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Influence of Vibration on Motor Responses in the Upper Arm Muscles under Stationary Conditions and during Voluntary and Evoked Arm Movements under Limb Unloading Conditions

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Abstract—Locomotion of mammals, including humans, is based on the rhythmic activity of spinal cord circuitries. The functioning of these circuitries depends on multimodal afferent information and on supraspinal influences from the motor cortex. Using the method of transcranial magnetic stimulation (TMS) of arm muscle areas in the motor cortex, we studied the motor evoked potentials (MEP) in the upper arm muscles in stationary conditions and during voluntary and vibration-evoked arm movements. The study included 13 healthy subjects under arm and leg unloading conditions. In the first series of experiments, with motionless limbs, the effect of vibration of left upper arm muscles on motor responses in these muscles was evaluated. In the second series of experiments, MEP were compared in the same muscles during voluntary and rhythmic movements generated by left arm m. triceps brachii vibration (the right arm was stationary). Motionless left arm vibration led to an increase in MEP values in both vibrated muscle and in most of the non-vibrated muscles. For most target muscles, MEP was greater with voluntary arm movements than with vibration-evoked movements. At the same time, a similar MEP modulation in the cycle of arm movements was observed in the same upper arm muscles during both types of arm movements. TMS of the motor cortex significantly potentiated arm movements generated by vibration, but its effect on voluntary movements was weaker. These results indicate significant differences in the degree of motor cortex involvement in voluntary and evoked arm movements. We suppose that evoked arm movements are largely due to spinal rather than central mechanisms of generation of rhythmic movements.

Keywords: motor cortex, transcranial magnetic stimulation, vibration, central pattern generator

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Locomotion of mammals, including humans, is based on the activity of spinal cord circuitries (central pattern generators, CPGs) [1, 2]. Although it has been shown that during locomotion spinal cord circuitries determine the pattern of limb muscle activity [2–4], supraspinal centers are an important necessary element of locomotor control in mammals. The motor cortex plays an essential role during walking [5–7], especially in rhythmic arm movements coupled with human walking [8]. Under certain conditions, for example, in a horizontal position of the body during limb unloading, the CPG may be activated by extrinsic noninvasive influences [9]. Such an external influence on afferent inputs can alter not only the state of spinal cord circuities, but also the state of motor cortical neurons [10].

One of the methods of activation of non-voluntary rhythmic leg [9] or arm [11] movements is vibration of limb muscles under unloading conditions and in the absence of the task of vertical stance maintenance. Involuntary leg movements may be generated in 50–80% of healthy subjects, and the possibility of activation of these movements seems to largely depend on the state of the CPG neurons of the corresponding level of the spinal cord, which, in turn, is considerably influenced by descending commands from the motor cortex [12]. Therefore, the generation and maintenance of non-voluntary rhythmic movements addresses the question as to the degree of motor cortex involvement in generated movements. Both voluntary and vibration-evoked movements under the same unloading conditions significantly increase proprioceptive impulsation of moving limbs. This increased proprioceptive input reaches the neurons of the spinal cord generator circuitries and, spreading in the rostral direction, enters the supraspinal structures, in particular, the motor cortical neurons. Using transcranial magnetic stimulation, it was shown that motor evoked potentials (MEP) during vibration-evoked non-voluntary rhythmic leg movements were less in size than

MEP during voluntary movements, which suggests a lesser contribution of the motor cortex to generation of rhythmic movements [10]. Since the motor cortex predominantly regulates upper rather than lower limb movements [13, 14], motor supraspinal commands determine the state of cervical spinal cord motoneurons to a larger degree than lumbar spinal cord motoneurons. In addition, cervical spinal cord motoneuron excitability may depend on the nature of rhythmic arm movements: generation of non-voluntary rhythmic upper limb movements entails lowered motor cortex involvement.

The method of transcranial magnetic stimulation (TMS) is used to study motor cortical excitability [8, 10, 15, 16]. TMS of the motor cortex induces short-latency pyramidal tract–mediated MEP in the target muscles [17]. Note that, during TMS, the force of a descending volley in corticospinal fibers depends on the level of excitability of stimulation-activated cortical neurons, as well as on the state of muscle at the moment of stimulus application. In the act of movement occurring with a greater involvement of the motor cortex, the MEP to background muscle activity ratio is higher than for movements with a lower motor cortex involvement [18]. The relationship between the magnitude of MEP and the nature of rhythmic movements may be an indicator of the state of the circuitries determining these movements.

The influence of arm muscle vibration on the excitability of neurons of motor cortex was studied in several studies. These studies were mainly conducted on forearm and hand muscles. Vibration of forearm muscles was shown to increase their MEP to TMS [19–22] and to influence the degree of activity of local inhibitory circuits investigated with paired TMS (short- and long-latency intracortical inhibition). The sensory input activated by muscle vibration is supposed to be directly addressed to the circuitries of the forearm area in the motor cortex [20]. On the contrary, in the antagonist muscle in relation to vibrated one, we observed an MEP decrease, which is supposed to be due to reciprocal interactions at the spinal level, as well as to inhibitory input from muscle afferents on corticospinal outputs to the antagonist muscle [23].

Most studies of the MEP–motor task relationship were conducted in a sitting or standing position. However, MEP to TMS in arm muscles is known to depend on the position of the body in space [24]. Kantak et al. investigated MEP in the upper arm (m. anterior deltoid) and hand (m. first dorsal interosseus) muscle in two body positions, sitting and standing. The transition from the sitting to the standing position was shown to modulate the magnitude of motor responses in proximal arm muscles. In addition, partial arm unloading also influences the excitability of the cortical neurons innervating upper limb muscles [25], and the degree of the unloading effect on MEP differs for different muscles. Since non-voluntary rhythmic arm movements were activated in this study under limb unloading conditions in the lateral lying position, the influence of vibration on corticomotor excitability could also differ from its influence in different body positions.

In this study, we estimated MEP in different upper arm muscles to TMS of the area of these muscles in the motor cortex under stationary conditions and during voluntary and evoked arm movements under limb unloading conditions.

METHODS

Thirteen subjects (11 men and two women aged 20–68 years) without motor disorders and neurological diseases took part in the experiments. All subjects were informed about the study procedure and gave their consent to participate in the experiment. The study was conducted in compliance with the ethical rules adopted by the Helsinki Declaration. The subjects lay on the right side with hanging upper and lower limbs in the arrangement that makes it possible to perform arm and leg movements in the horizontal plane [11] (Fig. 1a).

Two series of experiments were carried out on different days. Thirteen subjects were enrolled in the first series of experiments. Under stationary conditions, MEP evoked by TMS of the motor cortex were recorded in the left upper arm muscles: m. biceps brachii (BB); m. triceps brachii (TB); m. deltoideus anterior (DA); m. deltoideus posterior (DP) against the background of vibration of each of the muscles (at a frequency of 40–60 Hz and an amplitude of 0.8 mm) and without vibration. The vibrators based on a DMP-3-N1-01 direct current motor with eccentric on the shaft were used for muscle vibrostimulation. Seven subjects out of those enrolled in the first series took part in the second series of the experiments. In all these subjects, vibration generated non-voluntary rhythmic arm movements [11]. MEP to motor cortex TMS were recorded in the same arm muscles during voluntary and m. TB vibration-evoked rhythmic left arm movements, with the right arm being stationary. The vibration parameters were the same as in the first experiment. During vibration, the subjects were asked to relax and not to interfere with possible movement reactions to external effects.

In six subjects enrolled in the first series of the experiments, vibration did not generate arm movements. In these subjects, during vibration of each of the muscles in stationary relaxed arm, ten stimuli without vibration and ten stimuli against the background of vibration were applied in each trial (Fig. 1c). The stimuli were applied at a frequency of 0.4 Hz. Four trials were performed on every subject: vibration of each of the four left arm test muscles. The duration of each trial was 60 s. The subjects were allotted 30–60 s for rest between the trials. In the rest of the sub-

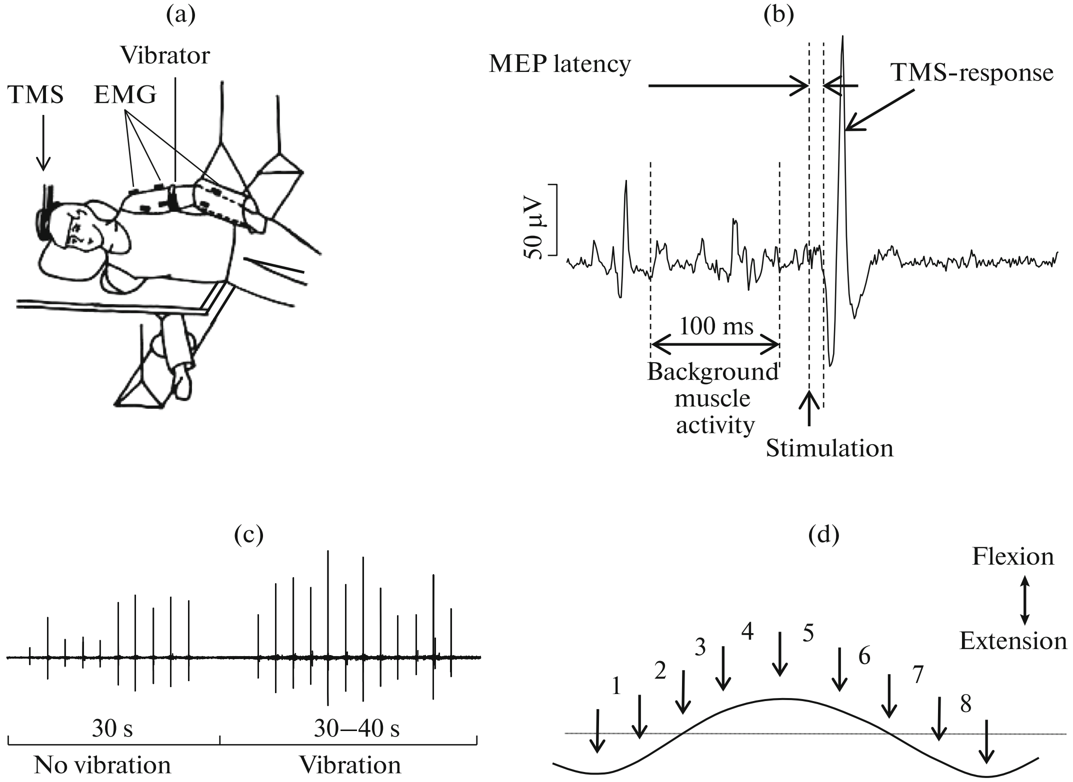

Fig. 1. Method of investigation. (a) The scheme of the experimental setup; (b) an example of muscle response to TMS; (c) the experimental protocol of stimulation under stationary conditions; (d) division of the arm movement cycle into intervals.

jects, vibration generated rhythmic arm movements. The latent period of the evoked rhythmic movement onset varied between 1 and 26 s in different subjects and in different trials [11]. That is why, after application of ten stimuli without vibration, two to five stimuli were applied against the background of vibration before the moment of movement onset. The trials with vibration were repeated until a total of ten stimuli were recorded against the background of vibration, which is a subthreshold for movement activation. The procedure was repeated on vibration of the next muscle.

In the second series of experiments, the motor cortex was stimulated against the background of evoked and voluntary rhythmic arm movements with the steady parameters (constant frequency and amplitude). In each trial, movements were recorded for 10 s without motor cortex stimulation, then for 40–60 s with TMS, and for 10 s without stimulation at the end of the recording against the background of rhythmic movements. The duration of each trial constituted 60–80 s. Ten trials during evoked arm movements and ten trials during voluntary arm movements were recorded. As the stimulation time was 40–60 s, an average of 16–20 stimuli per trial were applied to the motor cortex of each subject. In order to control the invariability of the coil position on the head of the subject, ten stimuli were each recorded on the stationary arm at the beginning and at the end of the second series of experiments.

The electrical muscle activity (EMG) of the left arm was recorded with surface bipolar electrodes using a Delsys wireless amplifier. Angular movements at the shoulder and elbow joints were recorded with potentiometric transducers. The data obtained were digitized at a frequency of 1000 Hz and entered into the computer for subsequent analysis.

Transcranial magnetic stimulation was carried out using a Magstim-200 magnetic stimulator (Schwarzer) (maximum magnetic field intensity on impulse, up to 2 T; duration of single impulses, 200 μs). An 8-shaped magnetic coil was used. The left arm muscle area in the motor cortex was stimulated. The coil was arranged tangentially to head surface (2 cm anteriorly and 2 cm on the right from the vertex) in a position optimal for MEP evocation in most upper arm muscles of stationary unloading arm. We adjusted the stimulus strength (55–65% of maximum stimulator output) so that evoked MEP would exceed the level of background activity at least twice. Stimulation startup was triggered according to the program. The stimuli were applied once in 2.5 s. Since the period of rhythmic arm movements was shorter (1.7 ± 0.2 s) than the period of interstimulus intervals [11], the stimuli was

Table 1. Averaged latent MEP periods (ms) with muscle vibration and without vibration

Muscle	Without vibration	With vibration
BB	16.8 ± 0.5	14.9 ± 0.4*
TB	17.6 ± 0.8	17.6 ± 0.6
DA	15.2 ± 0.4	14.8 ± 0.8
DP	16.2 ± 0.7	14.4 ± 0.8*

* Significant differences in the conditions with muscle vibration and without vibration.

applied the target in random order at different moments of the arm movement cycle.

The signals were filtrated with a 20–450 Hz-band pass (Butterworth 4th order 20-Hz high-pass and 450-Hz low-pass filters). To remove power supply and instrumental noises, the signal was filtered with Butterworth 6th order band-pass filter at 50, 74.05 Hz and multiple frequencies (filtration bandwidth for all frequencies was 1 Hz). To remove vibration noise, the signal was also filtered with Butterworth 6th order band-pass filter at a carrier frequency, as well as at 2-, 3-, and 4-multiple frequencies. Due to variation in the vibration noise frequency, the filtration bandpass bounds were adjusted separately in each experiment. When the data obtained for one subject were processed, the bounds of bandpass filters were not changed. The moment of stimulus application was determined by an artifact in the EMG (Fig. 1b). The magnitude of MEP was calculated as a difference between the EMG maximal and minimal value within an interval of 10 to 40 ms after stimulus application (Fig. 1b). Only those MEP that met the following requirements: (1) the amplitude no less than 12 μV and (2) the MEP amplitude is at least twice as high as the background activity amplitude of this muscle before stimulus application—were taken into account. The background activity of each muscle was calculated as the mean of the EMG reversed and filtered signal within the 10–110-ms interval preceding the stimulus.

In the second series of the experiments related to arm movements, the moment of stimulus application in the arm movement cycle was also determined. For this purpose, the arm movement cycle at the shoulder joint was broken up into eight equal intervals (Fig. 1d). The range of motion at the shoulder and elbow joints, as well as the arm movement period, was also calculated.

In each experiment, the maximum MEP magnitude was determined for each subject and in each muscle. In order to decrease between-subject variability, the responses in all the trials were expressed as a percentage of this maximum response. Since responses to stimulation depend on the level of activity of the target muscle at the moment of stimulus application [18, 26], we used different methods for analysis of the data obtained. First, we compared MEP for each muscle at similar levels of the background activity of this muscle with and without vibration. We did not succeed in making such a comparison for all the muscles, because mechanical muscle vibration, exciting I*a* afferents, resulted in some of the subjects in a slow increase in the EMG activity of stimulated muscle, i.e., in the tonic vibration reflex (TVR), or the antagonistic vibration reflex in its antagonist [27]. Therefore, for the muscles in which such an activity increase was observed, muscle responses were normalized by the background activity value for each stimulus, and the normalized responses were compared.

In order to compare the values of the background EMG-activity, MEP, as well as the latent periods of these responses, under stationary conditions with and without vibration, paired *t* test was used. To evaluate modulations in the background activity and MEP in different phases of the arm movement cycle, two-way ANOVA (the motor task type (voluntary, evoked movements) and the movement cycle interval (eight intervals)) was used. With a significant effect for a task, Fisher's LSD post-hoc test was used to determine the differences between the tasks at each interval. Paired *t* test was used for comparison of the arm movement period and the range of arm joint motion during voluntary and evoked movements. Pearson correlation coefficient was used for correlation analysis. The values in the study are presented as the mean ± the root-mean-square error. The level of significance was taken to be 0.05.

RESULTS

The influence of vibration on the magnitude of MEP in stationary arm muscles. With stationary arms, magnetic stimulation of the motor cortex evoked MEP in all subjects in mm. BB, TB, DA and in 11 of them in m. DP. Vibration of mm. BB and DP led to significant shortening of MEP latent periods in these muscles ($p < 0.05$, *t* test). The latent MEP periods for each muscle are shown in Table 1. Upon vibration of one of the muscles, only in separate non-vibrated muscles did we observe significant shortening of the MEP latent period: in m. TB (by 1.1 s) upon vibration of m. DA; in m. BB (by 1 s) and m. TB (by 0.9 s) upon vibration of m. DP.

Vibration influenced MEP not only in the vibrated muscle itself, but also in the other, non-vibrated, upper arm muscles. Note that these influences were different. An example of MEP modulation in the upper arm muscles influenced by vibration of m. BB in one of the subjects is shown in Fig. 2a. The averaged data for all the subjects on the influence of vibration of each of the muscles on MEP in it and in non-vibrated muscles are shown in Fig. 2b. Upon vibration of the target muscles, the MEP value was considerably greater than in the same muscle without vibration ($p < 0.05$). Such an increase could be determined by an increased activity of vibrated muscle due to TVR development, which was observed in seven subjects. The comparison of the MEP normalized to the background EMG activity with and without vibration showed the significance of the normalized MEP increase for m. BB ($p < 0.03$) (Fig. 2b, on the right). The background EMG activity in non-vibrated muscles did not change and was similar for two experimental conditions; significant MEP modulations were mainly facilitating.

MEP in voluntary and evoked arm movements. In both voluntary and evoked arm movements, we observed MEP in all the four target muscles of this arm. Figure 3 shows the amplitude and modulation of MEP (normalized to the maximum MEP in a given muscle) in different arm muscles and the background activity of the muscles corresponding to both types of movements. For all the muscles, MEP amplitude modulations, depending on the movement cycle phase, correlated with modulations in EMG activity (the correlation coefficients for mm. BB, TB, DA, DP, respectively, were $r = 0.91$, 0.85, 0.96, and 0.93 in voluntary movements and $r = 0.79$, 0.34, 0.76, and 0.89 in evoked movements). Similar MEP modulation was also observed in voluntary and evoked movements (the correlation coefficients: $r = 0.92$, 0.8, 0.97, and 0.95 for BB, TB, DA, DP, respectively) (Figs. 3a, 3b).

The level of EMG activity in vibrated m. TB was substantially higher than in evoked movements compared with its activity during voluntary movements (ANOVA, $F_{1,96} = 6.91$, $p = 0.01$). Significant differences were observed on all the cycle intervals, except 7. For both types of movements, MEP depended on the arm movement phase (ANOVA, $F_{7,96} = 6.92$, $p < 0.00001$), but no differences in MEP between the two types of arm movements were observed ($F_{1,96} = 0.14$, $p = 0.71$) (Fig. 3a). Comparison of responses normalized to the background activity of m. TB in voluntary and evoked movements revealed the motor task dependence of MEP ($F_{1,96} = 9.71$, $p < 0.002$): under evoked movement conditions, they were considerably more moderate than responses in voluntary movements on most intervals of the arm movement cycle ($p < 0.05$), except intervals 4 and 5.

Upon vibration of m. TB, the EMG activity against the background of which the stimulus was applied was substantially higher in its antagonist (BB) in four of seven subjects on most intervals of the vibration-evoked movement cycle than the activity on the corresponding intervals during voluntary arm movements. With regard to this difference, an increase in EMG activity was obtained for all the subjects on intervals 3–6 and a tendency to increase on interval 7 of the cycle ($F_{1,96} = 3.81, p < 0.05$) (Fig. 3a). Motor responses in m. BB depended on the motor task ($F_{1,96} = 3.28, p < 0.05$): despite the background EMG increase, MEP in the phase of the functional activity of this muscle (intervals 1–3), as well as on interval 8, were substantially lesser in non-voluntary than in voluntary move-

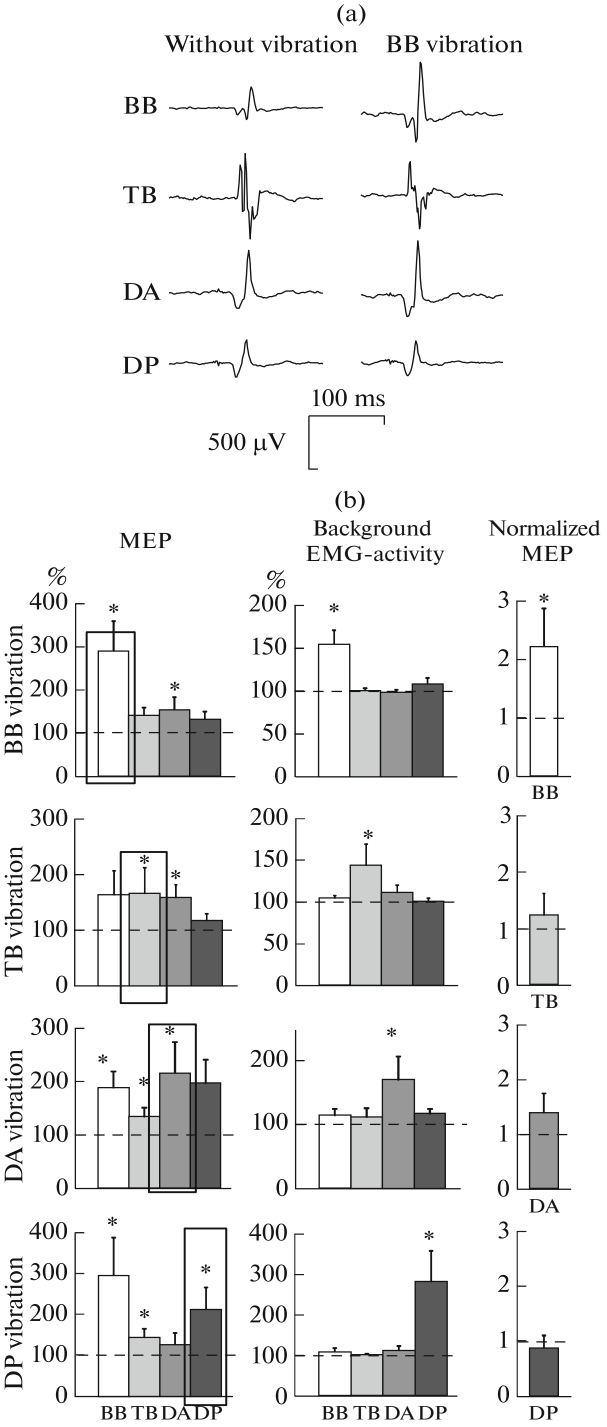

Fig. 2. Influence of vibration on the magnitude of MEP in stationary left arm muscles. (a) The MEP averaged by 10 stimuli without and with vibration of one of the arm muscles (BB) in one subject. (b) The MEP and the background activity of different arm muscles (percent of the corresponding values in the condition without vibration) averaged for all the subjects and the MEP normalized to the background activity in a given muscle (the right column) during vibration of each of the muscles. Vibrated muscle is in the box. * Significant differences in the conditions with muscle vibration and without vibration.

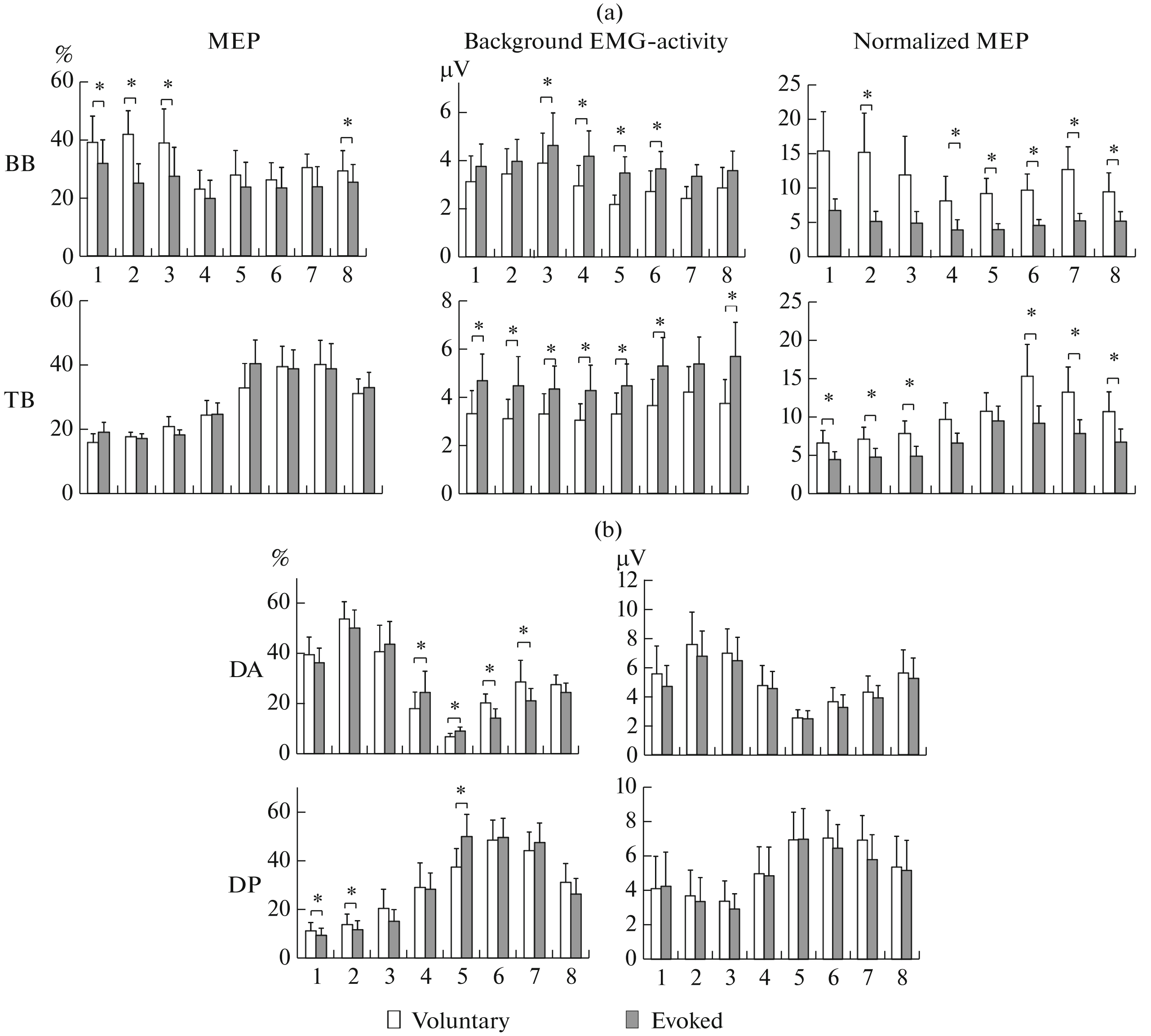

Fig. 3. MEP in voluntary and TB movements evoked by arm vibration: (a) for mm. BB and TB, the motor responses (percent of maximum MEP) and the background activity (μV) averaged for all the subjects and the MEP normalized to the background activity in a given muscle on each of the intervals of the arm movement cycle; (b) for mm. DP and DA, the MEP (% of maximum MEP) and the background activity (μV) averaged for all the subjects. * Significant differences in voluntary and vibration-evoked movement conditions.

ments ($p < 0.01$). Since differences in the background activity were observed, we compared the MEP normalized to the muscle background activity. The analysis showed that the normalized responses in evoked movements were considerably lesser on all intervals of the movement cycle ($p < 0.04$), except interval 3, where a tendency towards reduction was observed ($p = 0.08$).

The levels of EMG activity before stimulus application in m. DA in voluntary and evoked movements were close ($F_{1,96} = 0.48$, $p = 0.48$); the same was also observed for m. DP ($F_{1,96} = 0.17$, $p = 0.67$) (Fig. 3b). For both m. DA and m. DP, MEP modulation in the arm movement cycle was observed ($F_{7,96} = 8.96$, $p < 0.0001$). No significant MEP differences in both types of movements were observed in the phase of the highest m. DA activity. The differences between MEP in evoked and voluntary movements were observed on intervals 4–7. Note that on intervals 4 and 5, MEP in evoked movements were much more pronounced than in voluntary movements; on intervals 6, 7, substantially lesser (*t* test, $p < 0.03$). In m. DP in the phase of its activity on interval 5, MEP were much more significant in evoked movements than in voluntary movements ($p < 0.05$); however, on intervals 1, 2, on the contrary, they were by far more modest (*t* test, $p <$

0.03); a tendency to reduction was observed on interval 3 ($p < 0.09$).

The influence of TMS on the voluntary and evoked arm movement parameters. In seven subjects, vibration of m. TB evoked voluntary rhythmic unloading arm movements with a period of 1.4 to 2.1 s and an amplitude of motion of 6°–30° and 3°–12° at the shoulder and elbow joint, respectively, in different subjects (Figs. 4a, 4b). Motor cortex stimulation by single stimuli with a stationary unloading arm did not induce motor responses in it. However, when a stimulus was applied against the background of hanging arm movements (both evoked and voluntary), potentiation of movements was observed (Figs. 4a, 4b). As a result of stimulus application to the motor cortex, the activity of certain upper arm muscles was substantially increased; this was accompanied by a significant increase in the range of motion at the elbow and the shoulder joints (Fig. 4b). On the cessation of stimulation, we observed movement attenuation to the values close to the initial ones (Fig. 4a). No changes in the period of both voluntary and evoked movements were observed. The increase in the range of arm motion on stimulation of the motor cortex was more marked during evoked arm movements (from 13° ± 3° to 20° ± 5° and from 6° ± 2° to 12° ± 4° for the shoulder and elbow joint, respectively; $p < 0.03$, paired *t* test); in voluntary movements, a significant increase in the range of movements was observed at the shoulder joint only. The amplitude of evoked movements in arm joint on TMS application (vibration + TMS) was similar to that of voluntary arm movements on TMS (voluntary + TMS) ($p = 0.5$).

DISCUSSION

The application of vibration to stationary arm muscles under unloading conditions led to MEP modulation in both vibrated muscle itself and in some other muscles of the same arm. In all vibrated muscles, MEP was seen to be facilitated (Fig. 2b), and in nonvibrated muscle, the magnitude of MEP depended on which muscle was vibrated. Note that vibration of m. BB, as well as vibration of other muscles, exerted the greatest influence on MEP in this muscle in response to TMS.

What may the effect of muscle vibration on MEP in vibrated and other muscles be related to? As indicated above, the muscle motor response to TMS depends on muscle activity [26] and the motor cortex neural activity. Muscle vibration induced a substantial increase in muscle activity connected with increased impulsation of I*a* afferents; therefore, this increase had to make its contribution to MEP increase. However, the MEP increase in m. BB was associated not only with an increase in its activity as a result of vibration, because normalized responses in this muscle significantly increased. Moreover, the latency of MEP in this muscle (as in m. DP) was considerably decreased, which may be determined by an increased influence of descending input to the motoneuronal pools of these muscles [28]. Therefore, it may be suggested that, for m. BB, the motor cortex can make a contribution to its MEP increase due to increased corticomotor excitability of the representation of this muscle in motor cortex. A similar conclusion was made about subthreshold forearm muscle vibration, which did not change the background activity of the muscle [20–22], with the motor responses being increased in these muscles. The response increase occurred in certain non-vibrated arm muscles as well. Rosenkranz et al. [20] showed that sensory input from vibration of the hand flexor muscle did not influence motor cortical excitability of the representation of the hand muscles, which are not functionally connected with vibrated muscle. These authors applied very short, 1.5-s vibration with low amplitude of 0.5 mm. However, it was shown for hand muscles [21] that more prolonged vibration affected the neighboring muscles. In our study, vibration lasted about 30 s with higher amplitude, which resulted in a considerable degree of activation of muscle proprioceptors. In addition, the test muscles were functionally closely connected. Such an increased afferent input from vibrated muscle diverged to the adjacent areas representing arm muscles in the motor cortex. Therefore, under these experimental conditions, vibration of one muscle influenced the excitability of the neighboring areas, which caused MEP to increase in certain muscles (Fig. 2b). Nevertheless, it should be noted that we did not reveal the influence of vibration of any upper arm muscle on its antagonist. It is known that muscle vibration either does not influence the antagonist muscle at all [22] or exerts an inhibitory influence [21]. In addition, it was shown that activation of afferent muscles may suppress the excitability of antagonist-regulating cortical areas and contribute to the spinal pathways transmitting reciprocal inhibition [23]. The possible facilitating influence of upper arm vibration due to increased excitability of the other cortical areas does not seem to be manifested because of the activation of these inhibitory processes in both the spinal cord and cerebral cortex.

Our results also showed that muscle responses to TMS were modulated in the arm movement cycle and were greater during its voluntary movements than vibration-generated movements (Fig. 3). MEP differences in the two types of arm movements imply a lesser involvement of the motor cortex in evoked movements compared with voluntary movements. The high correlation of MEP modulation for upper arm muscles in the cycle between evoked and voluntary arm movements indicates that the operation of the generator of rhythmic arm movements is similarly modulated by afferent input (evoked movements) and central commands (voluntary movements).

What determines MEP differences in voluntary and evoked arm movements? The differences may be

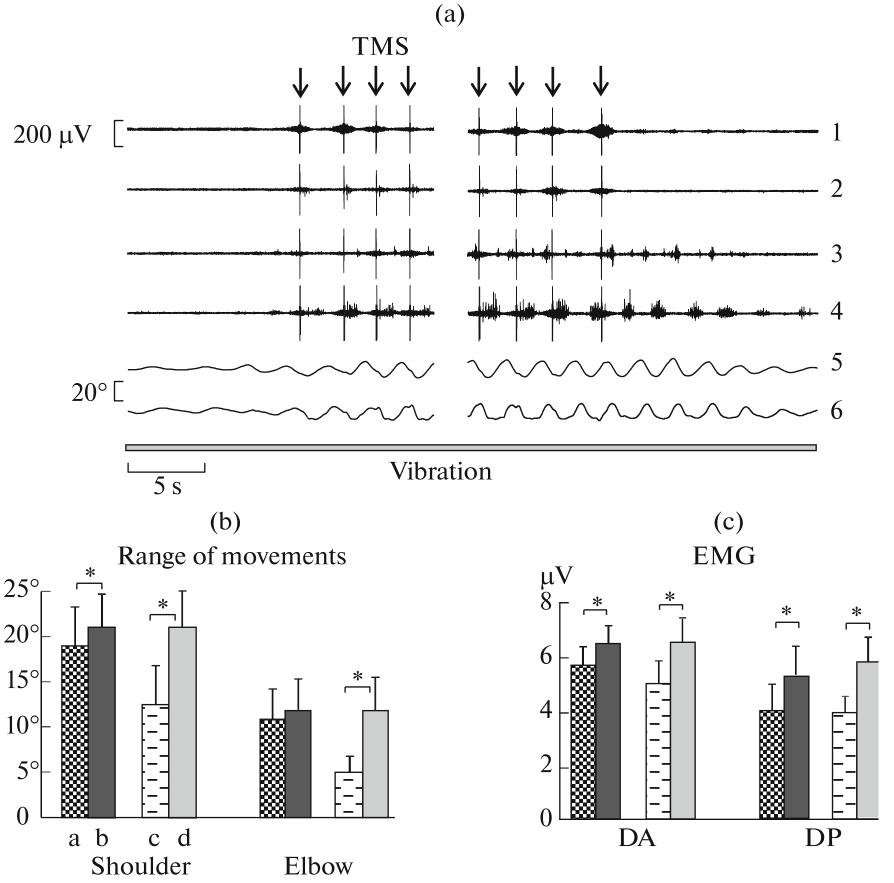

Fig. 4. Influence of TMS on the parameters of voluntary and evoked arm movements. (a) An example of the influence of TMS on the pattern of movements evoked by arm vibration in one typical subject. (1–4) EMG of the upper arm muscles (BB, TB, DA, DP); (5) angle change at the elbow joint; (6) angle change at the shoulder joint. Deviation up corresponds to joint flexion. (b) TMS-generated alterations in the kinematic and (c) electrophysiological arm movement parameters averaged for all the subjects in voluntary and evoked arm movements: a, voluntary movements without TMS; b, voluntary movements + TMS; c, evoked movements without TMS; d, evoked movements + TMS. * Significant differences in the conditions with and without TMS.

related to different levels of muscle activity at the moment of stimulus application, the influence of the increased afferent input activated by m. TB vibration on MEP in it, and the mediated influence on MEP in the other non-vibrated muscles, as well as with a different degree of excitability of the motor cortical neurons in different types of arm movements. For m. TB, the level of its activity was higher in evoked movements, but, nevertheless, MEP in evoked and voluntary movements in this muscle were similar and normalized responses were even considerably decreased in evoked movements (Fig. 3a). For m. BB, despite the differences in EMG activity on most intervals of the movement cycle and the potentiating influence of m. TB vibration on MEP in this muscle under stationary conditions, the authors also obtained the findings that normalized MEP during evoked movements were substantially decreased. For m. DA, with a similar level of the background activity, MEP in evoked movements were similar or less pronounced than those in voluntary movements on most cycle intervals, despite the fact that m. TB vibration potentiated the influence on m. DA responses under stationary conditions (Fig. 3b). However, in the phase of the extension onset at the shoulder, we observed an excess of MEP in evoked movements over MEP in voluntary movements, which may be linked to muscle stretch in this phase of motion and additional activation of I*a* afferents as a result of TB vibration. The results obtained reflect a different degree of involvement of the motor cortex in the regulation of voluntary and evoked movements and suggest that non-voluntary arm movements are largely determined by the spinal generator mechanisms of activation of rhythmic movements. Similar differences were obtained when we studied the involvement of the motor cortex in voluntary and vibration-evoked lower limb movements [10].

What is of interest is that corticomotor TMS significantly potentiated non-voluntary arm movements (Fig. 4). This effect could not be simply a consequence of direct influence of TMS on muscle contraction, because the authors applied the stimuli at different moments of the arm movement cycle and the period of stimulus application did not coincide with the period of its movements either. However, the influence of TMS on the variables of voluntary arm movements was decreased. An increase in the activity of the upper arm muscles was accompanied by alteration of the kinematic movement parameters (Fig. 4b). It is possible that increased activation of corticospinal neurons by transcranial magnetic stimulation may sum up with the activity of the neurons constituting the spinal generator of rhythmic arm movements, indicating the facilitating supraspinal influences. This suggestion agrees with the results of a number of studies, where it is also shown that corticomotor stimulation affects the characteristics of arm movements through interaction of the cortical mechanisms of control with the motor program localized at the spinal level [29, 30].

Better understanding of the mechanisms underlying the control of rhythmic limb movements in humans may be useful in clinical application in the recovery of motor arm and leg activity in patients with neurological deficits.

CONCLUSIONS

(1) The application of vibration to the muscles of stationary arm under its unloading conditions increases motor responses to TMS in both the vibrated muscle itself and in most non-vibrated muscles of this arm. Such an increased afferent input from an individual vibrated upper limb muscle diverges to the neighboring areas representing arm muscles in the motor cortex, thereby increasing the excitability of the adjacent areas.

(2) Similar MEP modulation in the upper arm muscles was observed in both voluntary and evoked movements in the cycle of arm movements. For most target muscles, MEP to TMS were more significant during voluntary arm movements than during vibration-generated arm movements. These results reflect significant differences in the degree of involvement of the motor cortex in voluntary and evoked movements. It may be suggested that non-voluntary arm movements are largely due to spinal rather than central mechanisms of generation of rhythmic movements.

(3) Motor cortical TMS substantially potentiates non-voluntary arm movements; its influence on voluntary arm movements is more modest. Such facilitating supraspinal influences seem to be connected with the summation of stimulation-increased activity of corticospinal neurons and vibration-activated proprioceptive input on the pattern-generating cervical spinal cord circuitries.

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