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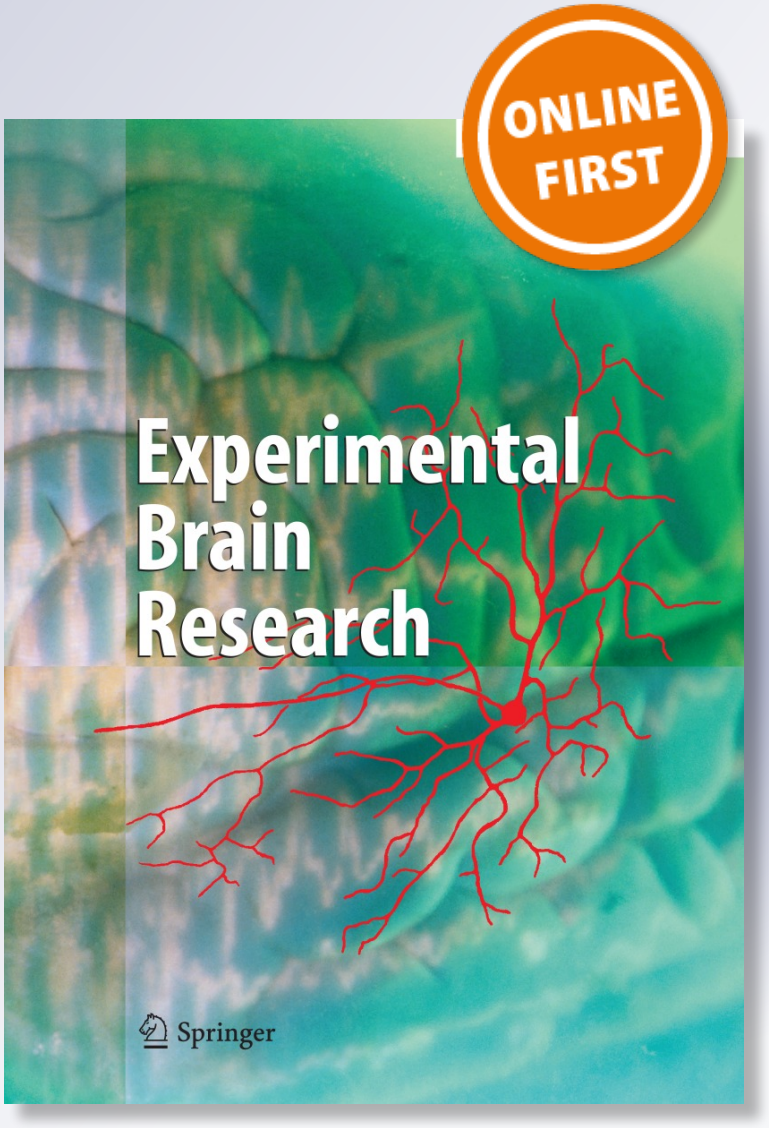

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RESEARCH ARTICLE

Prior history of FDI muscle contraction: different effect on MEP amplitude and muscle activity

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Abstract Motor evoked potentials (MEPs) in the right first dorsal interosseous (FDI) muscle elicited by transcranial magnetic stimulation of left motor cortex were assessed in ten healthy subjects during maintenance of a fixed FDI contraction level. Subjects maintained an integrated EMG (IEMG) level with visual feedback and reproduced this level by memory afterwards in the following tasks: stationary FDI muscle contraction at the level of 40 ± 5 % of its maximum voluntary contraction (MVC; 40 % task), at the level of 20 ± 5 % MVC (20 % task), and also when 20 % MVC was preceded by either no contraction (0–20 task), by stronger muscle contraction (40–20 task) or by no contraction with a previous strong contraction (40–0–20 task). The results show that the IEMG level was within the prescribed limits when 20 and 40 % stationary tasks were executed with and without visual feedback. In 0–20, 40–20, and 40–0–20 tasks, 20 % IEMG level was precisely controlled in the presence of visual feedback, but without visual feedback the IEMG and force during 20 % IEMG maintenance were significantly higher in the 40–0–20 task than those in 0–20 and 40–20 tasks. That is, without visual feedback, there were significant variations in muscle activity due to different prehistory of contraction. In stationary tasks, MEP amplitudes in 40 % task were higher than in 20 % task. MEPs did not differ significantly during maintenance of the 20 % level in tasks with different prehistory of muscle contraction with and without visual feedback. Thus, in spite of variations in muscle background activity due to different prehistory of contraction MEPs did not vary significantly. This dissociation suggests that the voluntary maintenance of IEMG level is determined not only by cortical mechanisms, as reflected by corticospinal excitability, but also by lower levels of CNS, where afferent signals and influences from other brain structures and spinal cord are convergent.

Keywords Transcranial magnetic stimulation · First dorsal interosseous muscle · Biofeedback · IEMG

Introduction

The investigations of motor cortex activity by means of transcranial magnetic stimulation (TMS) have shown the essential role of the motor cortex in fine muscle actions (Hess et al. 1987; Porter and Lemon 1993; Baker et al. 1995; Lemon et al. 1995; Tinazzi et al. 2003; Loh et al. 2010). This is highlighted by the facilitatory effect of hand muscles' voluntary contraction on motor evoked potentials (MEPs). The participation of motor cortex not only in voluntary muscle activation, but also in motor task planning (Bagce et al. 2013), motor imagery (Hashimoto and Rothwell 1999), motor learning (Muellbacher et al. 2001) is now generally accepted. Thus, the extra facilitatory effect on the MEP amplitude is observed during the motor tasks

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of high complexity, demonstrating the essential role of motor cortex on relatively high hierarchical level. However, data have been accumulated showing dissociation between muscle background activity and MEP amplitude not only during complex voluntary hand movements, but also during simple, automated motor actions, such as anticipatory postural adjustments (APAs; Kazennikov et al. 2005), corticospinal influences on abductor pollicis brevis (AbPB) and first dorsal interosseous (FDI) muscles decreased in several seconds during stationary finger grasp (Kazennikov and Levik 2009). The history of wrist flexors contraction can also alter cortical excitability, namely the reduction in the amplitude of the wrist flexor MEP response after conditioning contractions was shown (Stuart et al. 2002).

It was shown before that maintenance of finger muscle IEMG or force level is learned easily with visual feedback and is reproduced by memory afterwards (Talis et al. 2012). Additionally, matching performance without visual feedback is systematically affected by intervening forces (Park and Leonard 2008). The rationale for the present study was to analyze to what extent the prehistory of muscle activity could modify the relationship between EMG level and MEP amplitude. For this purpose, we examined the corticospinal excitability during the maintenance of a given level of voluntary activity in the FDI muscle preceded by this muscle's relaxation—contraction with and without visual feedback. We aimed to see MEP amplitude change during the muscle activity fluctuation caused by prehistory of muscle contraction. A short account of some of the present findings was published as an abstract (Talis et al. 2011).

Materials and methods

Subjects

Ten right-handed volunteers (7 males and 3 females, aged 20–55 years) with no history of neuromuscular disease participated in the experiment. Subjects gave informed consent to the experimental procedures, which were approved by the local ethics committee (at the Institute for Information Transmission Problems) and were applied in accordance with the Declaration of Helsinki.

Procedure

The subjects were seated comfortably in front of a computer screen with their right shoulder and elbow flexed, and forearm resting on a table. The hand was placed into a clamp with the proximal phalange of the index finger pressed against the force transducer on the stopper, and the third, fourth, and fifth fingers pressed against the other part of the stopper on the table (Fig. 1a). The stopper was not fixed to the table. Prior to the experiment, subjects were instructed to exert the maximum voluntary contraction (MVC) for 10 s with FDI muscle in response to the visual GO signal and generate the force by index finger abduction without using the whole hand, keeping palm and forearm steady on the table. This maximum force (F_{max}) and the corresponding EMG and IEMG of FDI muscle (EMG_{max} and $IEMG_{max}$) were considered as reference values for each subject. MVC of FDI muscle was repeated after the experiment to control fatigue (Fig. 1b).

After determination of the MVC, subjects performed one training trial in each of the stationary contractions at 20 and 40 % MVC with and without visual feedback. Visual feedback was given to subjects on the computer screen with boundaries of rectified and smoothed EMG activity. Without visual feedback, subjects reproduced the contraction of the muscle at 20 and 40 % MVC in front of the empty screen.

During the experiment, subjects executed five experimental tasks with and without visual feedback (Fig. 1b): (1) stationary contraction of 20 % MVC for 10 s (20 % task); (2) stationary contraction of 40 % MVC for 10 s (40 % task); (3) 40 % MVC contraction for 5 s, followed by 20 % MVC contraction for 5 s (40–20 task, total duration—10 s); (4) 40 % MVC contraction for 5 s, followed by muscle relaxation for 5 s and 20 % MVC contraction for 5 s (40–0–20 tasks, total duration—15 s); and (5) muscle relaxation for 5 s followed by 20 % MVC contraction for 5 s (0–20 task, total duration −10 s). After each trial without visual feedback, no information about the performance was given to the subject. Each subject performed the tasks in the same sequence.

Parameters recorded

EMG activity was recorded from the FDI muscle of the right hand with a pair of silver–silver chloride surface EMG electrodes. The pre-amplified EMG signal was band-pass filtered (50 Hz–1 kHz) prior to sampling at 2 kHz. The integrated EMG (rectified and averaged over 10 sample points, IEMG) was continuously monitored throughout the series of experiments to provide IEMG-based visual feedback. Force production was measured using a custom-made force transducer on a stopper and sampled at 2 kHz.

Measurement of motor excitability

Transcranial magnetic stimulation (TMS) was delivered by a Mags1 (Schwarzer, Germany, maximum output: 2T) using a figure 8-shaped magnetic coil (diameter of inner wings—7 cm). The coil was placed tangentially to the scalp, with the handle pointing postero-laterally at a 30° angle from the midline, and the direction of the current was

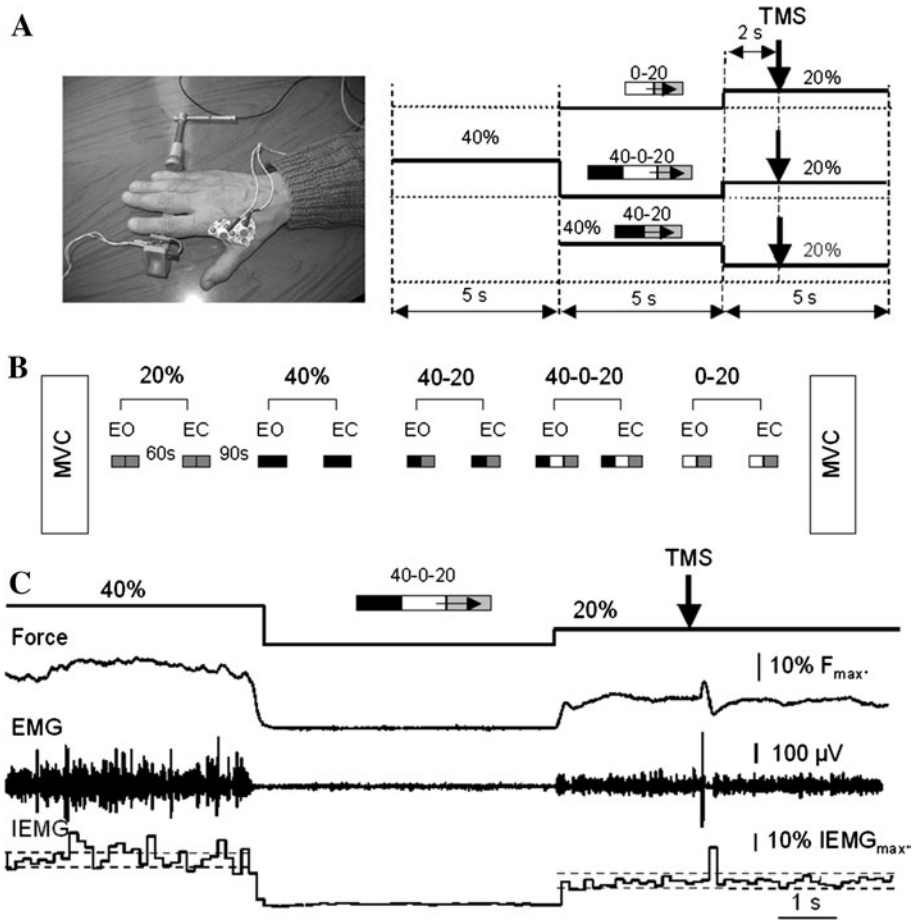

Fig. 1 Experimental paradigm. **a** *Left* Posture of the hand during performance of the task. *Right* schematic time course of the IEMG % produced during three tasks with different prehistory of muscle contraction. 20 and 40 % of IEMG FDI at maximum voluntary contraction (MVC). *Vertical lines* were presented to the subject, showing when the subject should relax or contract the muscle during each trial. *Vertical arrows* show the time of transcranial magnetic stimulation (TMS) application in different tasks. **b** Sequence of tasks. Each task was executed five times, one by one. *EO* eyes open, *EC* eyes closed. MVC was executed before and after all tasks. **c** One representative example of 40–0–20 task execution with visual feedback. *IEMG* integrated EMG. *Dashed horizontal lines* (10 % range of desired IEMG) and executed IEMG were presented to subjects in every task with visual feedback

clockwise when viewed from above. The position of the coil was adjusted on the scalp over the left M1 to find the optimum location of the right FDI muscle (usually 5–7 cm lateral to the midline along the interaural line) to produce MEPs in FDI muscle. The active motor threshold defined as the minimum intensity needed to evoke a MEP 3 times greater than background activity of FDI muscle in three out of five consecutive trials was measured in the tonically active FDI (about 20 % of MVC as assessed visually on the computer screen). It corresponded to the stimulation intensity from 30 to 40 % of maximum stimulator output depending on the subject and was used for each particular subject throughout the entire experiment. In order to stabilize the coil position during the experiment, the coil was fixed to the chair with a brace and taped to an elastic swim cap on the subject's head. The amplitude of MEPs was verified in 5 trials at 20 % MVC with visual feedback at the beginning and at the end of the experiment to ensure that the coil position remained steady. The stimulus was delivered at 2 s after setting of 20 % MVC level, that is, at 7 s after trial starts in 40–20, 0–20, and 20 % tasks; at 12 s after trial starts in 40–0–20 task. In 40 % tasks, TMS was delivered at 7 s after trial start (see also Fig. 1a, c).

Data analysis

The MEP amplitude was measured by calculating the peak-to-peak amplitude of EMG signal in the interval from 15 to 40 ms after the stimulus. In order to compare the MEP response across subjects, the MEP amplitude averaged for all trials with visual feedback at the level of 20 % MVC was considered to be 100 %, and the response in other tests was normalized to this "baseline calibration." In order to evaluate the task execution, we calculated the mean value of IEMG during 500 ms (between 2,000 and 2,500 ms after TMS—IEMG_Late). In order to relate the response to TMS to the voluntary activation of the muscle, we also evaluated the background level of muscle activity during 20 ms before TMS (mean value between 5 and 25 ms before TMS stimulus—EMG_Pre). Force signal was measured as a mean value between 2,000 and 2,500 ms after TMS stimulus (Force). The values of EMG_Pre, IEMG_Late, and Force were normalized to those at MVC.

Statistical analysis

To evaluate the effects of prehistory on 20 % muscle contraction, the two-way ANOVA with the first factor

"task"(40–20; 40–0–20; 0–20 and 20 % tasks) and the second factor "vision" (vision, no vision) was used. When significant effects were found, post hoc Tukey's testing was conducted to identify the loci of these effects. MEP amplitudes in two stationary tasks (20 and 40 %), as well as MEP responses at 20 % MVC and F_{max} at the beginning and at the end of the experiment, were also analyzed using paired *t* test. The level of statistical significance was set at 0.05.

Results

Steady coil position during the experiment revealed insignificant difference between MEP responses at 20 % MVC contraction at the beginning and at the end of the experiment (0.68 ± 0.12 and 0.70 ± 0.14 mV, respectively, paired *t* test, $p = 0.07$). Also, TMS-induced muscle response did not significantly affect the accuracy of task execution: the difference between EMG_Pre and IEMG_Late in all tasks with and without visual feedback was not significant (for instance without visual feedback, EMG_Pre was 0.18 ± 0.02; 0.29 ± 0.03; 0.20 ± 0.02; and 0.23 ± 0.02 % EMG_{max}, and IEMG_Late was 0.17 ± 0.01; 0.25 ± 0.01; 0.18 ± 0.01; and 0.22 ± 0.01 % $IEMG_{max}$ in 40–20, 40–0–20, 0–20, and 20 % tasks). There were no effects of fatigue on force production during the experiment: the difference between maximum force measurements before and after the experiment was not statistically significant (32.4 ± 4.3 and 34.6 ± 6.3 N, respectively, paired *t* test, $p = 0.57$).

Stationary contraction tasks

Figure 2 shows group mean data of background activity and MEP response of FDI muscle in two stationary contraction tasks. One can see that even if in visually guided 20 and 40 % tasks, the IEMG level was inside the desired corridor (Fig. 2a, dotted line), its average value was slightly less than 20 and 40 % EMG_{max} (17.6 ± 0.6 % and 37.1 ± 2.8 % EMG_{max}, correspondingly). On the contrary, without the visual feedback, the memorized level of muscle activity was reproduced with an overshoot of the prescribed level (22.8 ± 1.7 % and 41.9 ± 2.7 % EMG_{max}, in 20 and 40 % task, correspondingly), and also the difference between mean EMG level during 20 % task execution with and without visual feedback approached the level of significance (paired *t* test, $p < 0.05$).

MEP response in stationary tasks

MEP response in FDI muscle during 40 % task was higher than during 20 % task (paired *t* test, $p < 0.05$), but the double increase in muscle activity did not result in a double increase in MEPs: the mean normalized MEP amplitude during 20 % task was 0.98 ± 0.04 % and 1.52 ± 0.19 %—during 40 % task. A regression analysis of the individual averaged data (Fig. 3) showed a significant

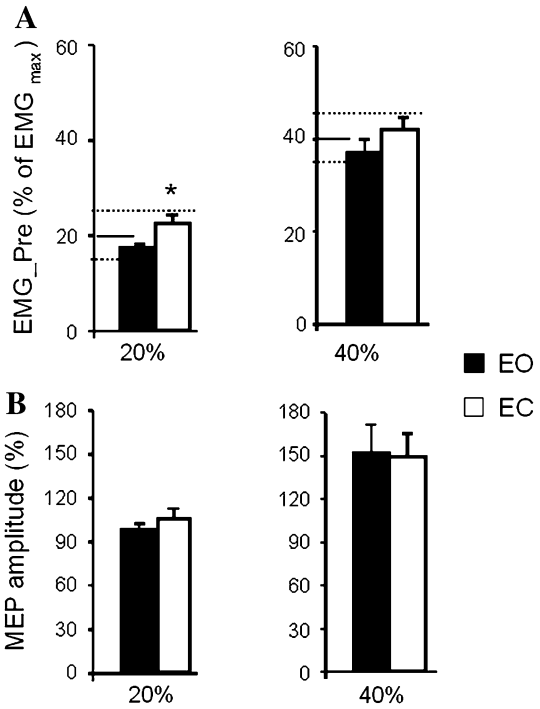

Fig. 2 Stationary FDI muscle contraction in 20 and 40 % tasks. The grand means of background FDI muscle activity, EMG_Pre (**a**) and MEP amplitude, MEPs (**b**) for all subjects ($n = 10$) during 40 and 20 % tasks with (EO) and without (EC) visual feedback. The values of EMG_Pre (%) were normalized to those at MVC, and the values of MEPs (%) were normalized to "baseline calibration" (see "Methods"). *$p < 0.05$

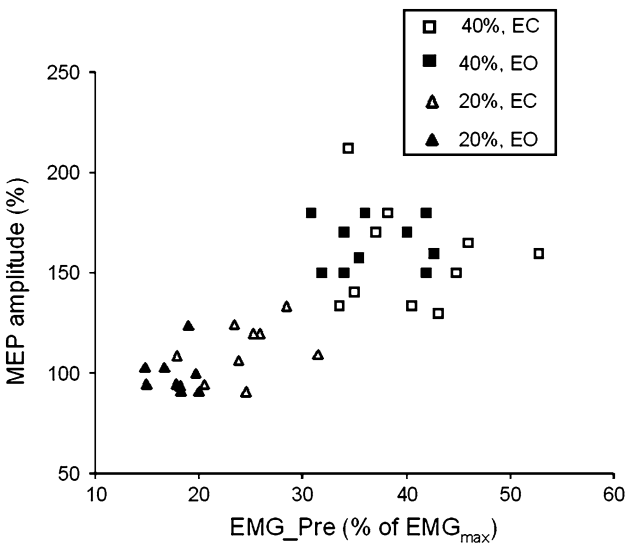

Fig. 3 Relationship between corticospinal excitability and background FDI muscle activity during 20 and 40 % tasks. EMG_Pre and MEP normalization as on Fig. 2

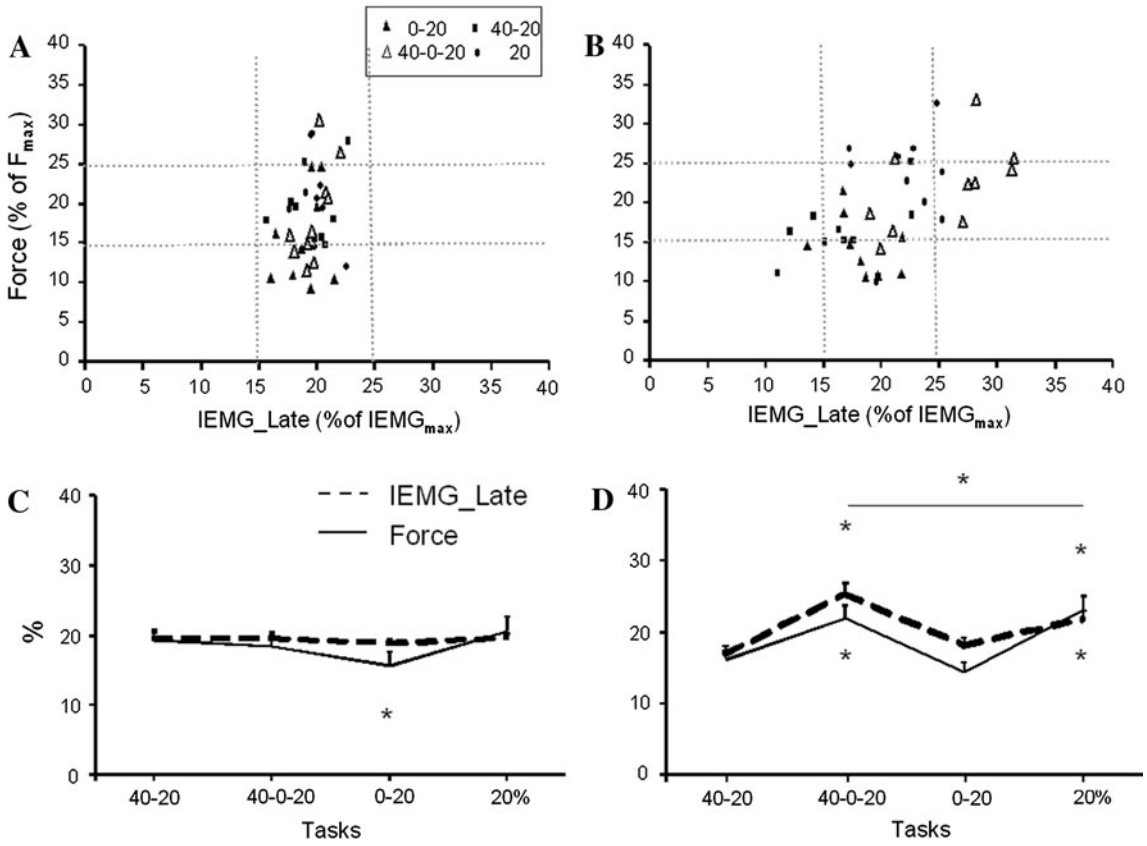

Fig. 4 Relationship between force and background FDI muscle activity in the tasks with different prehistory of muscle contraction. Average individual data of force and IEMG in 40–20, 40–0–20, 0–20, and 20 % tasks executed with visual feedback (**a**) and without it (**b**). *Dashed vertical lines* 15–25 % $IEMG_{max}$ corridor of desired performance. The grand means of IEMG_Late (*dashed line*) and force (*solid line*) of all subjects in 40–20, 40–0–20, 0–20, and 20 % tasks executed with visual feedback (**c**) and without it (**d**). The values of IEMG_Late and Force were normalized to those at MVC. *$p < 0.05$

increase in MEP response with background muscle activity increase (ANOVA, $F(1,37) = 15.06$, $p < 0.0005$). No significant difference in MEP responses between tasks with and without visual feedback, neither during 20 % nor during 40 % tasks, was found (paired t test, $p = 0.59$ and $p = 0.62$, correspondingly).

Tasks with different prehistory of muscle contraction

Figure 4a, b shows the individual averaged data and Fig. 4c, d—group mean data of force and muscle activity during the maintenance of 20 % MVC in 40–20, 40–0–20, and 0–20 tasks. One can see that as in stationary tasks, all subjects were able to accurately control 20 % MVC in the desired corridor in all tasks under visual feedback (ANOVA, $F(3, 24) = 0.84$, $p = 0.48$). When vision was occluded (Fig. 4b, d), the reproduction of 20 % MVC was different depending on the task (ANOVA, $F(3, 24) = 14.601$, $p < 0.0001$). Post hoc test revealed that 20 % $IEMG_{max}$ level in 40–0–20 and 20 % tasks was significantly higher than in 40–20 and 0–20 tasks, in turn in 40–0–20 task higher than in 20 % task ($p < 0.05$).

Force variation during IEMG reproduction

Force data presented in Fig. 4 show that even under visual feedback, muscle activity level was inside the desired corridor in all tasks, and the force exerted by finger muscle during the task execution has been changed (ANOVA, $F(3, 24) = 12.87$, $p < 0.0001$). Post hoc revealed significant decrease in force production during 0–20 task execution ($p < 0.05$). Without visual feedback, force level during 20 % MVC maintenance in 40–0–20 and 20 tasks was significantly higher than in 40–20 and 0–20 tasks ($p < 0.05$). Thus, muscle activity and force were not always related in the presence of visual feedback (Fig. 4c), but the force and muscle activity changed correspondingly when vision was occluded (Fig. 4d).

MEP in tasks with different prehistory of muscle contraction

Figure 5 shows group mean data of background activity and MEP response of FDI muscle in 40–20, 40–0–20, and 0–20

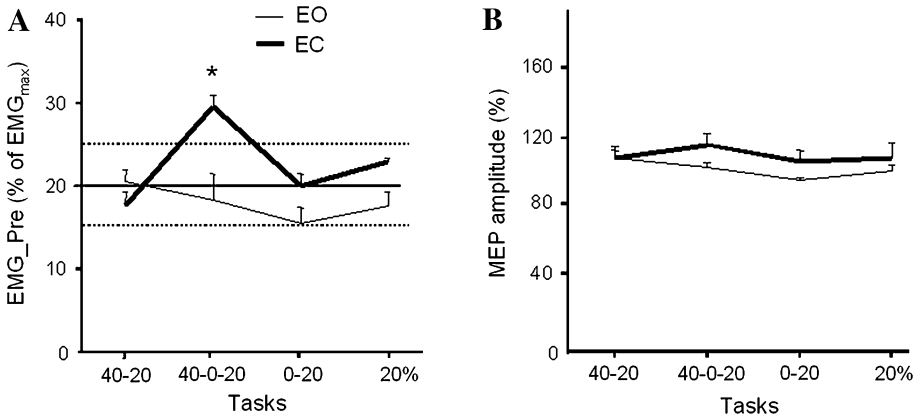

Fig. 5 Motor evoked potentials and background muscle activity during 20 % IEMG maintenance in the tasks with different prehistory of muscle contraction. Means and standard errors of background FDI muscle activity (EMG_Pre) (**a**) and MEPs (**b**) in 40–20, 40–0–20, 0–20, and 20 % tasks executed with visual feedback (*thin line*) and without visual feedback (*thick line*). MEP and EMG_Pre normalization as on Fig. 2. $^{*}p < 0.05$

tasks. One can see that in the visually guided tasks, FDI muscle activity, as well as its MEP response, did not significantly differ from task to task (Fig. 5, thin line). When vision was occluded (Fig. 5, thick line), MEP amplitude of FDI muscle still did not change in spite of the significant increase in background muscle activity during 20 % MVC reproduction in 40–0–20 task ($F(3,24) = 3.76$, $p < 0.05$).

Discussion

In this paper, we examined the corticospinal excitability during the maintenance of a given level of voluntary activity in the FDI muscle preceded by this muscle's relaxation—contraction with and without visual feedback. We analyzed MEP amplitude changes during the muscle activity fluctuation caused by prehistory of muscle contraction. Our data showed that FDI muscle activity deviations due to prehistory of muscle contraction were not accompanied by the corresponding change in corticospinal excitability. We found that strong muscle contraction followed by muscle relaxation resulted in a significant overshoot of the memorized 20 % MVC level; this misjudgement of muscle activity was not accompanied by a corresponding change in FDI MEP amplitude.

IEMG maintenance with and without visual feedback

With visual feedback, subjects maintained FDI muscle activity on 40 and 20 % MVC level for 10 s well inside ±5 % corridor with the tendency to keep IEMG mean level less than 40 and 20 % MVC, correspondingly. This result is similar to visual feedback IEMG control of AbPB muscle (Talis et al. 2012), where the variability index of 20 % task was also shown to be less than in 40 % task. When the task was executed by memory, the muscle activity level was also reproduced well inside the desired ±5 % corridor for 10 s with the tendency of mean IEMG level to be more than 40 or 20 % MVC, correspondingly (Fig. 2). Since the visually guided performance was executed with the undershoot and memory based performance, with the overshoot of the desired mean level of muscle activity, one can conclude that the fine control of finger muscles activity in the presence of visual feedback manifests itself in the suppression of excessive muscle contraction, and the consequent overestimation of the desired muscle activity level when vision was occluded.

The effect of finger muscle contraction's prehistory on the level of force reproduction by memory was demonstrated in research by Park and Leonard (2008). Their subjects were instructed to reproduce two reference forces (10 and 30 % MVCs) after four intervening forces (Zero, Half, Same, and Double the reference force) without visual feedback. The experiment showed that the reference force was overestimated in the task where the intervening force was double the size of the reference force. This result resembles the overshoot of the desired level in our 40–0–20 task. Considering that the 20 % level was better reproduced in the 40–20 task, than in the 40–0–20 task, one can conclude that it was not the level of reference force, but the duration of the relaxation period between reference and intervening force played an essential role in force level reproduction error of the Park and Leonard experiment. When the relaxation period of 5 s (or 1.5 s in Park and Leonard's paper) interrupted the step-wise memorized force change, the reference level was lost. In our experiment, not a force but IEMG signal was presented to the subject during visual feedback tasks. One can suppose that, not the FDI muscle activity but the resulting force was actually controlled, because the FDI muscle mainly produces index finger abduction. However, our experimental data showed that force and muscle activity did not always change together when visual feedback was available (Fig. 4c): at least in 0–20 task, the antogonist muscle coactivation may take place. On the other hand, without visual feedback, fine IEMG control has turned into force interaction between the interphalangeal joint and a support (Fig. 4d). Based on the force–support interaction, the

accuracy of the 20 % task execution with different prehistory of muscle contraction varies depending on the task: the IEMG and force level were significantly higher in the 40–0–20 task, than in the 40–20, 0–20, and 20 % tasks. In other words, strong muscle activation followed by relaxation led to the significant error during the intermediate IEMG level reproduction.

TMS-response and muscle contraction prehistory

FDI MEP amplitudes did not significantly change when the 20 % MVC level was overestimated in 40–0–20 tasks' performance without visual feedback (Fig. 5). There may be a methodological reason for this, namely due to the saturation of motor response in the FDI muscle (Turton and Lemon 1999), which was shown to be significantly greater than in more proximal muscles—biceps and the deltoid. If the rate of increases in FDI MEP amplitudes starts to slow down even at 10 % of MVC, it is possible that the majority of motor units of this small muscle were recruited at 20 % MVC, and this led to the smaller MEP increase at a higher force level. The regression analysis showed the relationship between MEP and EMG; however, this relationship was not direct: the double increase in background activity from 20 to 40 % MVC did not result in a proportional increase in FDI MEP amplitudes (Figs. 2, 3). Still, the contraction of the FDI in the 40–0–20 task could be accompanied by a proportional increase in MEPs. In our study, MEPs increased even at 40 % of MVC, so it is unlikely that the stability of MEP amplitudes in the explored tasks was related to saturation.

In our current research protocol, the subjects learned through the visual feedback session and reproduced the task from memory during the session without visual feedback. Taking into account that during memory reproduction, no feedback about the performance was given, the subjects extracted a certain template from memory and were explicitly sure about its accurate performance. It appeared that a certain combination of muscle contraction prehistory resulted in the significant error in performance, but this motor error was not accompanied by the corresponding MEP response change. It would be interesting to compare this effect with the virtual reality experiment, where the subjects flexed a virtual forefinger with the distorted visual feedback and learned to overcome it (Bagce et al. 2013). Analyzing FDI MEPs, authors have shown that the changes in corticospinal excitability were related to learning, but not a motor output or motor error. Investigation of APA before bimanual unloading, well known as a "barmen effect," has also shown motor cortex involvement into acquiring of the new unloading paradigm ("unnatural synergy"), but not into the over-learned unloading ("natural synergy"; Kazennikov et al. 2008).

In contrast to growing number of evidence that motor cortex is involved in motor learning, the number of studies questioning the role of motor cortex in the involuntary muscle action is quit rare. For instance, the subcortical origin of the involuntary deltoid muscle activity in the Kohnstamm phenomenon was demonstrated (Mathis et al. 1996). Motor cortex was shown to be actively involved in the vibratory reaction switch in elbow joint and vibratory-induced illusory movement (Naito et al. 1999); MEPs were shown to decrease due to long-lasting stationary finger grasp (Kazennikov and Levik 2009) and also due to the conditioning voluntary contraction of wrist flexor (Stuart et al. 2002).

Considering corticomotoneuronal excitability to be more related to the intended task than to the executed action, one can suppose that the motor command was the same during the execution of the desired level of a 20 % EMG in all experimental tasks of our study, but the real level of IEMG has changed due to the aftereffect of the preceding contraction. As a result, the level of background muscle activity varied depending on the prehistory of muscle contraction and was not related to the MEPs amplitude. Our finding is in line with the recently published TMS study by Janssen et al. (2013), where the subjects observing person's action exhibited the modulation of output to FDI that was consistent with the action specified rather the action observed. One of the possible explanations for the dissociation between variations in background muscle activity and MEPs response is that other brain structures and spinal cord were involved in the tasks with different prehistory of muscle contraction execution. Review by Prodoehl et al. (2009) showed that key basal ganglia nuclei are involved in parameterizing specific properties of precision grip force in norm (fMRI data) and pathology (Parkinson's disease, Huntington's disease, basal ganglia damage), namely prominent basal ganglia activation was demonstrated in the static force task, but not in a previous force task involving repetitive dynamic force pulses (Dettmers et al. 1996). Authors concluded that sustained exertion of a static force is an active process modulated, at least in part, by the basal ganglia.

In conclusion, the dissociation between FDI muscle activity variations due to different prehistory of contraction and the corresponding MEPs response in this muscle provides evidence that the level of activity in FDI muscle is not completely determined by the cortico-motoneuronal influence. The subcortical or low-level structures of CNS could possibly be involved in the proprioceptional control of this muscle activity.

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References

Bagce HF, Saleh S, Adamovich SV, Krakauer JW, Tunik E (2013) Corticospinal excitability is enhanced after visuomotor adaptation and depends on learning rather than performance or error. J Neurophysiol 109:1097–1106

Baker SN, Olivier E, Lemon RN (1995) Task-related variation in corticospinal output evoked by transcranial stimulation in the macaque monkey. J Physiol 488:795–801

Dettmers C, Lemon RN, Stephan KM, Fink GR, Frackowiak RS (1996) Cerebral activation during the exertion of sustained static force in man. NeuroReport 7:2103–2110

Hashimoto R, Rothwell JC (1999) Dynamic changes in corticospinal excitability during motor imagery. Exp Brain Res 125:75–81

Hess CW, Mills KR, Murray NMF (1987) Responses in small hand muscles from magnetic stimulation of the human brain. J Physiol 388:397–419

Janssen L, Steenbergen B, Carson RG (2013) Anticipatory planning reveals segmentation of cortical motor output during action observation. Cereb Cortex [Epub ahead of print] PMID: 23960201

Kazennikov OV, Levik YuS (2009) Study of motor cortex excitability in the load holding task. Hum Physiol 35(5):585–591 (in Russian)

Kazennikov OV, Solopova IA, Talis VL, Grishin AA, Ioffe ME (2005) TMS-responses during anticipatory postural adjustment in bimanual unloading in humans. Neurosci Lett 383:246–250

Kazennikov OV, Solopova IA, Talis VL, Ioffe ME (2008) Anticipatory postural adjustment before bimanual unloading reactions: the role of the motor cortex in motor learning. Exp Brain Res 186:215–223

Lemon RN, Johansson RS, Westling G (1995) Corticospinal control during reach, grasp and precision lift in man. J Neurosci 15(9):6145–6156

Loh MN, Kirsch L, Rothwell JC, Lemon RN, Davare M (2010) Information about the weight of grasped objects from vision and internal models interacts within the primary motor cortex. J Neurosci 30(20):6984–6990

Mathis J, Gurfinkel VS, Struppler A (1996) Facilitation of motor evoked potentials by postcontraction response (Kohnstamm phenomenon). Electroencephalogr Clin Neurophysiol 101(4):289–297

Muellbacher W, Ziemann U, Boroojerdi B, Cohen L, Hallett M (2001) Role of the human motor cortex in rapid motor learning. Exp Brain Res 136:431–438

Naito E, Ehrsson HH, Geyer S, Zilles K, Roland PE (1999) Illusory arm movements activate cortical motor areas: a positron emission tomography study. J Neurosci 19:6134–6144

Park W-H, Leonard CT (2008) The effect of intervening forces on finger perception. Neurosci Lett 438:286–289

Porter R, Lemon RN (1993) Corticospinal function and voluntary movement. Oxford University Press, Oxford

Prodoehl J, Corcos DM, Vaillancourt DE (2009) Basal ganglia mechanisms underlying precision grip force control. Neurosci Biobehav Rev 33(6):900–908

Stuart M, Butler JE, Collins DF, Taylor JL, Gandevia SC (2002) The history of contraction of the wrist flexors can change cortical excitability. J Physiol 545(Pt.3):731–737

Talis VL, Kazennikov OV, Castellote JM, Grishin AA, Ioffe ME (2011) The effect of preceding activity of m. first dorsal interosseous on its voluntary contraction and motor cortex excitability. Soc Neurosci Abstr 41:68

Talis VL, Castellote JM, Kazennikov OV, Grishin AA, Ioffe ME (2012) Control of different electromyogram levels of m. abductor pollicis brevis by means of visual feedback in healthy subjects. Zh Vyssh Nerv Deiat Im I P Pavlova 62(1):12–19

Tinazzi M, Farina S, Tamburin S, Facchini S, Fiaschi A, Restivo D, Berardelli A (2003) Task-dependent modulation of excitatory and inhibitory functions within the human primary motor cortex. Exp Brain Res 150:222–229

Turton A, Lemon RN (1999) The contribution of fast corticospinal input to the voluntary activation of proximal muscles in normal subjects and in stroke patients. Exp Brain Res 129:559–572