plasticity was attained in the skill group, while there were no significant changes in the endurance or in the control groups following PAS. As hypothesized, the change in the excitability (baseline MEP/post MEP) was significantly different between the skill and endurance groups. Sport background was the main separating factor of the skill and endurance groups and therefore, it is suggested that the different PAS-induced effects arise from exercise-specific adaptations in the corticomotoneuronal system.

The significantly greater plasticity induced by skill training is in line with what has been reported previously for professional musicians (Rosenkranz et al. 2007b). Musicians showed higher sensitivity towards induction of LTP-like plasticity compared to non-musicians when applying a PAS intervention on task-related hand muscles. There is convincing evidence from animal in vivo/in vitro and human studies that skill training increases the amount of neurotropic factors, synaptogenesis and map reorganization within the motor cortex, which drive the acquisition and performance of skilled movements (Monfils et al. 2005). These coordinated neuronal changes might also have led to higher motor cortex plasticity in the skillgroup in the present study since larger representation areas of tibialis anterior muscles have been observed in figure skaters when compared to controls (Vaalto et al. 2013). It has been demonstrated that these neuronal changes are not simply due to increased use of target muscles since motor map changes have not been observed in rats trained to continuously reach for an unattainable pellet (Kleim et al. 2004) nor in squirrel monkeys trained to retrieve food pellets from a large well despite 13 000 digit flexions during the course of training (Plautz et al. 2000). In addition, 30 days of running exercise have not been shown to alter motor maps in rats although running increases angiogenesis in the motor cortex (Kleim et al. 2002). This endurance training related increase in blood flow to the motor cortex has been shown to be accompanied by increased neurotropic factors that regulate neuronal activity as well as facilitate the survival

and differentiation of neurons (Erickson et al. 2012; Vaynman and Gomez-Pinilla 2005). Synaptogenesis is one separating factor between the skill and endurance training adaptations and can partly explain the different motor cortex plasticity changes in the present study.

However, some other factors are also likely to contribute to insignificant plasticity in the task-related muscle of endurance group because Cirillo et al. (2009) observed heightened plasticity in a task-unrelated, abductor pollicis brevis muscle in endurance-trained subjects compared to physically inactive subjects. Improved cognitive learning, but not motor learning, has been shown in endurance trained rats, when the motor learning task was task-related for running (Wikgren et al. 2012). It seems that the lower motor cortex plasticity induced by endurance training might be restricted only to task-related lower limb muscles, herein the reason for this still remains unknown. It should be noted that during the time course of repetitive training, the main focus of activity shifts from cortical towards subcortical motor regions as movements become more automatic (Floyer-Lea and Matthews 2004; Wu et al. 2004). Milton et al. (2007) compared brain activation in novice and expert golfers by whole-brain MRI and found that experts had focused and efficient organization of task-related neural networks while novices engaged wider brain areas during the same task. Schubert et al. (2008) found that after 4 week balance or ballistic strength training, motor cortical influence was reduced during the trained task and increased during a non-trained motor task. It seems that extensive repetitive type of practice over a long period of time leads to less of the neural network being recruited for movement control and this use reduction may also lead to lower plasticity of the particular brain area. It is also suggested by Kempermann et al. (2010) that physical activity promotes precursor cells, from which adult neurogenesis originates but the actual neurogenesis requires also cognitive challenges to be completed. Another explanation for lower motor cortex plasticity in the endurance group is that repeating the same movement sequences several hours per day could lead to over potentiation of synaptic transmission leaving no room for further LTP. Occluded LTP-like plasticity has been demonstrated by Beck et al. (2000) in human brain slices taken from epileptic focus, which had undergone excessive neuronal activity.

MEP increase did not reach statistical significance in the non-active control group which is in line with the study of Cirillo et al. (2009), where sedentary subjects were not facilitated after PAS intervention. In our previous study (Kumpulainen et al. 2012), where the subjects represented wide range of sports backgrounds, eight subjects were enough to show significant changes after identical PAS intervention. Even the change in the excitability (baseline MEP/post MEP) of the control group did not differ

significantly from the sport groups; it shows the crucial finding that the training adaptations of skill and endurance groups go opposite directions from the control group.

It is worth noticing that possible training adaptations in the supraspinal locomotor centers like cerebellum and brainstem are largely unknown. An animal study by Klintsova et al. (2004) showed different expression patterns of neurotropic factors in the cerebellum between skill and endurance-trained rats. Brain-derived neurotrophic factor increased in expression across the first training week in the cerebellar molecular layer in both groups while it remained elevated after 14 days of training in the skill group but not in the endurance group. The cerebellum is known to affect PAS-induced plasticity changes (Hamada et al. 2012), thus the training adaptations in the cerebellum might also affect the current results.

SLSR remained unchanged after the PAS intervention in both groups suggesting a lack of changes on the spinal level, which has also been shown in previous PAS-studies with F-waves, electrical brainstem stimulation (Stefan et al. 2000) and Hoffmann -reflexes (Mrachacz-Kersting et al. 2007). SLSR and its electrically evoked analog, the Hoffmann-reflex have been used in the past to assess potential training adaptations of the neuromuscular system. The biggest difference between these two reflexes is that the Hoffmann-reflex is less sensitive to changes in γ-activity because the muscle spindle is bypassed with direct nerve stimulation (Zehr 2002). However, their responses to interventions are generally reported to be similar though not identical. It is also very unlikely that with the same submaximal force level before and after PAS the spindle sensitivity would change.

As a fixed TMS intensity (120 % RMT) was used throughout the experiment to assess the possible changes within the corticospinal tract, it cannot be excluded that other intensities could have resulted in increased plasticity in the endurance group. However, the soleus muscle is a special muscle consisting mainly of slow twitch fibers, which are recruited progressively from rest to contraction strength close to 95 % of MVC (Oya et al. 2009). Thus, the recruitment of motor units should continue well-beyond the intensity of 120 % RMT in both subject groups and allow further increases in the soleus MEP amplitudes. Then again, higher intensities may have led to an even wider difference in the plastic changes in the motor cortex, since endurance training increases the type 1, low-threshold myosin heavy chain proportion in skeletal muscle (Ahtiainen et al. 2009). In addition, there were no significant differences in the MEP amplitudes at the intensity of 120 % RMT before the PAS between the groups suggesting that this is unlikely to be a major contributor to the results. A number of factors are known to influence PAS-induced plasticity changes, including history of synaptic activity, age, attention to the procedure, time of day the experiments were performed, gender, genetics

and regular exercise (Ridding and Ziemann 2010). Most of these factors were matched between the skill and endurance groups except the gender, genetics and the type of regular exercise. There is some evidence that females are somewhat more responsive to non-invasive brain stimulation (Ridding and Ziemann 2010). However, there were only 2 males less in the skill group and when only including females in the analysis, the result remains the same. There is still a significant change in the soleus MEP amplitudes in the 12 skill female subjects ($P = 0.02$) and insignificant in the 10 endurance female subjects ($P = 0.94$). It is not known whether these skill and endurance-trained athletes shared different brain-derived neurotrophic factor—polymorphisms, which are known to have a different influence on PAS-induced plasticity. However, it is known from numerous studies that endurance-trained subjects typically have enhanced plasticity in task-unrelated brain areas (Cirillo et al. 2009; Erickson et al. 2009; Kramer and Erickson 2007; Thomas et al. 2012), suggesting that it is very unlikely that the endurance athletes in the current study would carry unfavorable brain-derived neurotrophic factor——polymorphism. Taking all these arguments together, it seems reasonable to assume that a large proportion of the differential modulation of motor cortex plasticity is due to the different types of training backgrounds of the two groups.

Conclusions

The motor cortex is highly dynamic and adapts specifically to different types of motor training. PAS intervention revealed differential modulation of motor cortex plasticity in skill and endurance-trained athletes in this study. Understanding behavioral and neural signals that drive motor cortex plasticity will have important practical significance for guiding the development of novel therapeutic interventions for the treatment of various brain disorders and also the development of optimal coaching methods for elite athletes to achieve even better results. In fact, dance training has been implemented in the training program of young elite cross-country skiers by Alricsson et al. (2003), which improved many essential characteristics of the skiing performance such as speed, agility, joint mobility and muscle flexibility. The findings of the current study suggest that in the long-term, versatile skill training might induce preferable adaptations in the task-related areas of the motor cortex and thus might enhance rehabilitation and motor learning of muscle groups involved in the exercise.

Conflict of interest   The authors declare no conflict of interest.

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