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Improved sensorimotor adaptation after exhaustive exercise is accompanied by altered brain activity

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Running head: Motor adaptation after maximal exercise

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Abstract

Acute exercise has been shown to exhibit different effects on human sensorimotor behavior; however, the causes and mechanisms of the responses are often not clear. The primary aim of the present study was to determine the effects of incremental running until exhaustion on sensorimotor performance and adaptation in a tracking task. Subjects were randomly assigned to a running group (RG), a tracking group (TG), or a running followed by tracking group (RTG), with 10 subjects assigned to each group. Treadmill running velocity was initially set at $2.0 \text{ m}\cdot\text{s}^{-1}$, increasing by $0.5 \text{ m}\cdot\text{s}^{-1}$ every 5 min until exhaustion. Tracking consisted of 35 episodes (each 40 s) where the subjects' task was to track a visual target on a computer screen while the visual feedback was veridical (performance) or left-right reversed (adaptation). Resting electroencephalographic (EEG) activity was recorded before and after each experimental condition (running, tracking, rest). Tracking performance and the final amount of adaptation did not differ between groups. However, task adaptation was significantly faster in RTG compared to TG. In addition, increased alpha and beta power were observed following tracking in TG but not RTG although exhaustive running failed to induce significant changes in these frequency bands. Our results suggest that exhaustive running can facilitate adaptation processes in a manual tracking task. Attenuated cortical activation following tracking in the exercise condition was interpreted to indicate cortical efficiency and exercise-induced facilitation of selective central processes during actual task demands.

Keywords: exercise, sensorimotor adaptation, EEG, cortical activation, exhaustion, tracking

Introduction

Although numerous studies have examined the effects of prior exercise on the performance and acquisition of motor skills, the results have been very inconsistent. Some studies have suggested that low-intensity exercise can have a facilitative effect on motor performance and learning [1, 2], whereas others have demonstrated decrements in performance but not in learning of various motor tasks after moderately intense exercise [3–7]. In contrast, after high-intensity fatiguing exercise, both performance and/or learning has been found to be impaired [2, 4, 8–14]. Several authors have suggested an inverted U [15] effect of exercise intensity on motor performance and learning [1, 8, 11, 16]. Thus, with increasing levels of exercise, performance should improve up to an optimal or maximal point and then decline again with a further increase in exercise intensity and/or duration. Some authors have proposed that exercise prior to task performance elicits two concomitant effects: a beneficial effect of light exercise, possibly due to a general physiological warm-up, and a detrimental effect of high-intensity fatiguing exercise eventually as a result of the buildup of metabolites and altered acidity [1, 11]. However, metabolic changes were not measured and thus, the putative association between detrimental effects of higher-intensity exercise on motor behavior and the buildup of acid metabolites was not verified. Others have suggested that exercise is a stressor that degrades arousal of the central nervous system (CNS) and therefore, has an inverted U effect on motor performance and learning depending upon the intensity and/or duration of the preceding bout of exercise [16]. More recently, this same (inverted U) relationship has been hypothesized for the effect of exercise on reaction times and movement times during various choice- and simple-response reaction time tasks [17, 18]. While the inverted-U relationship may account for some findings, several other studies have shown improved performance [19, 20, 21, 22, 23] or learning [24] after intensive exercise. A common feature of these studies is that the bout of prior exercise did not incorporate the same muscle groups or movements that

were utilized during the subsequent motor task. Therefore, any changes in motor performance and/or learning in these studies are most likely characterized by functional modulation of the CNS following exercise.

Electrophysiological techniques such as electroencephalography (EEG) allow direct assessment of the brain electrocortical activity and provide a measure of CNS arousal. The EEG is usually categorized as either spontaneous activity or event-related potentials (ERPs). While ERP reveals diverse stimulus-locked changes in the EEG, spontaneous EEG activity with its typical frequency components (delta: 1–4 Hz; theta: 4–8 Hz; alpha: 8–13 Hz; beta: 13–35 Hz and gamma: > 35 Hz) is considered to be a good measure of psychophysiological state [25]. In the past, numerous studies were conducted using spontaneous EEG in order to measure cortical activation during performance of various self-paced visuomotor tasks like target shooting, archery and golf [26-31]. The major finding of these studies is that high performance in experts compared to poor performance in novices is accompanied by higher alpha power during the aiming period. In addition, a progressive raise in alpha power was noticed as performance improved after practice for diverse visuomotor tasks [32-35], primarily in those cortical regions that are nonspecific to the visuospatial task demands [34, 36, 37]. Since the alpha rhythm is typically attenuated by functional brain activity the above mentioned results suggest an inverse relationship between motor performance and cortical activation. This view is further supported by research applying imaging techniques such as positron emission tomography [38] or functional magnetic resonance imaging [39, 40], whereas the fMRI studies suggest a gradual shift from cortical to subcortical brain regions as motor skills develop. Based on the well-established stage structure of sensorimotor skill acquisition [41-44], Hatfield and Hillman [45] suggested that the observed decrease in cortical activation as a function of skill level reflects a reduction of cognitive effort due to automaticity of information processing and this may minimize potential interference with

visuomotor processes during task execution. The authors refer to this hypothesis as efficiency of psychomotor performance [45].

Most studies dealing with the effects of acute exercise on spontaneous EEG activity have reported increases in alpha power from pre to postexercise (reviewed in refs. 46, 47). The observed changes were interpreted as states of decreased cortical arousal probably reflecting relaxation, fatigue, affective change, and/or reduced anxiety [48–50]. In contrast to alpha, as yet, considerably less attention was paid to the beta frequency band although these waveforms are typically considered as a “desynchronization” of the EEG reflecting increased cortical activation [51-53]. In their meta-analysis Crabbe and Dishman [47] analyzed the results of those studies that measured beta activity and the cumulative evidence yielded an increase in beta activity following exercise, although less pronounced as compared to the alpha band (mean effect size 0.38 SD vs. 0.55 SD for alpha activity).

The main purpose of the present study was to determine the effects of exhaustive running on sensorimotor performance and adaptation in a visuomotor tracking task. Since tracking and exercise require action of different body parts, any change in motor behavior after running should, to a very large extent, be related to functional alteration of central states. Therefore, another purpose of this study was to examine cortical activation using EEG. With regard to previous studies, there should be at least an increase in alpha power after running. According to research detailing cortical states during superior visuomotor performance (see above), one would expect that an increase in alpha power after exercise should benefit subsequent motor behavior due to cortical efficiency. If so, then cortical activation is likely to be attenuated following tracking in the exercise condition.

Methods

Subjects and experimental overview

30 male sport and exercise science students from the German Sport University (mean and SD of age = 26 ± 4 years, body height = 183.1 ± 6.2 cm and body weight = 79.3 ± 7.6 kg) gave their informed consent to participate in the study which was approved by the University Research Ethics Committee. All participants were physically fit, recreational runners with 2-3 training sessions per week. They all were right-handed and unfamiliar with the experimental protocol and measurements. They did not report any neural disorders and none of them were taking medications.

Subjects were randomly assigned into a running group (RG), a tracking group (TG) or a running followed by tracking group (RTG), with 10 subjects in each group, respectively. The time course of the experimental procedure for each group is depicted in Fig. 1. Subjects in RTG performed an incremental running protocol on a treadmill until volitional exhaustion. This was followed by 35 episodes of an on-screen tracking task. Subjects in TG completed the tracking task without prior running, while subjects in RG completed the running protocol without tracking afterwards. This meant that RG and TG served as “control” groups for RTG. Continuous EEG was recorded for two minutes before running in RG and RTG, before and after tracking in TG and RTG, as well as before and after the rest period in RG. In another study in our laboratory we found no changes in EEG spectral power after an identical rest period [54]. Therefore, we abstained from adding a pre-assessment of EEG for the TG in the present study. During the experiment, subjects were not told how to proceed until completion of the EEG recordings. Thereby an effect on the EEG signal due to anticipation of a specific experimental condition was avoided.

EEG recordings and data analysis

Two min continuous EEG was recorded in a soundproofed, dark room. Subjects sat in a relaxed position with their eyes closed. Their position was stabilized by a back, arm and a head rest. The feet were placed flat on the ground in a parallel position. Bipolar EEG was recorded from 19 sites (Fp1, Fp2, Fz, F3, F4, C3, C4, Cz, P3, P4, Pz, F7, F8, T7, T8, P7, P8, O1, O2) using an EEG-Cap (Electro-Cap International, Inc., Eaton, USA) with the electrodes positioned according to the international 10:20 system [55]. An electrode located within the triangle of Fp1, Fp2 and Fz was used as the reference site. To reduce the impedance between scalp and electrodes, impedance reducing gel (Electro-GelTM, Electro-Cap International, Inc., Eaton, USA) was applied to the electrodes until the impedances of all electrodes were below 5 k Ω . The cap was worn by subjects for the entire experimental period, including resting and exercise periods.

The analogue EEG signal was amplified and converted to a digital signal with an A-D conversion rate of 256 Hz (Digital EEG Amplifier, Braintronics B.V., HL Almere, NL). Data was recorded with the Neurofile XP System (IT Med, Usingen, Germany). During EEG recordings subjects were monitored using a video camera that was triggered by the EEG system. For data analysis Brain Vision Analyzer software (Brain Products, Munich, Germany) was used with the high and low band pass filters set at 1 Hz and 40 Hz (24 dB/octave), respectively. The 2 min continuous EEGs of each subject were visually inspected and artifacts were rejected using an automatic artifact detection method with a gradient $< 35\mu\text{V}$ as well as $100\mu\text{V}$ and $-100\mu\text{V}$ as a maximum and minimum amplitude, respectively. The synchronized video tapes of each artifactual segment were inspected before rejecting the artifact. This check revealed that the most common artifact was “swallowing” (particularly after running). After artifact rejection the EEG data was epoched into segments of 4 s allowing 0.5 s overlap

between segments. Each segment was then fast Fourier transformed (FFT) using a 10% Hanning window in order to determine spectral power. Next, the FFT-segments of each electrode were averaged to obtain the mean spectral power of each site. Finally, the overall alpha (7.5 - 12.5 Hz) and beta (12.5 - 35 Hz) power were calculated as a mean across all electrodes. Identical or very similar recording and analyzing methods of the EEG were reported in many other studies [54, 56-58].

Treadmill running protocol

Before running, all subjects were familiarized with the treadmill (Woodway, Weil am Rhein, Germany) and running protocol. Subjects wore a safety belt in case of a fall. The protocol started at a running velocity of $2.0 \text{ m}\cdot\text{s}^{-1}$ which was increased with each stage by $0.5 \text{ m}\cdot\text{s}^{-1}$ until exhaustion was reached. Each stage lasted 5 min and stages were separated by 30 s breaks for blood collection. The first two running stages provide a very solid warm-up phase for young and physically fit subjects. The selected stage duration of 5 min ensures a lactate steady-state after each stage (see [59]).

Blood lactate, heart rate and rating of perceived exertion

At rest, after each running stage and immediately upon the cessation of the running protocol, 20 μl capillary blood was sampled from a lancet puncture of the earlobe. Lactate concentration (BLa^-) was determined according to the enzymatic-amperometric principle with the Biosen C_Line (EKF Diagnostic, Barleben/Magdeburg, Germany). At each time point, immediately prior to blood sampling, rating of perceived exertion was assessed using the 6-20 Borg scale. Heart rate (HR) was measured continuously with an ECG accurate wireless heart rate monitor (S810i, Polar Electro, Kempele, Finland).

Manual tracking

Subjects sat in front of a computer screen, watching a visual target (red dot of 2 cm diameter) that moved smoothly and with constant angular velocity across the screen. Three different trajectories were presented to the subjects in a quasi-random and counterbalanced order to ensure that the path of the target was unpredictable. Each tracking episode lasted 40 s with a 20 s break between the episodes. In their dominant hand, subjects held an optical computer mouse which controlled the cursor (blue dot of 2 cm diameter) on the screen. The participants' task was to track the target with the cursor as accurately as possible. The x- and y-position of target and cursor was sampled every 40 ms. Manual performance of each tracking episode was quantified as root mean square error (RMSE). The first 2 s of each tracking episode were excluded from analysis in order to eliminate the effect that an initial misplacement of the cursor may have had on the calculated RMSE. The RMSE was presented to the subjects on the screen in the pause between each of the subsequent tracking episodes. During the first five tracking episodes the target and cursor motion were not manipulated and these episodes were used to assess task performance. In the subsequent 30 tracking episodes the cursor control was left-right reversed. Thus, a hand movement to the right led to a cursor displacement to the left. Movements in the vertical plane did not change. These tracking episodes were used to assess task adaptation. Participants were informed immediately after the performance trials that cursor control will be perturbed for the subsequent episodes. However, no further information about the type of perturbation was given to them in order to avoid pure strategic control [60-62]. For statistical analysis, the 35 tracking episodes were divided into seven blocks of five successive episodes. Thus, the RMSE of the first block represented the subjects' performance, whereas RMSE of blocks 2-7 was a measure of adaptation to the left-right reversal. Similar tracking paradigms were also used in several previous studies [44, 54, 63, 64].

Statistics

Variables recorded during treadmill running were analyzed using *t*-tests for unpaired datasets. Tracking errors during the performance and adaptation phases of the tracking task were assessed using analysis of variance (ANOVA) with the between-factor GROUP and the within-factor BLOCK. EEG activity was analyzed in two steps. First, an ANOVA with the factors GROUP (RTG, RG) and TIME (pre and postrunning) was calculated in order to test for the effects of exercise on alpha and beta power, respectively. Second, an ANOVA with the factors GROUP (TG, RTG, RG) and TIME (pre and posttracking in RTG and TG as well as pre and postrest in RG) was conducted in order to examine the course of alpha and beta power from before to after tracking, tracking following running and rest in TG, RTG and RG, respectively. Significant main effects and interactions were further analyzed using the Fischer's LSD post hoc tests.

Results

Incremental running

At the point of exhaustion, subjects in the RTG reached a mean running velocity of 4.2 ± 0.26 $\text{m}\cdot\text{s}^{-1}$ (26.0 ± 3.7 min running duration) and reported a mean RPE value of 19.7 ± 0.7 . Their HR_{max} was 199 ± 4.0 $\text{beats}\cdot\text{min}^{-1}$ with a corresponding $\text{BLa}^{-}_{\text{max}}$ of 10.5 ± 2.2 $\text{mmol}\cdot\text{l}^{-1}$. In RG, exhaustion occurred at a mean running velocity of 4.4 ± 0.21 $\text{m}\cdot\text{s}^{-1}$ (28.7 ± 2.1 min running duration). The subjects in this group reported a maximum RPE value of 19.5 ± 0.9 , had a HR_{max} of 194.7 ± 6.1 $\text{beats}\cdot\text{min}^{-1}$ and a $\text{BLa}^{-}_{\text{max}}$ of 10.4 ± 1.9 $\text{mmol}\cdot\text{l}^{-1}$. Subjects' aerobic capacity was determined by calculating each individual's running velocity at the 4 $\text{mmol}\cdot\text{l}^{-1}$ lactate threshold [59] using an exponential regression. According to this analysis subjects reached the 4 $\text{mmol}\cdot\text{l}^{-1}$ threshold at 3.3 ± 0.47 $\text{m}\cdot\text{s}^{-1}$ and 3.4 ± 0.50 $\text{m}\cdot\text{s}^{-1}$ in the RTG and RG, respectively. *t*-tests for unpaired datasets confirmed that there were no differences between RTG and RG for any of the above reported variables.

Tracking performance

Fig. 2 shows raw tracking data as an example of one subject. The distance between cursor and target was small under normal visual feedback (left), severely increased immediately after the introduction of the left-right reversed visual feedback (middle), but recovered after a practice period (right). Mean across subjects RMSE of each block during the performance and adaptation phases of the tracking task in TG and RTG are shown in Fig. 3. There was a significant GROUP x BLOCK interaction ($F(6,108) = 2.25$, $p < 0.05$). Tracking errors were small during the performance phase, with no difference between groups, and then increased

abruptly at the onset of reversed visual feedback. RMSE was substantially lower in the RTG compared to TG for the first two tracking blocks under reversed visual feedback ($p < 0.05$). This difference gradually diminished over the following blocks with similar errors between TG and RTG by the end of tracking. RMSE gradually returned towards initial values from block 2 onwards without reaching them at the end of adaptation. In RTG there was no difference in RMSE from block 4 to 5. Such a plateau in the recovery of tracking error did not occur until block 5 and 6 in TG.

EEG spectral power

Alpha and beta power of each group and measuring time is shown in Fig. 4. The ANOVA with the factors GROUP (RTG, RG) and TIME (pre and postrunning) yielded no significant main effects either for alpha or beta power, indicating that exhaustive running had no effects on resting cortical states in the present study. A second ANOVA with the factors GROUP (TG, RTG and RG) and TIME (pre and posttracking in RTG, TG as well as pre and postrest in RG) revealed a significant GROUP x TIME interaction for both alpha ($F(2, 27) = 4.24$; $p < 0.05$) and beta power ($F(2, 27) = 7.11$; $p < 0.01$). Post hoc tests on the significant interactions showed increases in both alpha ($p < 0.01$) and beta ($p < 0.001$) power from pre to posttracking in TG, whereas in RTG alpha power remained unchanged and beta power even decreased ($p < 0.05$) after tracking. There were no changes after the rest period in RG for either alpha or beta power.

Discussion

Past research revealed conflicting results of the effects of intensive exercise on subsequent motor behavior. In the present study, we evaluated the effect of exhaustive running on performance and adaptation in a tracking task. Task adaptation was faster in the exercising group, as indicated by the smaller tracking error during the first two blocks of adaptation and a quicker attainment of a RMSE plateau between two subsequent tracking blocks (see Fig. 3). These results are in agreement with those obtained by Benson [24], who found improved learning of a juggling task after intensive cycling. Despite this agreement, numerous previous studies have reported impaired performance and/or adaptation after high-intensity exercise [2, 4, 8–14]. However, in all of these later studies, the bout of prior exercise was performed using muscle groups that were also required during the subsequent motor task. This raises the possibility that the detrimental effects of exercise on motor behavior in those studies were due to local neuromuscular fatigue. As the upper limbs are only marginally loaded during running, they would not be expected to be fatigued and negatively affected in their function during a subsequent tracking. A systemic warm-up effect of running might have contributed to improved arm and hand motor adaptation. Among other factors, such a warm-up would imply a rise in body temperature and thus, increased speed of chemical reactions, oxygen uptake, and neural drive [65].

Unlike task adaptation, baseline performance (block 1; episodes 1-5) did not differ between groups. This finding may indicate that controlling the cursor of a computer mouse under normal conditions (veridical visual feedback) is a highly automatized everyday task for university students. Therefore, it is probably not sufficiently sensitive to prior exercise.

In addition to the above-mentioned warm-up effect, the mechanisms underlying the means by which maximal running influenced task adaptation are probably located in the brain. In the present study, exercise failed to induce significant spectral power changes. This is somewhat surprising in that most studies reported increases in alpha activity following exercise [46, 47]. Several methodological differences could be responsible for this disagreement. Most of the previous studies used low- to moderate-intensity exercise protocols, whereas we used a protocol that included maximal exercise intensity. Furthermore, most studies calculated spectrum power only for specific scalp locations and not for the entire scalp, as we did here. Another possible explanation for the failure to find a systematic EEG change after exercise could be the interval nature of the exercise. Previous studies that reported postexercise increases in alpha activity mostly used continuous exercise protocols [66-68]. Despite these methodological aspects, Mechau et al. [56] demonstrated that during incremental running, overall lower alpha and beta power first increase and then gradually return toward baseline values at higher running intensities with increasing lactate accumulation. With respect to these findings, it appears possible that after maximal exercise, resting alpha and beta power could be similar to or even lower than baseline values.

Although exercise failed to induce significant spectral power changes, the TG and the RTG showed substantially different EEG responses from before to after tracking. In TG, both alpha and beta power increased significantly, while in RTG, alpha power remained unchanged and beta power even decreased after tracking (Fig. 4). Particularly in TG, these results are difficult to interpret with respect to the traditional arousal interpretation of the EEG, according to which alpha and beta oscillations characterize decreased and increased cortical activation, respectively [51-53]. However, over the last two decades, convincing evidence has emerged that alpha activity also reflects numerous mental processes, including working memory or top-down influence on perceptual processes [69-72], whereas beta activity has been suggested

to be an adequate index of information processing at the cognitive level as well as emotional processes [71-73]. With respect to these findings, it is possible that subjects in TG were cognitively and/or emotionally aroused following tracking. Unlike in TG, in RTG the unchanged alpha and decreased beta power may indicate a rather relaxed and inactive cortical state after the tracking task. This differential response between TG and RTG is not related to physical recovery from the exercise bout, since spectral power did not change after the rest period in RG. Furthermore, adaptation occurred in both groups, and its degree did not differ between TG and RTG for the last three tracking blocks, suggesting that altered cortical activity following tracking is probably not specific to memory processes. However, it is conceivable that the above-described differences in EEG activity between TG and RTG following tracking may be a result of exercise-induced changes in cortical states during actual task demands but not necessarily during rest. Studies detailing the psychophysiological state of elite performers found that high psychomotor performance is associated with lower levels of cortical activation probably due to psychomotor efficiency (see Introduction) and reduced mental effort in order to fulfill task demands [36, 37, 45]. Therefore, enhanced task adaptation in RTG may reflect an increased quality of central information processing following exercise probably resulting in rather relaxed cortical states after tracking in the exercise condition. This view is further supported by a relatively large number of studies that were able to demonstrate an exercise-induced facilitation of selective central processes. For example, it is well known that sensorimotor performance and adaptation very much depends on the ability of a person to focus attention on the task [43, 74]. Accordingly, it has been shown in previous studies that allocation of attentional resources, as measured by P300 amplitude of ERP is enhanced after exercise [75-78]. In addition to attention, it is widely accepted that adaptive motor improvement results from at least two distinct processes: (a) perceptual-motor recalibration (alternatively called spatial alignment) and (b) strategic control [60-62]. While recalibration denotes progressive adjustments of an “internal model” [79], strategic control involves,

among other aspects, movement corrections based on sensory feedback and cognitive processes. Moreover, neural correlates of cognitive operations were found to be partially recruited during motor performance [80, 81]. It has been shown that exercise has the potential to facilitate selective cognitive processes [18, 82-84] which in turn may enhance sensorimotor adaptation. After all, motivational properties of augmented feedback about goal achievement (i.e., knowledge of result after each tracking episode) are also known to play an important role in motor performance and adaptation [43]. In this context, it is important to note that the results of numerous studies indicate diverse psychological benefits of acute exercise, including positive affective responsivity and anxiety reduction [85-88]. Moreover, Crabbe et al. [89] suggested recently that emotional arousal during exposure to unpleasant stimuli may be reduced after exercise. Such an effect would have been quite beneficial after the introduction of task perturbation when subjects had to accept a sudden increase in tracking error.

Conclusion

The main finding of this study is that maximal exercise can facilitate sensorimotor adaptation in a tracking task that does not incorporate muscle groups and movements that were utilized during the exercise bout. This beneficial effect of exercise on task adaptation was accompanied by attenuated cortical activation after tracking. In combination, these results were interpreted to probably indicate exercise-induced cortical efficiency and amelioration of task-relevant central processes such as attention, cognition and motivation. Future studies should measure EEG during actual task performance to allow further interpretation of the EEG data. Also, additional assessment of affective/emotional states may be helpful in order to deconfound the role of the motivational system on motor behavior following exercise.

Figures

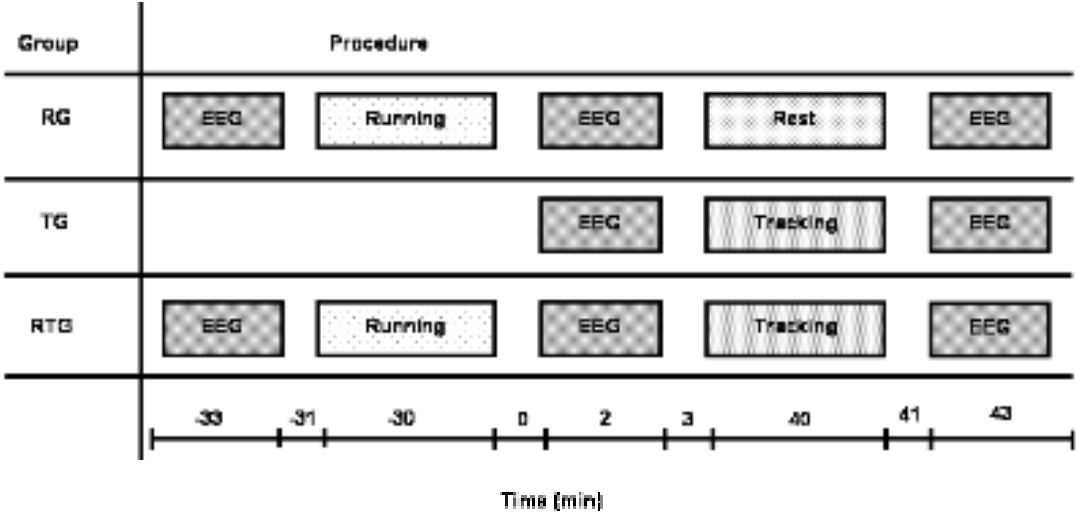


Fig. 1. Procedure and time course of the experimental setup for each group.

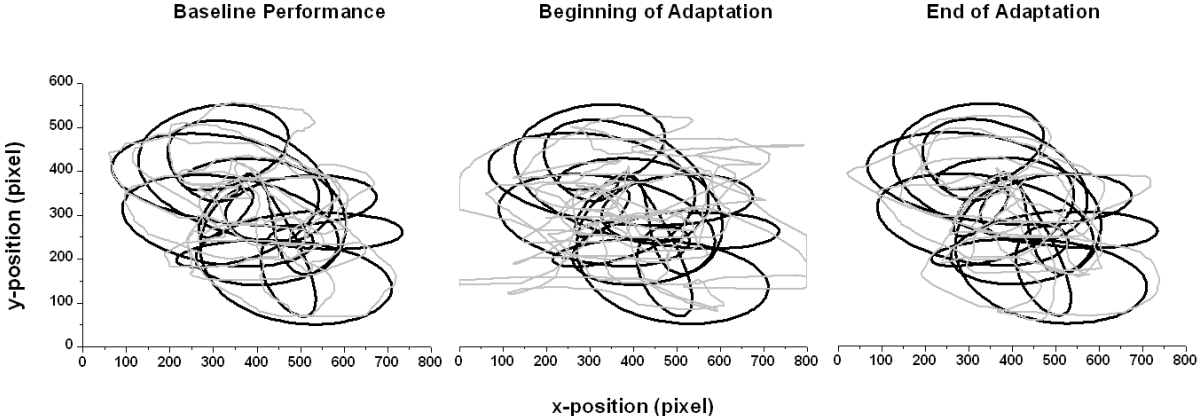


Fig. 2. Tracking trajectories: an example of one subject before (left), immediately after (middle) and by the end (right) of left-right reversed visual feedback. The target trajectory is represented by the bold and the trajectory of the cursor by the thin line.

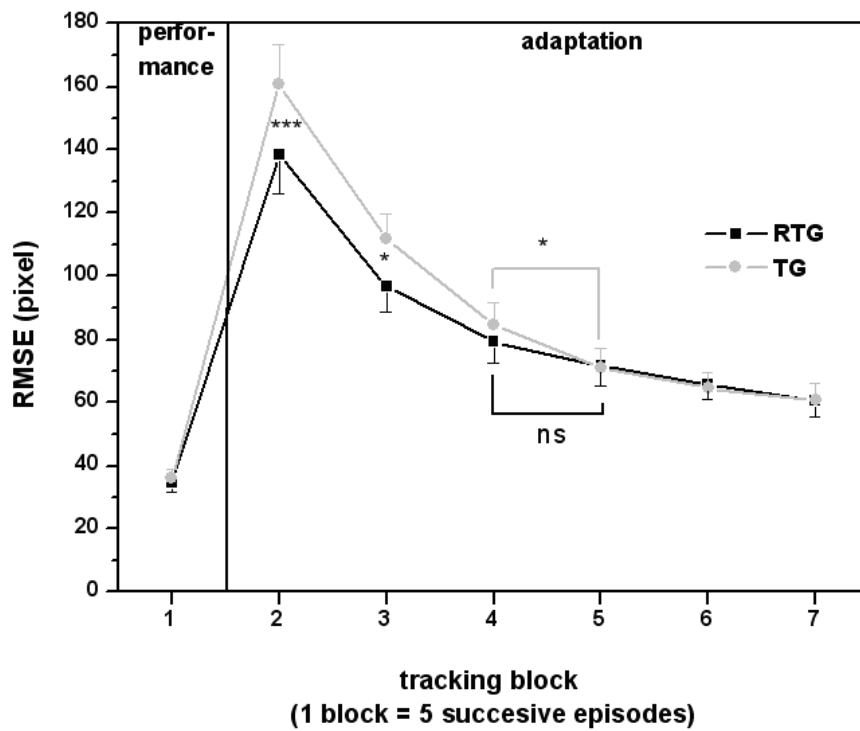


Fig. 3. Subjects' tracking error before (block 1) and during task adaptation (blocks 2-7). Each data point represents the mean RMSE across five subsequent tracking episodes and across subjects. Vertical bars represent the standard error. * $p < 0.05$; *** $p < 0.001$; ns = not significant.

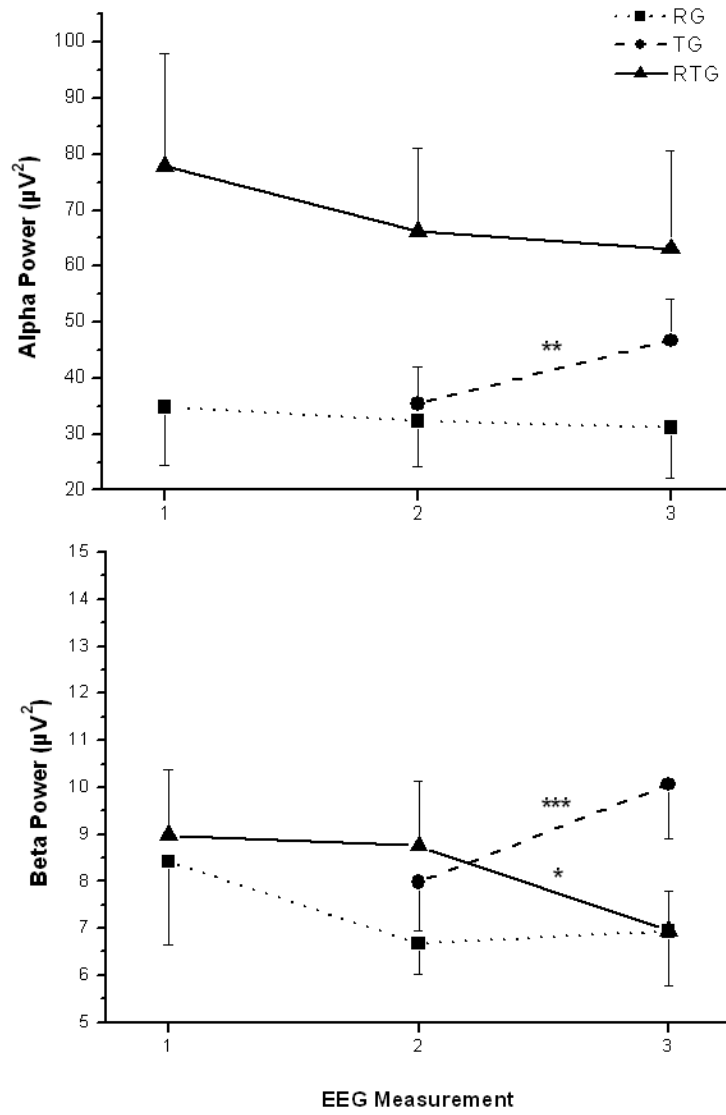


Fig. 4. Alpha and beta power of each group and measurement time. Vertical bars represent the standard error. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

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