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Mechanism of Anticipatory Adjustments of the H Reflexes of the Shin Muscles in Humans Related to Voluntary Movements in the Contralateral Ankle Joint

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In healthy adults, we recorded H reflexes from the *mm. sloeus* and *tibialis longus*; the reflexes were evoked by transcutaneous stimulation of the *n. tibialis comm.* and *n. peroneus comm.*, respectively. Changes in the magnitude of the H reflexes were measured, and background EMG activity was recorded from the tested muscles within a premotor period of voluntary plantar flexion of the foot of the contralateral lower limb performed by a light signal. The EMG activity appearing in the *m. soleus* of the latter lower limb served as the index of beginning of the conditioning movement. Anticipatory facilitation of the H reflexes in both tested muscles, which began 60-90 msec before initiation of the conditioning contralateral movement, was observed. The magnitudes of these reflexes increased gradually and reached their maxima synchronously with the greatest EMG level in the contralateral *m. soleus*. Background EMGs recorded from both tested muscles demonstrated no significant changes within the premotor period. The above-described results show that anticipatory facilitation of the H reflexes of the shin muscles within the mentioned period of the voluntary movement of the contralateral lower limb is related to changes developing in the presynaptic components of the arcs of these reflexes. It is hypothesized that such changes result from weakening of background presynaptic inhibition in the terminals of 1a afferents of the testes muscles under the influence of descending activity coming from the supraspinal structures. Weakening of presynaptic inhibition promotes facilitation of the afferent signals arriving from proprioceptors and providing regulation of changes in the nervous system within the premotor period.

INTRODUCTION

Bilateral interlimb interaction plays an important role in realization of various types of movements. This interaction is based on conjugate bilateral activity of spinal neuronal networks, both simple (like chains of reciprocal inhibition) and complex (e.g., motor generators of patterned movements). Patterns of such activity are preprogrammed genetically. Under natural conditions, interlimb interaction is also regulated by influences from the descending systems and afferent signals coming from the periphery. Coordination of movements of the right and left lower extremities in humans has been studied under various conditions, with an immobile body position [1, 2], at veloergometric exercises [3, 4], in the course of locomotion (walking) [5-8], etc. It is known that coordination of the movements is realized not only immediately in the course of their realization, but also within a premotor period, where the movement *per se* is still absent. Within this interval, a few anticipatory changes in the CNS directed toward optimization of the future movement are observed. Among them, anticipatory postural adjustments first described by the Gurfikel's group [9] have been studied in most detail. The patterns of such adjustments and their role in the control of the lower limb movements were examined in a few studies; biomechanical techniques and EMG recording were mostly used for this purpose [10-14].

The H reflexometry is one of the methods allowing experimenters to study signal transmission in the spinal neuronal networks of humans within the period corresponding to resolving of the tasks related to the control of movements [15, 16]. The H reflex is a reflex reaction of the muscle to electrical stimulation of its own afferent 1a fibers; its arc

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is monosynaptic (two-neuronal), which makes the analysis of the respective events simpler, as compared with other reflex reactions. This approach has been extensively used in the studies of premotor changes in the CNS. For example, it was shown that the H reflex recorded from *m. soleus* is facilitated a few tens of milliseconds before the beginning of movements in the contralateral ankle joint [17-19]. At present, the mechanism of this phenomenon and its physiological importance still remain unclear from a few aspects. Our study was aimed at elucidation of this question.

METHODS

Tests were carried out on 26 healthy adult volunteers of both sexes. During the experiment, the subjects lay on a couch, on the stomach, with the feet hanging down. The effects of a conditioning voluntary movement of the contralateral lower foot performed as a simple sensorimotor reaction were examined. According to preliminary instructions, the subjects performed, after a light signal (flash of a light-emitting diode), maximally rapid plantar flexion of the foot contralateral with respect to the side of recording of the H reflex, with immediate subsequent extension. Identification of the beginning of the conditioning movement of the foot was provided by recording EMG activity from the above *m. sloeus*. For this purpose, bipolar surface electrodes (diameter 10 mm) with interelectrode distance 15 mm were used. EMG signals were amplified and addressed to one of the inputs of a two-channel digital oscillograph (Handiscope HS3, Tie-Pie engineering, Netherlands) connected to a PC. The appearance of the first EMG oscillations after an interval corresponding to the latency of the sensorimotor reaction was considered an index of the movement beginning.

In the first experimental series, we recorded the H reflex from the tested *m. soleus* in a parallel mode with the conditioning voluntary movement of the foot of the contralateral lower limb. The *n. tibialis comm.* was stimulated transcutaneously through a monopolar electrode in the region of the popliteal dimple; current pulses were 1 msec long. EMG responses of the *m. soleus* corresponding to the H reflex were recorded by bipolar electrodes. After amplification, the respective signals were addressed to the second input of the oscillograph; their full (peak-to-peak) amplitude was measured. Test stimuli evoking the H reflex were synchronized with the light signal. The *n. tibialis* was stimulated at different time intervals after this signal; the intervals between subsequent trials were 50 to 60 sec long. The control value of the H reflex (in the absence of the light signal and conditioning contralateral movement) was measured after each group of three or four trials. The normalized amplitudes under control conditions (with no movement of the contralateral foot) were taken as 100%.

In the second experimental series, we examined, in a similar way, the effects of the voluntary movement of the contralateral lower limb on the H reflex recorded from the *m. tibialis long*. The reflex was evoked by transcutaneous monopolar stimulation of the *n. peroneus comm.* in the popliteal dimple and recorded by bipolar electrodes from the middle part of the mentioned muscle. The voluntary movement of the foot of the contralateral lower limb was analogous to that in the first series of tests. The first oscillations in EMG in the contralateral *m. soleus* also served as an index of beginning of the conditioning movement. Upon complete relaxation of the muscles of the lower limb at the side of testing, there were no EMG activities in both *m.soleus* and *m. tibialis* at this side. This is why we recorded the respective EMG activity under conditions of light voluntary tonic plantar or back flexion of the foot maintained during the premotor period and conditioning movement of the contralateral lower limb. EMGs were amplified and addressed to the second channel of the oscillograph. The EMG signals were processed using Origin 8.6 software; these signals were off-line full-wave rectified and subjected to low-frequency filtration. The area under the integral curve rounding the processed EMG of the examined muscle served as the index of the intensity of the respective EMG. The normalized magnitudes of such EMGs were calculated; the EMG intensity before presentation of the light signal was taken as 100%. In each test, results of 10 trials were processed. The means for the H reflex amplitude and EMG intensity and the respective s.e.m. values were calculated in each series of the tests.

RESULTS

According to the results of testing, noticeable facilitation was observed before the beginning of voluntary plantar flexion of the contralateral foot.

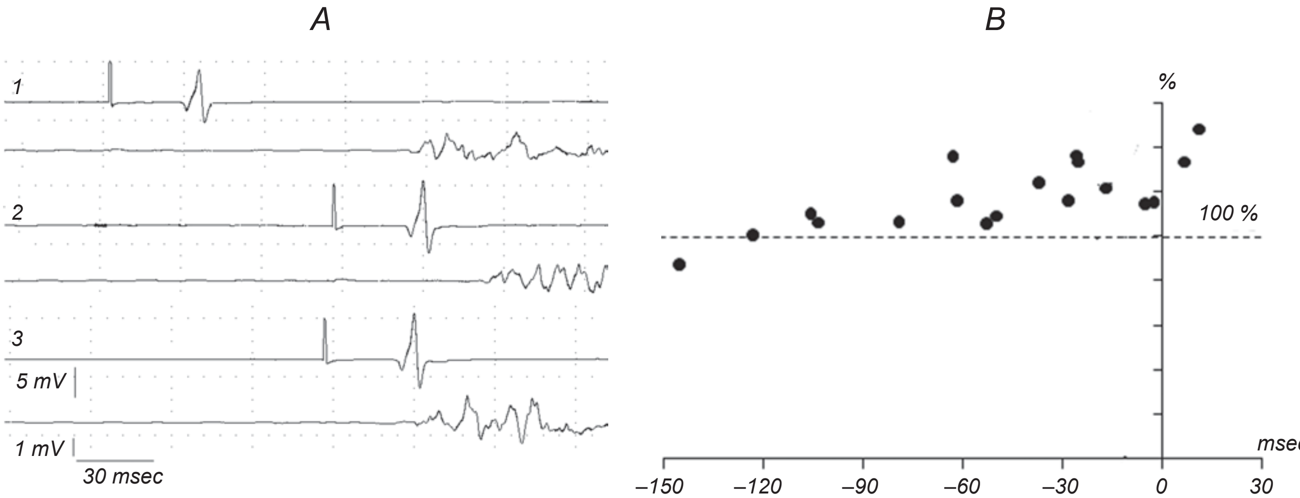

Fig. 1. Anticipatory changes in the H reflex of the *m. soleus* related to voluntary plantar flexion of the foot of the contralateral lower limb. A) Results of three trials (1-3) in one of the series; upper curve) tested H reflex recorded from the *m. soleus*; lower curve) EMG recorded from the contralateral *m. soleus* at voluntary plantar flexion of the foot. The H reflex was elicited at 123 (1), 63 (2), and 36 (3) msec before the appearance of the first EMG oscillations. B) Results of all trials of the experiment. Abscissa) Interval between application of testing stimuli and appearance of EMG activity in the contralateral *m. soleus*, msec; ordinate) normalized magnitude of the H reflex, %; the value of this reflex in the absence of foot flexion is taken as 100%.

The amplitude of the reflex began to increase approximately on the 90th msec before initiation of the conditioning movement. Figure 1 illustrates the results of a representative test. Testing stimuli were applied at different intervals after presentation of the light signal covering the entire premotor period, and the interval between test stimulation and appearance of the first EMG oscillations in the contralateral *m. soleus* was measured in each trial. Results of three trials from this group of realizations are shown (A). In this group, the mean magnitude of the tested H reflex on the 123rd msec before the beginning of the voluntary contralateral foot movement corresponded to 100% of the control value (1); on the 63th msec, this value was 138% (2), and on the 36th msec, 142% (3). In panel B, results of all trials of this group are summarized. As can be seen, the amplitude of the H reflex increased gradually within the premotor period and reached the maximum at the beginning of realization of the conditioning movement.

We compared the dynamics of changes in the H reflex and of the intensity of background EMG of the tested muscle within the premotor period, i.e., at the same time intervals before the beginning of the conditioning movement where anticipatory facilitation of the H reflex was observed.

Figure 2 shows averaged results of two series

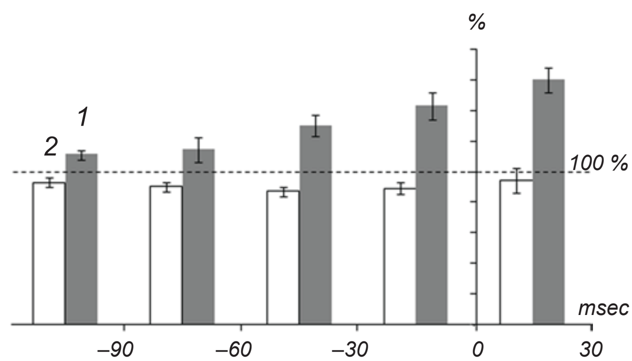

Fig. 2. Dynamics of the normalized magnitude of the H reflex recorded from the *m. soleus* and intensity of its background EMG within the premotor period of the voluntary movement of the contralateral lower limb. Abscissa) Interval, msec, with respect to the beginning of EMG corresponding to voluntary flexion of the contralateral foot; ordinate) averaged magnitude of the H reflex recorded from the tested soleus muscle, % (12 tested subjects) and averaged intensity of background EMG recorded from the same muscle, % (5 subjects), 1 and 2, respectively.

in which the *m. soleus* was the tested muscle. Measurements of the H reflex recorded from this muscle within the premotor period demonstrated clear anticipatory facilitation of the mentioned reflex (Fig. 1 shows results of one of the tests in this series). The averaged normalized amplitude of the H reflex of the *m. soleus* evoked at the 90 msec before the movement beginning was 111 ± 3% of the control; at 90-60 msec, this was 114

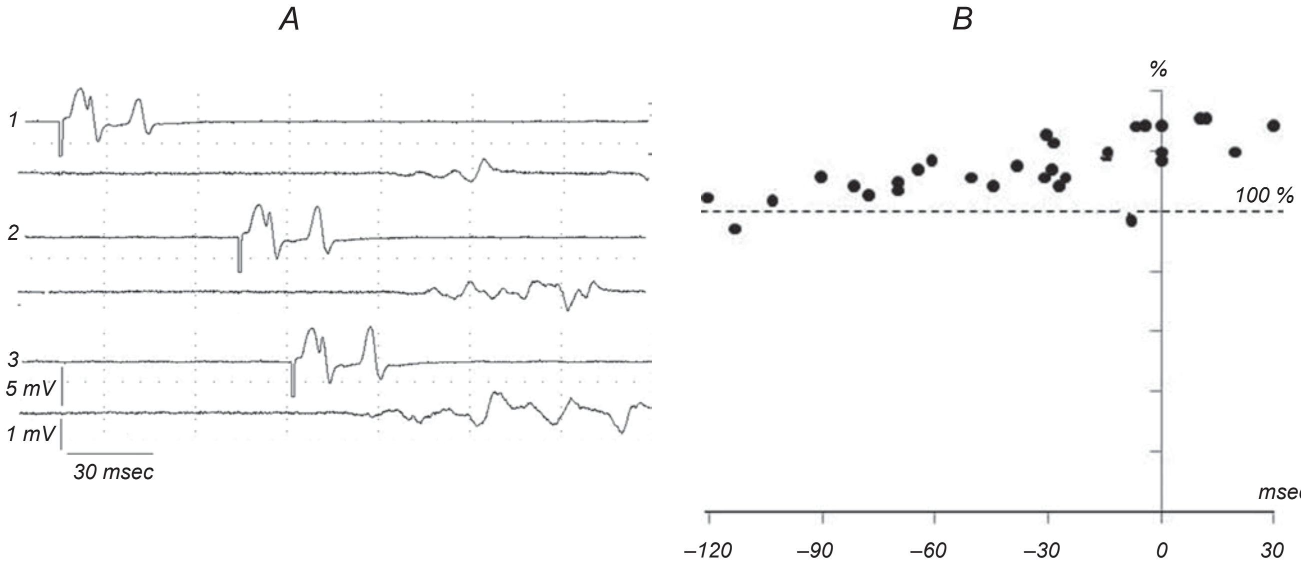

Fig. 3. Anticipatory changes in the H reflex of the *m. tibialis longus* related to voluntary flexion of the contralateral foot. A) Results of three trials (1-3) in one of the series; upper curve) tested H reflex recorded from the *m. tibialis long.*; lower curve) EMG recorded from the contralateral *m. soleus* at voluntary plantar flexion of the foot. The H reflex was elicited at 120 (1), 67 (2), and 25 (3) msec before the appearance of the first EMG oscillations. B) Results of all trials in this experiment. Other designations are the same as in Fig. 1.

± 8%, at 60-30 msec, this was 130 ± 7%, at less than 30 msec, 143 ± 9%, and against the background of the realized movement, this was 160 ± 8%. At the same time, the intensity of background EMG within intervals longer than 90, 90-60, 60-30, and less than 30 msec corresponded to 90 ± 3, 87 ± 3, 90 ± 3, and 94 ± 8% of the control, respectively. In other words, the intensity of background EMG in the tested muscle, in contrast to the value of the H reflex recorded from the same muscle, demonstrated no increase both within the premotor period and synchronously with the voluntary movement of the contralateral limb.

Anticipatory changes in the H reflex amplitude and in the intensity of background EMG were examined in the same mode also in the *m. tibialis long.* The conditioning movement was the same, i.e., plantar flexion of the contralateral foot. It was found that changes in the H reflex of this muscle were, in principle, similar to those described above. Figure 3A illustrates results of three trials of a series characterizing the dynamics of the H reflex. In contrast to the H reflex in the *m. soleus*, the analogous reflex in the *m. tibialis* was recorded after the M response of this muscle. In the illustrated trials, the test intervals corresponded to 120, 67, and 25 msec before the first EMG oscillations in the contralateral *m. soleus* (1-3, respectively). The

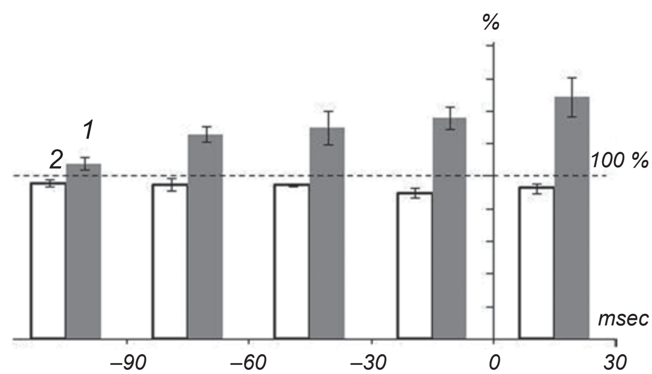

Fig. 4. Dynamics of the normalized magnitude of the H reflex of the *m. tibialis long.* (1, 5 subjects) and intensity of its background EMG within the premotor period of the voluntary movement of the contralateral foot (2, 4 subjects). Other designations are the same as in Fig. 2.

response magnitudes at these intervals were 101, 136, and 147% of the control value, respectively. Panel B of Fig. 3 shows the results of all trials in this experiment; clear facilitation of the tested H reflex within the premotor period is also obvious.

In Fig. 4, averaged data on changes in the H reflex of the *m. tibialis long.* and of background EMG recorded from the latter within the premotor period are shown. As can be seen, the reflex in this muscle, similarly to that in the *m. soleus*, demonstrated clear anticipatory facilitation. At intervals longer than 90 msec before the beginning of the conditioning movement, the magnitude of this reflex corresponded to 108 ± 4% of the control. At 90-60 msec, the respective value was 126 ± 5%, at 60-30 msec, 130 ± 10%, at intervals shorter than 30 msec, 136 ± 7%, and against the background of the conditioning movement, 149 ± 12%. The intensity of EMG recorded from the *m. tibialis*, similarly to that in the *m. soleus*, demonstrated no significant changes both within the premotor period and during the conditioning movement. At the intervals longer than 90, 90-60, 60-30, shorter than 30 msec before the beginning of the movement, and against the background of the latter, the respective figures were 96 ± 2, 95 ± 4, 95 ± 10, 90 ± 3, and 93 ± 3% of the control. Thus, such results are indicative of significant differences between the relatively stable level of background EMG activity of the tested muscles and clear positive dynamics of their H reflexes within the limits of the premotor period of the voluntary movement of the contralateral lower limb.

DISCUSSION

In our tests, we examined the amplitude characteristics of the H reflexes and background EMGs in the shin muscles of humans within the premotor period for the conditioning voluntary movements of the contralateral lower extremity. The subjects, after receiving the visual (light) signal, performed plantar flexion of the contralateral foot (a simple sensorimotor reaction). It should be taken into account that the tests were carried out in the lying position of the subjects, when the lower limbs did not perform a support function. It is obvious that the conditioning movements in this case cannot result in any noticeable change in the position of the body in space. Ninety to sixty milliseconds before the beginning of the above movement, clear facilitation of the H reflexes in both tested muscles, *soleus* and *tibialis*, began to be observed. The amplitude of these reflex reactions gradually increased during the premotor period of the conditioning voluntary foot movement and reached the maximum synchronously with the initial phase of realization of this motion. The following circumstance deserves attention: Changes in the magnitude of the H reflexes in both soleal and tibial muscles (i.e., functionally, in the antagonists) were unidirectional. This fact shows that anticipatory facilitation of the H reflexes is of a nonspecific nature (with respect to reciprocal interaction of the shin muscles) and is realized in the reflex arcs of both extensors and flexors of the ankle joint.

The relatively simple structure of the arcs of the H reflex (their nonspecific pattern) makes easier the analysis of physiological mechanisms of anticipatory facilitation of this reaction. It is obvious that there are only two alternative interpretations. The first is an increase in the excitability of the motoneuronal pool of the tested muscle. Such a shift could be provided by central motor commands that are able to move the membrane potential of motoneurons toward a critical level of depolarization. Another interpretation takes into account possible modulation of the excitatory influences of 1a afferent fibers (presynaptic components of the arcs of the H reflex) on motoneurons. The results of our tests prove that precisely the second interpretation is valid. The intensity of background EMG in the tested muscles demonstrated no increase within the premotor period of the contralateral movement, whereas such a change should be expected if the excitability of the corresponding motoneurons increases. Therefore, our findings allow us to conclude that anticipatory facilitation of the H reflex related to the movements of the contralateral lower limb are explained by the processes developing in the presynaptic, but not in the postsynaptic, part of the studied reflex arc. It can be postulated that this shift results from certain weakening of background presynaptic inhibition of 1a afferent fiber terminals (which are the components of the H reflex arc), and this weakening is induced by the action of central descending commands. An analogous conclusion was made after examination of facilitation of the H reflex in the *m. soleus*, which preceded a voluntary movement of the ipsilateral lower limb [21]. The above-described tests also show that weakening of presynaptic inhibition develops in a generalized mode. This weakening is related to the movements of both ipsilateral (see above) and contralateral lower limbs and covers the reflex arcs of both flexors and extensors of the ankle joint.

Activation of the supraspinal structures is a probable reason for the weakening of presynaptic inhibition. In experiments on animals, suppression of depolarization of primary 1a afferents was demonstrated after stimulation of the red nucleus [22, 23], brainstem reticular formation, and pyramidal tract [23]. Effects of stimulation of the motor and sensory cortical regions showed that activation of some sites in these zones provides suppression of depolarization of terminals of segmental 1a primary afferents [24]. Such sites are intermingled with other ones; stimulation of the latter does not provide the above effects. These data allow one to hypothesize that the centrifugal influences determining modulation of the H reflexes within the premotor period can act via changing the level of presynaptic inhibition of 1a afferent fibers.

Despite the clearly visible facilitation of the H reflex in the soleus muscle found in our experiments within the premotor period, the tone of this muscle showed no signs of rise during this time interval (the intensity of background EEG recorded from this muscle did not increase). Considering this, the question on the physiological importance of anticipatory weakening of background presynaptic inhibition in 1a afferents of the H reflex arc is quite natural. It can be assumed that such weakening, with no increase in the muscle tone, reflects changes in the sensory sphere. Due to partial elimination of presynaptic inhibition, conditions for transmission of afferent signals from proprioceptors to the CNS should be improved. As was recently shown, information coming from these receptors within the premotor period is rather important for the processes realized at this time in the CNS [25, 26]. As was shown in the above-cited reports, afferent signals from muscle spindles play a significant role in on-line control of the motor commands determining the pattern of the postural rearrangements preceding voluntary movements.

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