

# Anticipatory postural adjustment: the role of motor cortex in the natural and learned bimanual unloading

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**Abstract** Anticipatory postural adjustment (APA) during bimanual action is observed when participants hold an object in one hand and then lift that object with the other hand. The decrease in activity of a forearm flexor muscle prior to an active forearm unloading acts to stabilize the forearm position. Recent studies have investigated the influence of the corticospinal system on muscle activity during APA through transcranial magnetic stimulation. It was shown that at different times during APA, the amplitude of motor-evoked potentials in the forearm flexors decreased in conjunction with the decrease of muscle activity. If the unloading is triggered via an electromagnet by lifting an equal weight by the other arm, the anticipatory postural adjustment is learned through the repetition of unloading (three series of 20 trials). Using the transcranial magnetic stimulation, we examined changes in the motor-evoked potential in the forearm flexors before and after APA learning. Motor-evoked potential amplitude did not significantly change as forearm flexor activity decreased. The motor-evoked potential/background electromyogram ratio, however, increased in the final learning session in comparison to the initial learning session and stationary loading. The present results corroborate a hypothesis on the fundamental role of the motor cortex in the suppression of

synergies that interfere with the execution of the new coordination in the process of motor learning.

**Keywords** Bimanual unloading · Anticipatory postural adjustment · Transcranial magnetic stimulation · Learning

## Introduction

The role of the motor cortex in motor learning is being intensively studied (Carrol et al. 2001; Pascual-Leone 2001). Most studies have focused on how the acquisition of new fine motor skills or practicing complex movement leads to plasticity in the motor cortex (Pascual-Leone et al. 1995; Kleim et al. 2002; Kang et al. 2004; Ljubisavljevic 2006), depending on the types of movements and characteristics of training (Tyc and Boyadian 2006). The specificity of the motor cortex in learning new tasks, however, is still not clear. The earlier animal experiments on this subject suggest that the motor cortex inhibits inappropriate synergies during the learning of new motor patterns (Ioffe et al. 2002). According to this hypothesis, the motor cortex plasticity during the acquisition of a new motor skill provides inhibition of synergies and coordination interfering with the movement being learned. The corticospinal command should include parameters of both appropriate muscle activation and inhibition of inappropriate muscle groups. Though a number of data are in favor of this hypothesis for movement and postural tasks (see Ioffe et al. 2002), this idea was not directly checked in the neurophysiological experiments. Thus, it seemed to be important to test this hypothesis by the examination of motor cortex excitability during the process of learning a new motor task: particularly during learning a new pattern

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of anticipatory postural adjustment (APA). It is known that the soleus H-reflex appeared to be inhibited during the anticipatory phase before arm movement. This inhibition is suggested to be produced by the descending motor command (Kawanishi et al. 1999). However, the motor cortex excitability during the learning of a new APA pattern was not previously studied.

In contrast to skilled learning, which typically recruits attention and memory, a discrete, simple and known movement can be learned through repetition in a short experimental session (Classen et al. 1998). A good example of a simple learned movement is bimanual unloading, well known as a “barmen effect” (Hugon et al. 1982; Dufosse et al. 1985): if a subject unloads the forearm by use of the contralateral arm, the unloaded forearm maintains an almost stable position due to the anticipatory inhibition of the biceps activity to the unloading. This “natural synergy” is shown to be established in childhood (Schmitz and Assaiante 2002). If the unloading is done through a mechanical linkage, the postural arm stabilization is initially absent and could be learned through the experimental session (Paulignan et al. 1989; Vialett et al. 1992; Ioffe et al. 1996; Massion et al. 1999).

To evaluate the role of the motor cortex in APA in the preceding paper, we investigated the motor potentials (MEPs) evoked by transcranial magnetic stimulation (TMS) in the forearm flexors at the time of the “natural synergy” in bimanual unloading (Kazennikov et al. 2005). No specific changes were found in the cortical excitability, so MEP amplitude decreased in parallel to changes in the background EMG. However, it was shown earlier that if the bimanual unloading is learned, then the postural adjustment is specifically impaired in patients with lesions of the cortico-spinal system, and not as apparent in patients with lesions of the basal ganglia or other brain structures (Vialett et al. 1992; Massion et al. 1999). These data suggest a predominant role of the motor cortex in learning new patterns of postural adjustment. In the present study, we compared APAs during natural bimanual unloading (“natural” APA) with learned unloading (“learned” APA), and also with the TMS-response in these tasks. Left-hand manipulation during the unloading task could be associated with enhanced activity in the right motor cortex, which could influence the excitability of the left motor cortex (Sohn et al. 2003). Taking this into account, we examined the inter-cortical interaction in the additional “contralateral” test when the postural forearm was stationary loaded and the contralateral forearm lifted the 1-kg weight.

Thus, the purpose of the present work was to study the role of the motor cortex in learning a new APA that provides the inhibition of muscle activity prior to unloading. To accomplish this, we compared the excitability of cortical representation of the elbow flexors during natural and

learned bimanual unloading. In this paper we present the additional data of the experiment (Kazennikov et al. 2005) what concerned “natural synergy” in order to compare it with the data of the current experiment. In the experiment with “natural synergy” a subject’s forearm was loaded with a 1-kg weight in a suspended basket. On command, the subject grasped a handle on top of the basket with the contralateral index finger and thumb, and lifted the basket. That part of data from the previous experiment, used for comparing with the present data concerns the characteristics of MEP response delivered at the moment of the finger touching the basket (test ACT-O from active unloading task, see Kazennikov et al. 2005). Also data of “contralateral” task, namely—the characteristics of MEP response delivered during lifting of an equivalent weight by the contralateral arm while the ipsilateral forearm was statically loaded and held stationary (task CONTRA in Kazennikov et al. 2005), was compared with the data of “contralateral” test of the present experiment.

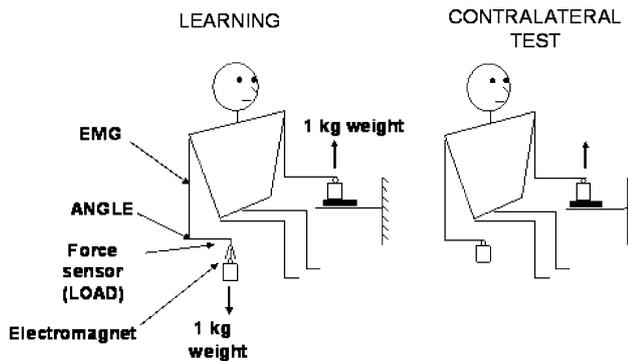
## Materials and methods

### Subjects

Ten, right-handed, healthy subjects [35–55 years, 8 males, height  $173 \pm 9$  cm, weight  $69 \pm 8$  kg (mean  $\pm$  SD)] participated in this experiment. The subjects had no history of neurological disorders and gave informed consent prior to testing. The experimental procedures corresponded to the ethical principles of the Declaration of Helsinki.

### Experimental setup and tasks

Experimental setup is presented in Fig. 1. The subjects were seated comfortably in an armchair with their eyes closed and with the head supported by a headrest, so that the head was relatively immobilized, and the possible head rotation did not exceed  $1^\circ$ . The subject’s right (postural) upper arm was gently pushed backward against a support placed above the elbow. In this position, the angle between the upper arm and vertical line was  $20^\circ$ , and the wrist was placed horizontally in a semi-prone position. Both arms were fixed by elastic bands to the backward support placed above the elbow. A basket was fixed on the postural forearm and was loaded by 1 kg weight by means of an electromagnet (Fig. 1, left panel). The subjects were instructed to maintain the horizontal and semi-pronated position of the loaded forearm during the whole session. Another 1-kg weight was firmly fixed to the left forearm. The left forearm was stretched out on the table. In the basic experimental condition (learning), the subject was instructed to lift the left



**Fig. 1** Experimental set up. *Left panel:* the subjects sat with eyes closed and with their right (postural) forearm loaded with a 1-kg weight by means of an electromagnet. The subjects were instructed to maintain the horizontal position of the postural forearm and to lift the left forearm with the 1-kg weight from the table in response to beep. Weight increase on the left forearm to half of its initial value triggered disconnection of electromagnet and load release from the postural forearm. *Right panel:* the subjects held the postural forearm in a stationary horizontal position with a 1-kg weight and lifted the 1-kg weight with the contralateral forearm

forearm approximately 10 cm above the table, as fast as possible, in response to an auditory beep. The weight increase on the left forearm to half of its initial value triggered the disconnection of the electromagnet ( $T_0$ ) and load release from the right forearm. Time delay between  $T_0$  and load release was about 15 ms.

The learning process consisted of three sequential sessions (LEARN1, LEARN2, LEARN3) including 20 trials each. The inter-trial interval was 5–7 s, and intervals between sessions were 5–7 min. Transcranial magnetic stimulation was delivered at the beginning (during the first five trials of LEARN1) and at the end (during the last ten trials of the LEARN3 sessions) of learning. No TMS was delivered during LEARN2 session (see below).

There were also two other conditions, where the electromagnet was continuously “on”:

- Subjects held the forearm in horizontal position with 1-kg weight (Stationary loading, LOAD). LOAD trials were executed by the subject at the beginning (five trials) and at the end of the experiment (five trials)
- Subjects held the postural forearm in a stationary horizontal position with a 1-kg weight, and lifted the 1-kg weight with the contralateral forearm (CONTRA). CONTRA trials were executed by the subject before (five trials) and after learning (ten trials) (Fig. 1, right panel).

#### Parameters recorded

Angular position of the elbow joint of the postural forearm was measured by a potentiometer-based goniometer. A

force sensor was placed between the basket and the right forearm to measure the force acting on the forearm. Surface EMG was recorded from the *biceps brachii* m. of the postural (right) forearm (BB). The preamplified EMG signal was bandpass filtered (50 Hz–1 kHz) prior to sampling at 2 kHz. Force and angular signals were sampled at 500 Hz. EMG; force and angular signals were recorded in the interval 500 ms before and 2,500 ms after the “beep” in the Learning and CONTRA sessions. In the LOAD session, TMS was delivered at 500 ms after recording began.

#### Transcranial magnetic stimulation

Transcranial magnetic stimulation (TMS) was delivered by a Mags1 (Schwarzer, Germany, maximum output: 2T) using a 9-cm round coil. Fine adjustments of coil position were routinely made for individual subjects, to identify the optimal location. The coil was placed tangentially to the scalp, with the handle pointing posterolaterally at a 30° angle from the midline. The coil was positioned over the vertex and the direction of the current was clockwise when viewed from above. The coil was then moved over the hemisphere to determine the optimal position for eliciting MEPs on the TMS that were 3–5 times bigger than the activity of the right biceps brachii with the forearm unweighted and elbow at 90° flexion. The stimulation intensity was set at 40–50% of maximum stimulator output and was used at this intensity throughout the whole experiment. In order to stabilize the coil position during the experiment, the coil was fixed to the chair by a brace and scotch-taped to an elastic swim cap on the subject’s head. MEP amplitude was verified in the LOAD condition to ensure that the coil position remained steady.

During the learning sessions TMS was delivered at  $T_0$ . TMS was delivered during the first five trials of LEARN1 and during the last ten trials of the LEARN3 sessions. No TMS was delivered in LEARN2. The CONTRA test before learning consisted of five trials with TMS, and the CONTRA test after learning consisted of ten trials, with TMS delivered during the last five trials. Also, TMS was produced during the first five and last five trials in the LOAD sessions. In summary, each subject was stimulated 35 times. The duration of the experiment was about 40 min.

#### Data analysis

The learning process was quantified by the means of two indexes: the amplitude of elbow angular displacement, and the amount of inhibition of muscle activity. The amplitude

of elbow angular displacement was calculated as the difference between the mean value of the elbow angular position during the last 100 ms before unloading and its maximal value on the interval 100–200 ms after unloading. In order to calculate the amount of inhibition of biceps activity before unloading, the EMG of biceps activity in the interval 5–20 ms before  $T_0$  (BG2) was compared to the interval 200–450 ms before  $T_0$  (BG1). The effect of practice was assessed by the analyses of three blocks of trials: trials 1–20 (LEARN1), trials 21–40 (LEARN2), and trials 41–60 (LEARN3). The learning process was quantified using exponential curves by equation

$$A \exp(t/\tau), \quad (1)$$

where  $t$  and  $\tau$  are the number of trials for angular displacement. This analysis was used in order to have a measure of the learning time constants. In order to compare APAs in “natural” and “learned” unloading, the trials without TMS were viewed off-line on a monitor screen. For further analysis, the amount of biceps activity inhibition prior to unloading (BG2/BG1) and the duration of anticipatory biceps activity inhibition (from the first visible decrease in the rectified EMG (Aruin and Latash 1995) until the start of unloading) were calculated.

Changes in biceps muscle TMS-response in LEARN1, LEARN3, LOAD and CONTRA sessions were quantified through two indexes: MEP amplitude, and the background activity of the biceps muscle (BG2). The MEP amplitude was measured by calculating the peak-to-peak amplitude of the EMG signal in the interval from 15 to 50 ms after the stimulus.

In order to pool the data across subjects for statistical analysis, the background activity in the LOAD trials was averaged across all trials of each subject and was taken as 100%. The background activity in each of the other series was expressed as the percentage of this value. In order to compare the MEP response across subjects, the MEP amplitude averaged across all LOAD trials was considered to be 100% and the response in other tests was expressed as a percentage of this value.

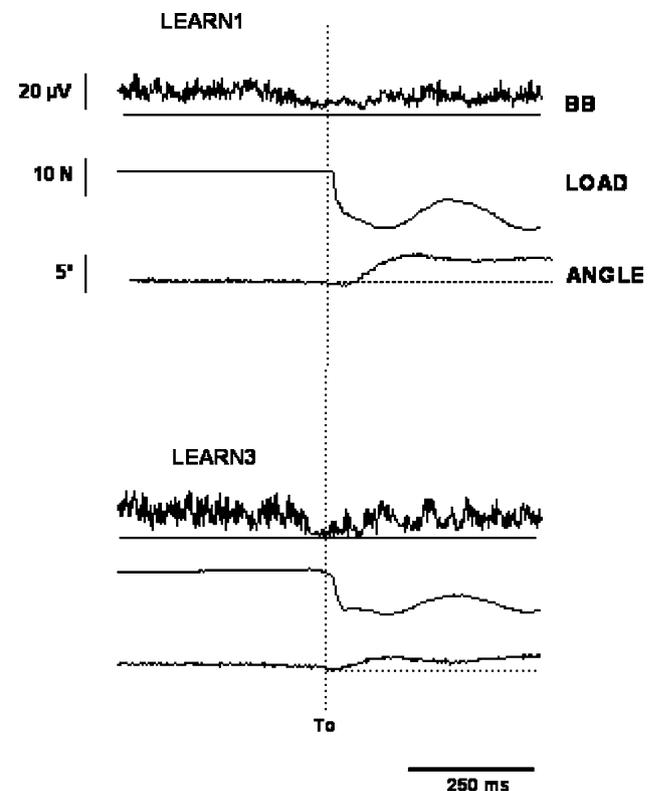
### Statistical analysis

The amplitude of forearm movement and activity of the biceps muscle during learning were analyzed using one-way ANOVA [factors: number of learning sessions (LEARN1, LEARN2, LEARN3)]. MEP amplitudes at the beginning (LEARN1) and at the end of learning (LEARN3) were analyzed using paired  $t$  test. The amount and duration of anticipatory inhibition in “natural” and “learned” APAs were also analyzed by means of non-paired  $t$  test. The level of statistical significance was set at 0.05.

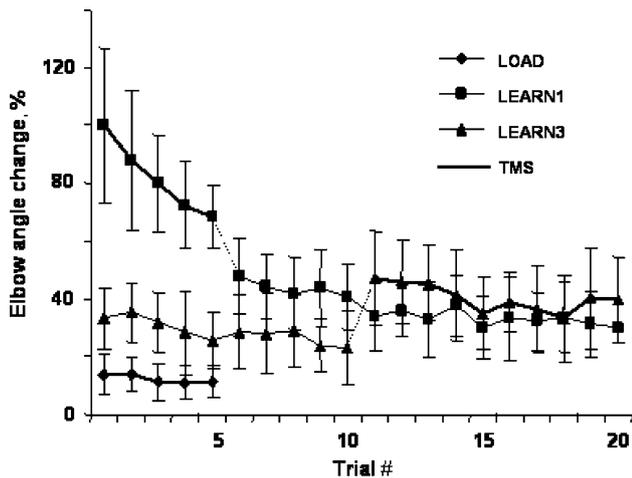
## Results

### Elbow angular displacement and EMG activity during forearm stabilization learning

Figure 2 shows EMG specimen recordings of the biceps muscle, forearm loading, and elbow angular position of the right (postural) arm in the averaged data of the first (LEARN1) and final (LEARN3) sessions of learning. During learning, the amount of biceps activity inhibition increased and the inhibition became better synchronized with the time of unloading. Even though the unloading profiles were similar at the beginning and at the end of learning sessions, practice at the final stage of learning resulted in less elbow flexion after the unloading due to anticipatory biceps activity inhibition. Changes in the amplitude of elbow flexion in sequential trials of the first, second and third learning sessions as well as in the LOAD session are exhibited on Fig. 3. Although a progressive decrease of the elbow angle is observed in the first five trials of the first learning session (up to 68%), the following learning was less intensive. The total decrease of the elbow



**Fig. 2** Elbow angular position and EMG patterns in the process of learning. EMG of biceps brachii (BB) and elbow angular position of the right (postural) arm (ANGLE) averaged across all trials of LEARN1 and LEARN3 sessions for a representative subject. The alignment was done according to the time of disconnection of the electromagnet ( $T_0$ , dotted line)



**Fig. 3** Averaged amplitude of maximal elbow angular displacement after unloading in sequential trials in LEARN1 and LEARN3 sessions and in the control session (LOAD). Thick lines join the trials with TMS. Abscissa—sequential trials; ordinate—the mean and standard deviations of the relative amplitude of elbow angular displacement normalized to the amplitude in the first trial of the first session calculated from all subjects. Note the elbow angular displacement increase up to 20% due to TMS (compare trials 5 and 6 of first series and trials 10 and 11 of third series)

angle in the first learning session was equal to 66%, but in the third learning session it was only 19% of the initial values. Elbow angular displacement after unloading increased due to TMS (see difference between trials 5 and 6 of LEARN1 and between trials 10 and 11 of LEARN3). Note that the same amount of elbow angular displacement increase occurred during the LOAD session accompanied by TMS (circles on Fig. 3).

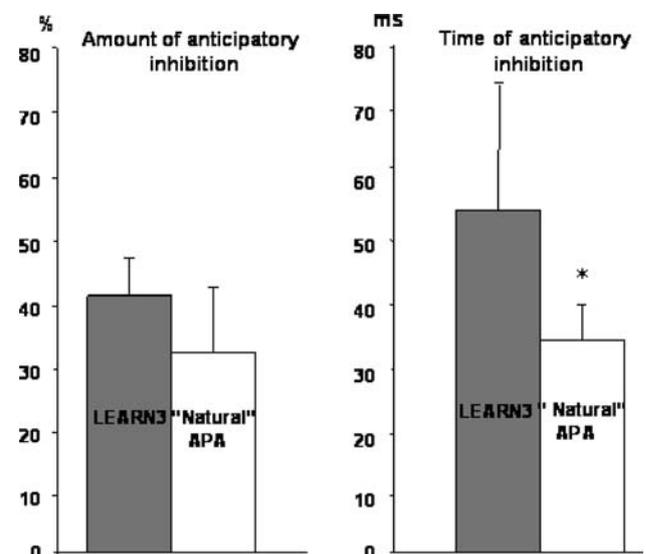
There was a statistically significant change in the amplitude of elbow angular displacement after unloading ( $7.1 \pm 1.0^\circ$ ,  $6.6 \pm 1.1^\circ$ ,  $4.9 \pm 0.6^\circ$  averaged across all trials in LEARN1, LEARN2 and LEARN3 session, correspondingly, ANOVA,  $F_{(2,18)} = 21.44$ ,  $P < 0.05$ ), due to the decrease of biceps muscles activity in preparation for action. The approximation of the learning process using the exponential curves has shown that the elbow angle was changed in LEARN1 significantly (mean time constant  $\tau$  (Eq. 1) across subjects was  $22 \pm 15$  trials) and the changes were less pronounced in LEARN2 and LEARN3 sessions. In the first trial of the first learning session, the amplitude of biceps activity before unloading (BG2) did not significantly differ from the amplitude of biceps activity a long time before unloading (BG1) ( $P = 0.87$ ); in the process of learning, however, BG2 decreased significantly up to  $76 \pm 25$ ,  $72 \pm 25$  and  $55 \pm 19\%$  of BG1 in LEARN1, LEARN2 and LEARN3, correspondingly (ANOVA,  $F_{(2,18)} = 7.00$ ,  $P < 0.05$ ). The activity of the biceps muscles at 200–450 ms prior to unloading (BG1) was not changed across all three learning sessions (ANOVA,  $F_{(2,18)} = 1.77$ ,  $P = 0.2$ ).

### Comparison of APAs in “natural” and “learned” bimanual unloading

The inhibition of biceps activity preceding forearm unloading could not be detected in 2% of trials during “natural APA” (see also Hugon et al. 1982) or in 20% of the trials during learning sessions. The differences between APAs in “natural” and “learned” bimanual unloading, therefore, was calculated by using the other 98% of natural unloading trials and 80% of learning sessions. Figure 4 (left panel) shows that the amount of biceps activity inhibition prior to unloading in “natural APA” and those learned through the experimental session were not significantly different ( $P > 0.14$ , non-paired  $t$  test); however, the duration of anticipatory biceps activity inhibition in learned unloading was significantly greater than in natural unloading ( $P < 0.05$ , non-paired  $t$  test) (Fig. 4, right panel).

### Changes of the amplitude of motor-evoked potential (MEP) in the process of learning

TMS of the motor cortex evoked a biphasic MEP in the biceps m. with a latency of 16–18 ms, which was not changed in the process of learning. MEP amplitude already decreased up to 73% of the MEP amplitude in the LOAD condition ( $P < 0.05$ ) during the first trial of the first learning session (as above mentioned there was no biceps activity inhibition at that time). In the process of learning,

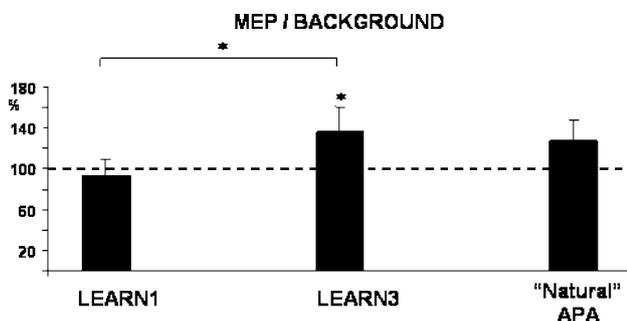


**Fig. 4** Comparison of anticipatory inhibition of background EMG activity (BG2/BG1) and the duration of the anticipatory inhibition in “learned” and “natural” APAs. In this figure and the following figures, the graphs represent the grand mean with standard deviation bars

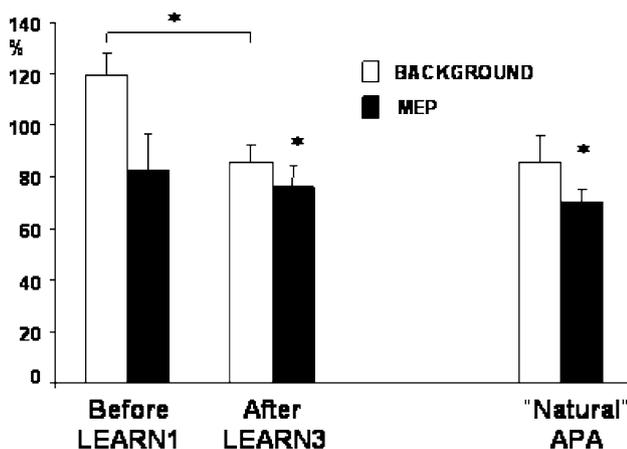
the MEP amplitude decreased in LEARN1 and LEARN3 sessions up to  $69 \pm 30$  and  $57 \pm 30\%$  of that in the LOAD condition, respectively, but the difference between MEP amplitudes in LEARN3 and LEARN1 sessions did not achieve the level of significance ( $P = 0.28$ ). However, the MEP/ BG2 ratio in LEARN3 session was significantly higher than in the LEARN1 session and in the LOAD ( $P < 0.05$ , paired  $t$  test). In the LEARN3 session, the MEP/ BG2 ratio was approximately equal to the natural APA ratio (Fig. 5).

#### MEP amplitude change in the contralateral test

Figure 6 shows the MEP amplitude and the corresponding background EMG activity in the CONTRA test before and



**Fig. 5** Ratio MEP/background muscle activity in the “learned” and in the “natural” APA experiments. Asterisk upon the column indicates the significant difference between the MEP/background ratio in current and LOAD conditions. MEP amplitude averaged across all LOAD trials was considered to be 100% and the response in other tests was expressed as a percentage of this value



**Fig. 6** MEP response and background muscle activity in the contra lateral test before and after learning and in the “natural” APA experiment. MEPs amplitude and EMG background activity are expressed as a percentage of those in the LOAD condition. Asterisk upon the column indicates the significant difference between MEP in current and LOAD conditions

after learning and in the “natural APA “experiment. Before learning, the left arm lifting 1-kg without right arm unloading resulted in an increase of right biceps muscle activity up to 40–50% of background muscle activity (BG1) in some subjects. Averaged across all subjects this increase of muscle activity consisted of 19% and was not significant ( $P = 0.13$ ). Before learning, the average MEP amplitude in the CONTRA test decreased up to 83% of the MEP amplitude in LOAD, but the difference between MEP amplitude in the CONTRA and LOAD conditions did not achieve the level of significance ( $P = 0.27$ ). After learning, the postural arm biceps activity (BG2) in the CONTRA session decreased. Averaged across all subjects, this decrease consisted of 86% of BG1 and was significantly less than it was in the CONTRA test before learning ( $P < 0.05$ , paired  $t$  test). MEP amplitude in the CONTRA session after learning was 76% of the MEP amplitude in LOAD, and it was significant ( $P < 0.05$ , paired  $t$  test). The relationship between MEP and ongoing muscle activity in the CONTRA test after learning corresponds to those in “natural” APA.

#### Discussion

It was shown in the previous study (Kazennikov et al. 2005) that in the active bimanual unloading (“natural” synergy), MEP amplitude decreased with the decrease of muscle activity during APA. This does not suggest the active participation of the motor cortex in APA during natural unloading. Also, a study of bimanual unloading in stroke patients revealed that forearm stabilization in the natural synergy is mainly disturbed after basal ganglia, but not motor cortex, lesions (Ioffe et al. 2002). This corresponds to the data by Diedrichsen et al. (2005) demonstrating that APA during natural unloading is intact in acallosal patients, which suggests its subcortical organization. In the meantime, APA formation after learning is impeded in patients with lesions involving the motor cortex and internal capsule (Massion et al. 1999; Ioffe et al. 2002) and with cerebellar lesions (Diedrichsen et al. 2005). These data suggest that the motor cortex and cerebellum are mainly involved in learning new synergies for forearm stabilization but are not involved in the realization of the natural synergy.

The results of the present study show that during the learning procedure, MEP amplitude starts to decrease at just the beginning in the first trial—i.e. before the real learning starts and before any decrease of EMG activity. Possibly, this initial suppression of the motor cortex excitability is a result of interhemispheric influence from the contralateral motor cortex accompanying the command to lift left forearm. This assumption is confirmed by a

similar decrease of MEP amplitude in the contralateral test. MEP amplitude continues to decrease in the process of learning. However, in contrast to the natural synergy, MEP amplitude decrease in the process of learning was not proportional to the EMG decrease. Particularly, biceps muscle activity decreased significantly greater than MEP amplitude. As a result, the ratio MEP/background EMG increased in the process of learning (Fig. 5). This suggests an active involvement of the motor cortex in the organization of a new EMG pattern of APA during forearm stabilization learning.

The motor cortex participation in the control of posture is shown in animals (see review by Deliagina et al. 2006) and humans (Horak and Macpherson 1996). The primary motor cortex was shown to be connected to specialized, but not automated movements. In unusual condition, the increase of the motor cortex activity during standing on the rocking platform was shown (Solopova et al. 2003). Thus, postural instability requires a high hierarchical level of posture control. In animals, the activity of pyramidal tract neurons was specifically related to the control of posture during the platform tilting (Beloozerova et al. 2005). In stroke patients, enhanced activity of the motor cortex was shown during motor function recovery (Liepert et al. 2006). The above-presented data are in line with the known data about motor cortex involvement into acquisition of the new postural skills and its minor participation in the control of the well-learned postural patterns. Perhaps, the motor cortex is involved in the APA adaptation, as it was shown during standing of amputees by Aruin et al. (1997) and during walking of healthy subjects in new environmental constraints by Zettel et al. (2002). Let us note that in order to achieve forearm stabilization, it is necessary to prevent biceps muscle shortening after the unloading. A way to organize this is to decrease the biceps muscle activity during APA. The APA pattern does, in fact, result in biceps activity inhibition just before unloading. Perhaps a way to accomplish this is to decrease the motor cortex activity, which will result in a decrease of the biceps activity. This way may possibly be realized by the MEP decrease in the process of learning. Liepert et al. (1998) showed that the learned inhibition of a hand muscle during activation of another muscle is associated with the decrease of MEP amplitude in the inhibited muscle, as a result of the increase of intracortical inhibition and the decrease of intracortical facilitation. According to Davey et al. (1994), low levels of TMS may produce suppression of voluntary muscle activity. The authors propose that this is a result of the activation of intracortical mechanism that reduces corticospinal output to the muscle. Tamarova et al. (2007) showed that GABAergic system of the motor cortex reduces the posture-related responses of pyramidal tract neurons. Soto et al. (2006) revealed the decrease of

intracortical inhibition during both voluntary and postural activations of m. soleus.

Thus, cortical inhibition plays a role in the organization of muscle inhibitory reactions. In our experiments, however, MEP amplitude decrease was not linked with muscle activity decrease. This suggests that some other active process in the motor cortex participates in organization of the APA pattern.

Perhaps the motor cortex not only decreases its activity, but also actively organizes inhibition of the biceps EMG in the process of learning. The previous animal experiments suggested that the specificity of the motor cortex in learning new motor tasks is shown by inhibition of inappropriate synergies, which prevent the performance of a new movement (Ioffe et al. 2002). The above-presented data suggest that the increase of the MEP/background ratio is a result of increase of the motor cortex activity during learning a new pattern, which provides inhibition of biceps activity (cortical motor engram, according to Monfils et al. 2005). Motor cortex activation reaches maximum at the last learning session, but the most intensive learning takes place in the first session. This suggests that the new cortical pattern needs some time to be formed. Perhaps the most intensive learning in the first session is provided by initial inhibition of the motor cortex activity.

However, the motor cortex is not the only brain structure taking part in learning a new postural pattern during bimanual unloading. The cerebellum plays an important role in this process as well. Diedrichsen et al. (2005) revealed that while over-learned anticipatory adjustments are preserved after cerebellar lesions, adaptation of this response and the acquisition of a novel coordination requires the cerebellum ipsilateral to the postural hand. The role of cerebellum in learning new postural tasks is reviewed elsewhere (Ioffe et al. 2007).

The limitation of the present study is the influence of the TMS on the process of learning. The similar effect was shown earlier by Romaguere et al. 2004 where TMS impulses influenced the velocity of the kinesthetic illusion. In our experiment TMS produced the additional elbow movement. It is clearly shown in Fig. 3, where elbow flexion increase up to 20% due to TMS in LEARN3 sessions. Presumably, that might influence the acquisition of new APA. The question arises, whether this effect might be a result of circular coil stimulation. However, the stimulation produced local flexion of biceps muscle, so this suggests that the spread of the stimulus did not influence the results considerably.

Let us note that the weight lifting by the contralateral arm in the CONTRA test before learning was accompanied by increased muscle activity in the postural arm, but the amplitude of the MEP was decreased (Fig. 6). The decrease of MEP amplitude was perhaps a result of

interhemispheric inhibition of the motor cortex, whereas the increase of EMG was evoked by segmental interaction. However, after learning, the CONTRA test was accompanied by a decrease of postural arm biceps activity and a rather small decrease of the MEP. As a result, the MEP and background muscle activity became similar to that in natural APA. This suggests that after learning, the lifting of the weight by the other arm accompanied by the inhibition of the muscle activity is independent of whether unloading will be or not.

## Conclusions

The results of this study reveal that in contrast to natural bimanual unloading, the motor cortex plays an active role in learned forearm stabilization in a new bimanual unloading procedure. The inhibition of the biceps muscle activity of the postural arm occurs in two steps. The first step corresponds to the decrease of the motor cortex activity, partly by interhemispheric influences during the lifting of a weight by the other arm, and also by intracortical processes. The second step presumably consists of the organization of a new motor cortex activity pattern (cortical motor engram), which suppresses the muscle activity. This process may be attributed to the increase of the MEP/background ratio in the process of learning.

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