Modulation of H Reflex of Pretibial Muscles and Reciprocal Ia Inhibition of Soleus Muscle During Voluntary Teeth Clenching in Humans

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Takada, Yoshiyuki, Takao Miyahara, Tatsuya Tanaka, Takashi Ohyama, and Yoshio Nakamura. Modulation of H reflex of pretibial muscles and reciprocal Ia inhibition of soleus muscle during voluntary teeth clenching in humans. *J. Neurophysiol.* 83: 2063–2070, 2000. A previous study has demonstrated that the soleus H reflex is facilitated in association with voluntary teeth clenching in proportion with biting force in humans. The present study tried to elucidate the functional significance of this facilitation of the soleus H reflex, by examining *1*) whether the facilitation of the H reflex is reciprocal or nonreciprocal between the ankle extensors and flexors and *2*) whether the reciprocal Ia inhibition of crural muscles is facilitated or depressed in association with voluntary teeth clenching. The H reflex of the pretibial muscles was evoked by stimulation of the common peroneal nerve in seven healthy subjects with no oral dysfunction. The pretibial H reflex was facilitated in association with voluntary teeth clenching in a force-dependent manner. The facilitation started preceding the onset of electromyographic activity of the masseter muscle. Stimulation of the common peroneal nerve at low intensities subthreshold for evoking the M wave of the pretibial muscles inhibited the soleus H reflex after a short latency corresponding with a disynaptic inhibition, indicating that the reciprocal Ia inhibition was depressed in association with voluntary teeth clenching. Thus, the present study has shown that voluntary teeth clenching evokes a nonreciprocal facilitation of ankle extensor and flexor muscles and attenuated reciprocal Ia inhibition from the pretibial muscles to the soleus muscle. It is concluded that voluntary teeth clenching contributes to improve stability of stance rather than smoothness of movements.

INTRODUCTION

Clenching of the teeth is often observed in association with voluntary movements requiring strong efforts—e.g., during weight lifting. With the development of sports medicine, an increasing number of analyses have recently been made of the possible correlation of teeth clenching with efficiency of motor performance as well as muscle strength of the extremities (Miyahara et al. 1996). A previous study in our laboratory has demonstrated that the human soleus H reflex is facilitated in association with voluntary teeth clenching (Miyahara et al. 1996). The facilitation started preceding the onset of the masseter electromyographic (EMG) activity and increased in magnitude linearly with the increment of biting force. However, the functional significance of this facilitation in motor control has remained to be studied.

In association with locomotion, ankle flexors and extensors are activated alternately during stance and swing phases, respectively. During the stance phase, the ankle extensors contract and ankle flexors relax to extend the ankle joint for propulsion of the body mass. On the other hand, during the swing phase the ankle flexors contract and the extensors relax. Thus, the reciprocal inhibition plays a major role for smooth performance of locomotion. In contrast, to stabilize the posture, the ankle extensors and flexors co-contract to fix the ankle joint, as seen in the positive supporting reaction.

It has been reported in humans that in association with voluntary extension and flexion of the ankle joint, the soleus H reflex is facilitated and inhibited, respectively (Tanaka 1983). It is also known that the gain of H reflexes of lower limbs is modulated in a phase-dependent manner during stepping, walking, and running in humans (Brooke et al. 1997). In addition, the reciprocal group Ia inhibition of the soleus H reflex by stimulation of the lowest threshold fibers in the common peroneal nerve was demonstrated in patients with bilateral athetosis in the resting condition (Mizuno et al. 1971) and during voluntary contraction of pretibial muscles in healthy subjects (Tanaka 1974).

Thus, to reveal the significance of the facilitation of the soleus H reflex in association with voluntary teeth clenching, we studied whether the facilitation of H reflexes of leg muscles in association with voluntary teeth clenching is reciprocal or nonreciprocal between ankle extensors and flexors. We also studied whether the reciprocal Ia inhibition from the pretibial muscles to the soleus H reflex (Tanaka 1974) is depressed or facilitated in association with voluntary teeth clenching.

METHODS

Subjects and materials

Experiments were performed on seven healthy male volunteers, aged 25–30 yr, who had all given informed consent to participate in the study. Five of them participated in both the first and second series of experiments. One of the remaining two subjects participated only in the first series, and the other in the second series only. Subjects were comfortably seated in a reclining chair. The angle of the knee and foot joints on both sides was kept constant at ~120° and 100°, respectively, by means of an immobile footplate. The head rested on a

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headrest, and the forearm and hand rested on an armrest. The armrest and the footplate served to keep the muscles of the arm and leg relaxed during the resting period in the experiment.

In the first series of experiments, in which we studied modulation of the H reflex of the pretibial muscles during voluntary teeth clenching, EMG activity was recorded from the pretibial and masseter muscles on the right side with bipolar surface cup electrodes (diameter: 8.0 mm) placed 3 cm apart longitudinally over the middle part of the tibialis anterior muscle and over the masseter muscle just below the zygomatic arch. The EMG activity was amplified with conventional amplifiers (time constant: 0.03 s; high cut frequency: 10 kHz).

The H reflex of the pretibial muscles was evoked on the right side with a pair of surface electrodes (diameter: 8.0 mm) taped to the skin along the common peroneal nerve: the cathode positioned at the head of the fibula and the anode 2.5 cm apart distally. A ring silver plate was placed around the skin between the stimulating and recording electrodes as the ground electrode, to reduce the artifact because of spread of the stimulating current along the surface of the skin. The stimulating pulse of 0.5 ms was used at an intensity 1.1 times the threshold (×*T*) for the M wave. At this stimulus intensity, a small M wave was obtained together with the H reflex; this M wave was used to monitor the stability of the stimulating condition.

In the second series of experiments, we studied modulation of the reciprocal Ia inhibition from the afferents of the pretibial muscles to the soleus muscle during voluntary teeth clenching. The same type of bipolar surface recording electrodes as used in the first series were placed 3 cm apart longitudinally over the right soleus muscle just below the gastrocnemius muscle belly to record the soleus H reflex, in addition to the stimulating and recording electrodes used for the H reflex of the pretibial muscles in the first series. A surface stimulating electrode (diameter: 8.0 mm) was positioned in the popliteal fossa over the tibial nerve as a cathode and a silver plate (35.0 × 45.0 mm) placed on the patellar region as an anode, to evoke the soleus H reflex. Test stimulating pulses of 1.0 ms in duration were applied to the tibial nerve at intensities that evoked the H reflex with an amplitude ~30% of the maximum M wave. The conditioning stimulating pulse was applied to the common peroneal nerve at an intensity of 0.95 × *T* for the M wave of the pretibial muscles. Experimental data were simultaneously recorded on a data recorder (Sony PC216A, flat frequency response: DC, 5.0 kHz) and on a floppy disk through an A/D converter (Canopus ADX-98E, 10 kHz per channel) with the use of a microcomputer (NEC-98 model 60). Hard copies of records were obtained with a thermal array recorder (Nihon Kohden RJA-1300, flat frequency response: DC, 10 kHz).

Experimental procedures

Experimental procedures were similar to those in our previous study (Miyahara et al. 1996). The strength of teeth clenching with the upper teeth against the lower teeth was monitored by the amplitude of the full-wave–rectified, integrated masseter EMG, because it is known that there is a rectilinear relationship between the amplitude of the masseter EMG and bite force during isometric contraction (Moller 1966). Two vertical cursors were shown on the computer display in front of the subject (Fig. 1*A*). The cursor in the *top* half of the display (target cursor) consisted of a pair of vertical lines; the center between them indicated the instructed force level, and each line corresponded to the instructed force level ±5.0% of the maximum contraction of the masseter muscle. The level of maximum contraction was defined as the mean amplitude of the full-wave–rectified, integrated masseter EMG during voluntary teeth clenching with maximum effort for 3 s. The strength was set from 25 to 100% of the maximum contraction in 25% steps. The cursor at the *bottom* half of the display (force cursor) continuously indicated the instantaneous amplitude of the full-wave–rectified, integrated masseter EMG during the instructed muscle contraction. It moved from the left to the right on the display with an increase in contraction of the masseter muscle. The left and right ends

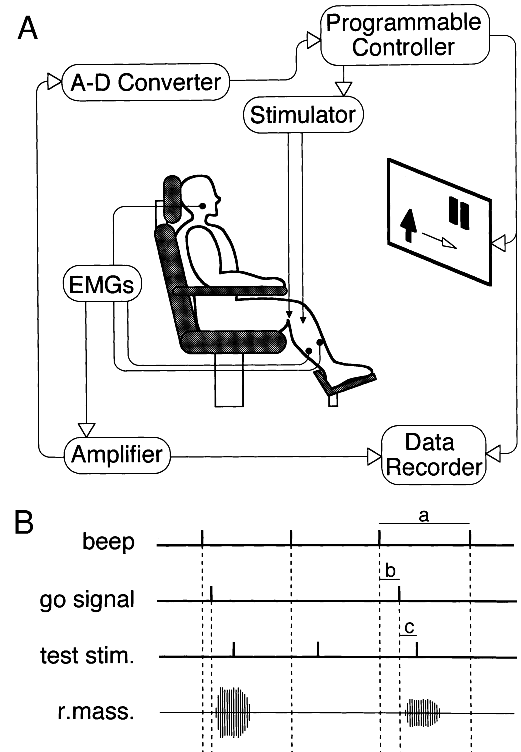

FIG. 1. Experimental setup and protocol. *A*: stimulation and recording setup controlled by a programmable controller (NEC-H98 model 60). *B*: temporal relations among 3 kinds of applied stimuli with respect to voluntary teeth clenching (r. mass): warning signal (beep), imperative stimulus (go signal), and stimulation of the common peroneal nerve (test stim.).

of the display corresponded to the 0 and 100% levels of the voluntary muscle contraction, respectively. In advance of each experiment, the subject was instructed to match the position of the force cursor between the pair of target cursors as soon as possible by adjusting the strength of contraction of the masseter muscle.

The subject maintained the jaw in the rest position during the resting period when neither cursor was shown in the display. The start of the trial was indicated by a warning signal of beep (1 kHz for 300 ms), which was given at a constant interval of 10 s (Fig. 1*Ba*). After various intervals from the warning signal (Fig. 1*Bb*), both the target and force cursors were shown simultaneously on the display as the go signal. The target cursor was shown at the position representing the instructed level of contraction of the masseter muscle, and the force cursor at the left end of the display corresponding to the null biting force during the rest period. In response to the go signal, the subject quickly matched the force cursor to a position between two vertical lines of the target cursor by adjusting the strength of contraction of the masseter muscle (Fig. 1*B*, *bottom trace*) and kept this level until the test stimulus was given or for ~3 s when the test stimulus was not given. A session consisted of 20–30 trials, and a series of 6–12 sessions was performed in a day with a 5-min interval after each session.

In the first series, a trial consisted of one of the following three tasks: *1*) test stimulus to the common peroneal nerve without teeth clenching—i.e., null biting force (control trial), *2*) test stimulus with teeth clenching (conditioned trial), and *3*) no test stimulus with teeth clenching. Neither the subject nor the experimenter could predict which task would be required in the next trial or when the next go signal would be given, because the delay of the go signal (Fig. 1*Bb*) as well as test stimulation of the common peroneal nerve from the go signal (Fig. 1*Bc*) in each trial was ordered randomly by the computer. Before starting a session, both *1*) the number of trials in the session and *2*) the number of trials in which either conditioning or test stimulus was not given were randomly determined.

In the trials to study the relation between the biting force and the magnitude of the pretibial H reflex, the interval between the warning signal and the go signal was set from 0.5 to 3.0 s in 0.5-s steps in random sequence (Fig. 1*B*, *2nd* and *3rd traces*). In the trials to study the time course of modulation of magnitude of the pretibial H reflex with respect to the onset of masseter EMG, the subject was instructed to clench his teeth at a strength of 75% of the maximum effort. The interval between the go signal and the stimulation of the common peroneal nerve was varied randomly from 1 s before the go signal to 3 s after it.

In the second series, trials consisted of the following four kinds: *1*) test stimulation of the tibial nerve without teeth clenching, *2*) test stimulation with teeth clenching, *3*) conditioning stimulation of the common peroneal nerve followed by test stimulation of the tibial nerve without teeth clenching, and *4*) the same as *3*) with teeth clenching. As in the first series, the sequence of these four kinds of trial was randomized by a computer in advance of each session. The level of masseter contraction was set at 70% of the maximum voluntary contraction throughout this series of experiments.

Data analysis

The difference in magnitude of the H reflexes of the pretibial and soleus muscles between the control trials without teeth clenching and the conditioned trials with teeth clenching was statistically tested by one-way ANOVA followed by Scheffé's *F* test, Welch's *t*-test and a paired *t*-test. Except for the results of the experiments, in which the time course of modulation of amplitude of the pretibial H reflex was studied, the results in those trials were excluded from the analysis, in which *1*) the masseter EMG activity was present before the go signal, *2*) the test stimulus applied before the masseter EMG reached the instructed level, and *3*) the level of the masseter EMG activity was outside the instructed level.

RESULTS

Modulation of H reflex of pretibial muscles during voluntary teeth clenching

In the first series of experiments, we studied whether the H reflex of the pretibial muscles was modulated in association with voluntary teeth clenching. Figure 2 illustrates an example of the EMG of the pretibial muscles evoked by stimulation of the common peroneal nerve. It consisted of two successive

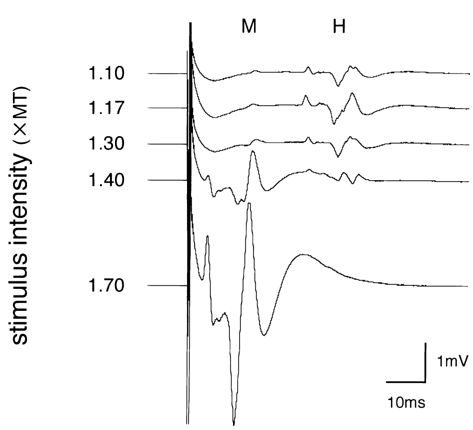

FIG. 2. Elecgromyogram (EMG) evoked in the pretibial muscles by stimulation of the common peroneal nerve obtained from a subject. Stimulus intensity is shown on the *left* by multiples of the threshold intensity for the M wave (×M*T*). Each trace is the averaged record of 6 sweeps.

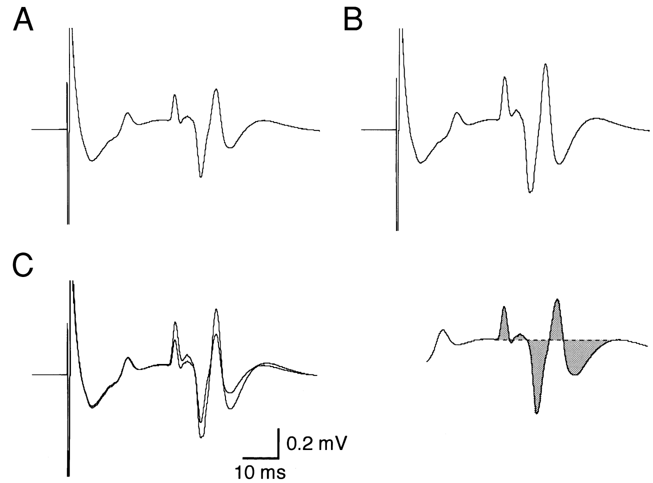

FIG. 3. Modulation of H reflex in pretibial muscles during voluntary teeth clenching. M wave and H reflex were evoked at intensity 1.1 × *T* for M wave. *A*: EMG obtained without teeth clenching. *B*: EMG obtained during maximum voluntary teeth clenching. In *A* and *B*, the records were obtained by averaging 30 and 18 traces, respectively. *C*: superimposed record of *A* and *B*. Shaded area in *inset*: magnitude of H reflex.

responses: an early and a late response. At low stimulus intensities, the early response had a rather simple wave form with a latency of ~15 ms, whereas the late response consisted of a pair of component waves after a latency of ~30 ms. Each component wave of the late response had the same threshold of 0.90–0.95 × *T* as the early response. Both the early and late responses increased in magnitude in parallel with an increase in stimulus intensity at a range lower than ~1.2 × *T* for the early response. Beyond this level, the early response steadily increased in magnitude with a further increase in stimulus intensity, whereas the late response gradually diminished to finally disappear as the stimulus intensity was increased. Because these properties corresponded to those of the M wave and the H reflex in other limb muscles, we regarded the early and late responses as the M wave and the H reflex of the pretibial muscles, respectively.

At higher stimulus intensities, the M wave showed a notable change with an increase in stimulus intensity: in addition to an increase in amplitude of the M wave that was induced at lower stimulus intensities, another wave appeared after a shorter latency and increased in amplitude with an increase in stimulus intensity. Thus at high stimulus intensities, the M wave itself consisted of a pair of distinct component waves.

We tested modulation of the pretibial H reflex evoked by stimulation at intensity of 1.1 × *T* for the H reflex during voluntary teeth clenching. As shown in Fig. 3, every component wave comprising the pretibial H reflex (Fig. 3*A*) increased in amplitude during maximum voluntary teeth clenching (Fig. 3*B*), which is seen in the superimposed record of *both traces* in *A* and *B* (Fig. 3*C*).

The magnitude of the pretibial H reflex, was defined as the area lying between the EMG trace and a straight line extending from the onset of the first deflection to the peak of the last deflection (the shaded area of the *inset* in Fig. 3). It increased in parallel with the strength of teeth clenching. Figure 4*A* is a scatter diagram of the magnitude of pretibial H reflex against the force level of teeth clenching obtained from a subject. The mean H reflex magnitudes at the force levels of 25, 50, 75, and

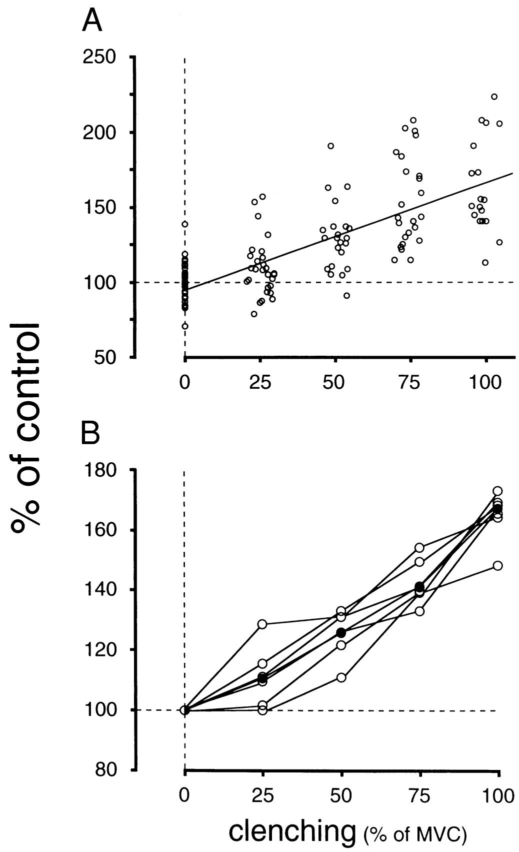

FIG. 4. Correlation between the facilitation of pretibial H reflex and strength of teeth clenching. Abscissa, strength of teeth clenching expressed in percent of maximum voluntary teeth clenching; ordinate, magnitude of tibialis anterior H reflex expressed in percent of the mean control value of magnitude without teeth clenching. *A*: data obtained from 1 subject. Each circle represents the result of each trial in a subject who was instructed to clench teeth at intensities of 25, 50, 75, and 100% of maximum voluntary teeth clenching. The numbers of trials in the resting condition and at levels of contraction of 25, 50, 75, and 100% of maximum voluntary contraction were 30, 28, 22, 24, and 18, respectively. Solid straight line is the regression line obtained by the least-square method applied to all the points. *B*: data obtained from 6 subjects. Each open circle represents the mean value of magnitude of pretibial H reflexes obtained at each instructed level of strength of teeth clenching. Strength of teeth clenching is expressed at each instructed level, although in a majority of trials strength did not exactly match with instructed level. Trials in which actual strength of teeth clenching showed a deviation from an instructed level <5% of the maximum were lumped together to each instructed level; those showing a ≥5% deviation from each instructed level were discarded. Open circles represent the mode of modulation in each subject; each circle shows the mean value of magnitude of 10–55 trials. Filled circles represent grand mean values of magnitude of 6 subjects at each strength of teeth clenching.

100% of the maximum voluntary contraction were 109.5, 130.0, 154.0, and 163.3% of the control magnitude, respectively. Compared with the magnitude of the control H reflex without teeth clenching, it was larger during the teeth clenching as a whole at all strengths of teeth clenching than the control magnitude without teeth clenching ($P < 0.05$), and steadily increased with an increase in strength of teeth clenching with a significant difference between one level and the level after the next (i.e., between 0 and 50%, 25 and 75%, and 50 and 100%; $P < 0.05$). The correlation coefficient was 0.72 ($P < 0.05$). Figure 4*B* shows the correlation between the strength of teeth clenching and the mean values of magnitude of the pretibial H reflex at respective intensity level in each of six tested subjects (open circles); in each subject there was a significant positive correlation between the magnitude of the H reflex and the stimulus intensity ($r = 0.49–0.74$, $P < 0.05$). The filled circles represent the grand mean values of the magnitude of all the six subjects against the strength of teeth clenching; a significant positive correlation was found between the magnitude of the H reflex and the stimulus intensity ($r = 0.94$, $P < 0.05$).

Time course of modulation of the pretibial H reflex in association with teeth clenching

Figure 5 shows the time course of the modulation of magnitude of the pretibial H reflex in relation to EMG activity of the masseter muscle during teeth clenching at an intensity of 75% of the maximum in a subject. The onset of the masseter EMG activity is shown as 0 on the abscissa. Each circle in Fig. 5*A* represents the magnitude of the reflex as a percent of the control amplitude at the time when the test stimulus was applied. As seen in Fig. 5*B*, which shows the plot in Fig. 5*A* on an expanded time base, the increase in magnitude of the pretibial H reflex apparently started at >200 ms before the onset of the masseter EMG activity, reached a peak ~60 ms

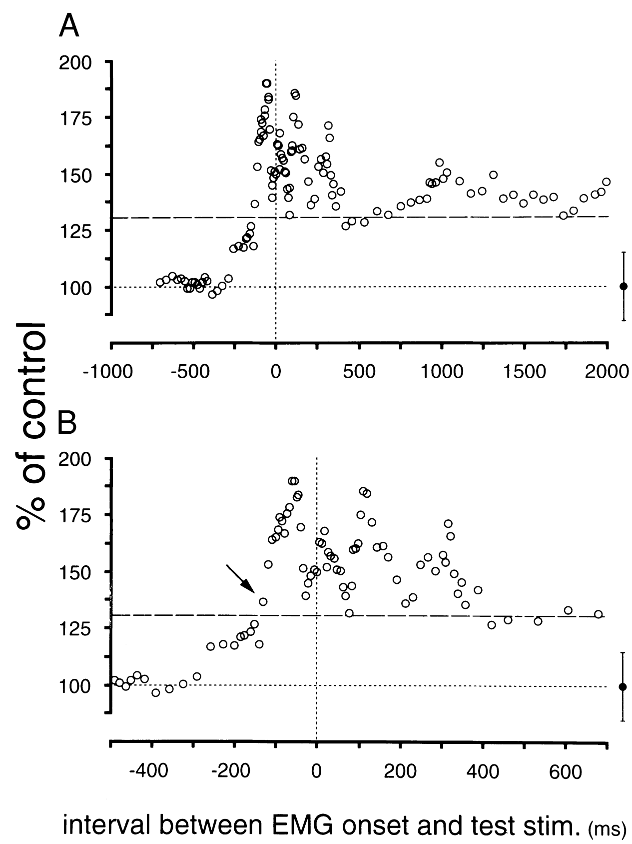

FIG. 5. Time course of modulation of the pretibial H reflex with respect to the onset of the masseter EMG. *A*: amplitude of the pretibial H reflex evoked by test stimulation at the respective intervals from the onset of the masseter EMG. Abscissa, interval between test stimulation and the onset of the masseter EMG that was taken as *time 0* (vertical dotted line); plus and minus signs show that the test stimulation followed and preceded the onset of EMG activity, respectively. Ordinate, amplitude of pretibial H reflex shown as percent of the control (horizontal dotted line) *B*: data in *A* on an expanded time base. Circle indicated by arrow shows the time when the amplitude exceeded the control value by +2 SD (horizontal broken line). Vertical bars above and below the filled circle showing the control value in *B* indicate ±1 SD.

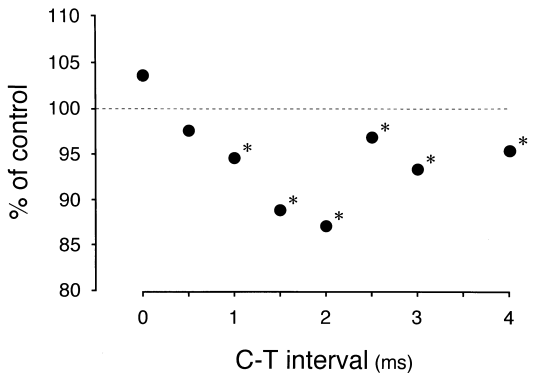

FIG. 6. Time course of reciprocal inhibition of soleus H reflex evoked by conditioning stimulation of common peroneal nerve. Abscissa, conditioning-test interval; ordinate, amplitude of soleus H reflex in percent of control value. Each filled circle represents the mean value of the results in 14–23 trials. Control amplitude was set ~30% of that of the maximum M wave, which was expressed as 100%. *, significant decrease in amplitude of the soleus H reflex is shown compared with the control value ($P < 0.05$).

before the onset, and then declined to a plateau ~400 ms after the onset. If we take the control value +2 SD as the minimum value of a significant increase in magnitude, the increase started at 124 ms before the onset of the masseter EMG activity (Fig. 5*B*, arrow). In the six tested subjects, the magnitude of the pretibial H reflex started to increase at 83–124 ms before the onset of the EMG activity (99.3 ± 15.7 ms, mean ± 1 SD).

Modulation of the soleus H reflex by stimulation of the common peroneal nerve

Conditioning stimulation of the common peroneal nerve at an intensity subthreshold for the M wave of the pretibial muscles depressed the soleus H reflex. Figure 6 shows an example of the time course of the depression of the soleus H reflex induced by conditioning stimulation of the common peroneal nerve at an intensity of 0.95 × *T* for the M wave of the pretibial muscles in a subject. It started at a conditioning-testing interval of 1.0 ms and reached a peak at 2.0 ms, then gradually tended to return to the control level, although the depression was still present at an interval of 4.0 ms ($P < 0.05$).

Figure 7 shows the results obtained from a session in a subject. The soleus H reflex was depressed by conditioning stimulation of the common peroneal nerve at an intensity subthreshold for the M wave of the pretibial muscles under the conditions with teeth clenching (*right*) and without (*left*). The control soleus H reflex obtained without teeth clenching (amplitude: 4.20 mV; *top left*) was depressed by conditioning stimulation of the common peroneal nerve applied 2.0 ms preceding test stimulation to the tibial nerve (amplitude: 3.53 mV; *bottom left*). The facilitated soleus H reflex during teeth clenching (amplitude: 5.08 mV; *top right*) was also depressed by stimulation of the common peroneal nerve (amplitude: 4.38 mV) at the same intensity as used during the rest control condition without teeth clenching (*bottom right*). Although the soleus H reflex was depressed not only in trials without teeth clenching but also in those with teeth clenching, the depression was reduced from 19.0% in trials without teeth clenching to 13.8% in those with teeth clenching.

In this subject, the depression of the soleus H reflex was compared among all the trials without teeth clenching and those with teeth clenching (Fig. 8*A*). The mean amplitude of the soleus H reflex was reduced to 86.2% ($n = 75$) of the control ($n = 79$) in the trials without teeth clenching, whereas during teeth clenching the mean amplitude was reduced to 93.1% ($n = 82$) of the facilitated amplitude ($n = 84$) of the soleus H reflex. Although the depression was significant in both conditions, the soleus H reflex was less depressed during teeth clenching ($P < 0.05$)—i.e., the soleus H reflex was partially disinhibited in association with the teeth clenching. Figure 8*B* shows the depression of the soleus H reflex without teeth clenching (open circles) and during teeth clenching (filled circles) in each of all the six tested subjects, showing a significant reduction of the depression of the soleus H reflex during teeth clenching ($P < 0.05$).

To exclude the possibility that the reduction of the depression is simply due to an increased amplitude of the soleus H reflex during teeth clenching, the relation of the magnitude of depression of the soleus H reflex to its amplitude was studied. Figure 9*A* illustrates the relation of the amplitude of the control soleus H reflex (open circles) and the conditioned soleus H reflex (filled circles) with the intensity of test stimulation of the tibial nerve in a subject. Although the amplitude increased with stimulus intensity in both control and conditioned soleus H reflexes, it was smaller in the conditioned H reflex in the range from 10 to 70% of the maximum magnitude of M wave except for 15 and 67% ($P < 0.05$). However, the reduction was clearly dependent on the amplitude of the soleus H reflex. As shown in Fig. 9*B*, the depression was increased until the amplitude of the

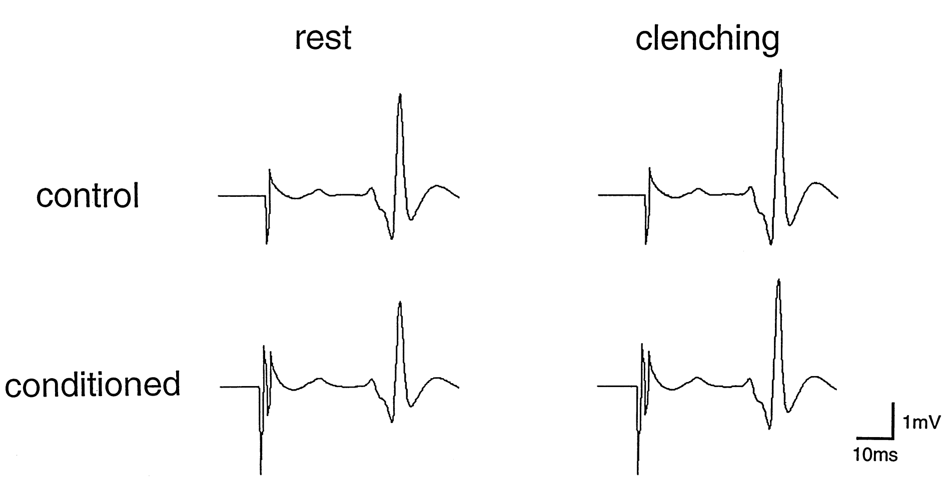

FIG. 7. Modulation of reciprocal inhibition of soleus H reflex by voluntary teeth clenching. Intensity of test stimulation of tibial nerve was set to evoke soleus H reflex with an amplitude of ~30% of the maximum M wave; conditioning stimulation of the common peroneal nerve was applied 2.0 ms before test stimulation of the tibial nerve at an intensity of 0.95 × *T* for evoking M wave in the tibialis anterior muscle. *Left* and *right*: data obtained without teeth clenching and during teeth clenching, respectively. *Top*: control records evoked by test stimulation only; *bottom*: records conditioned by stimulation of the common peroneal nerve. Each panel shows averaged record of 17 (*top left*), 19 (*bottom left*), 15 (*top right*), and 15 (*bottom left*) traces.

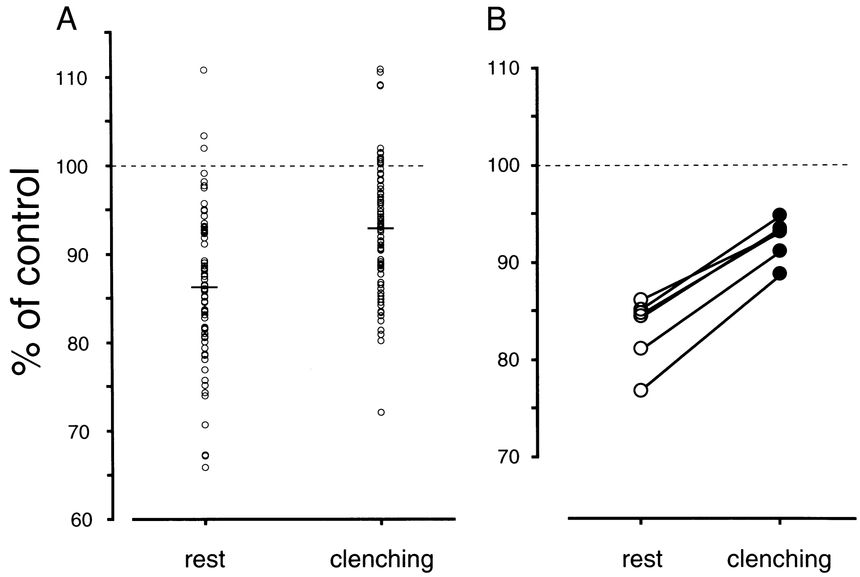

FIG. 8. Decrease in the amount of reciprocal inhibition of soleus H reflex during voluntary teeth clenching. *A*: data obtained from the same subject as shown in Fig. 7. Each open circle represents the amplitude of the soleus H reflex conditioned by stimulation of the common peroneal nerve expressed in percent of mean amplitude in the resting condition in each trial without teeth clenching (rest) and during teeth clenching (clenching). Horizontal bars represent the mean values in the respective condition. *B*: data obtained from 6 subjects. Test stimulation was applied to the tibial nerve at an intensity that evoked the soleus H reflex with amplitude of ∼30% of the maximum M wave. Conditioning stimulation was applied to the common peroneal nerve at an intensity of 0.95 × *T* to evoke M wave in the tibialis anterior muscle, 2.0 ms preceding test stimulation. Open circles represent the mean amplitude of the conditioned soleus H reflex in percent of the control amplitude without teeth clenching; filled circles represent the mean amplitude of the soleus H reflex expressed in percent of the control amplitude during teeth clenching. Each pair of open and filled circles shows the results obtained from one subject. Open and filled circles, representing the results obtained from each subject, consists, from *top* to *bottom*, of 75 and 84, 38 and 37, 34 and 39, 13 and 21, 90 and 86, and 38 and 28 trials, respectively.

soleus H reflex reached ∼50% of the maximum M wave (correlation coefficient: 0.95, $P < 0.01$). Beyond this level, however, the inhibition tended to decrease with an increase in amplitude of the soleus H reflex.

Because the amplitude of the soleus H reflex never exceeded 45% of the maximum M wave even during teeth clenching in the present study, the reduction of depression of the soleus H reflex in association with teeth clenching showed a change in the opposite direction to that expected simply from an increase in amplitude of the soleus H reflex.

DISCUSSION

The present study has demonstrated that *1*) the pretibial H reflex is facilitated during voluntary teeth clenching in proportion with the strength of biting force monitored by the amplitude of the masseter EMG, *2*) the facilitation started preceding the onset of masseter EMG activity, and *3*) the depression of the soleus H reflex induced by conditioning stimulation of the common peroneal nerve at an intensity subthreshold for evoking the M wave in the pretibial muscles is reduced during voluntary teeth clenching.

Modulation of pretibial H reflex during voluntary teeth clenching

It was reported that the H reflex could be evoked in the pretibial muscles in selected subjects as well as during voluntary contraction of these muscles (Davies 1985; Deschuytere and Rossele 1971; Pierrot-Deseilligny et al. 1973, 1981; Schieppati and Crenna 1985; Tanaka 1974; Upton et al. 1971). In the present study, transcutaneous stimulation of the common peroneal nerve evoked a pair of successive EMG responses recorded from the bipolar surface electrode placed on the belly of the tibialis anterior muscle: an early and a late response. Both these responses appeared after the latencies comparable to those reported in the studies described, and the relation between the stimulus intensity and the magnitude of the early and late responses was essentially the same as that of the M wave and H reflex of other limb muscles. Thus, the present study confirmed that the M wave and H reflex could be evoked by transcutaneous stimulation of the common peroneal nerve in healthy subjects at rest.

It was noted in this study that the H reflex recorded from the surface over the tibialis anterior muscle consisted of a pair of distinct waves separated from each other by a rather silent period. This pattern is in sharp contrast to the soleus H reflex, which consists of a single wave. The difference in waveform may be due to a difference in composition of muscle fiber types as well as spinal motoneurons between the two muscles in humans. It has been reported that the number of type II fibers amounts to 27% (Johnson et al. 1973) or 34% (Henriksson-Larsén et al. 1985) of all the fibers in the tibialis anterior muscle, whereas it is only 12.3% in the soleus muscle in humans (Henriksson-Larsén et al. 1985). Thus a significant portion of the fibers consisted of type II fibers in the tibialis anterior muscle, whereas nearly all the fibers are type I in the soleus muscle. The group of motoneurons innervating the type I fibers have axons with slower conduction velocities than those innervating the type II fibers. The volley monosynaptically evoked in the two groups by stimulation of the common peroneal nerve arrives at the tibialis anterior muscle after appreciably different latencies. It has been reported that stim-

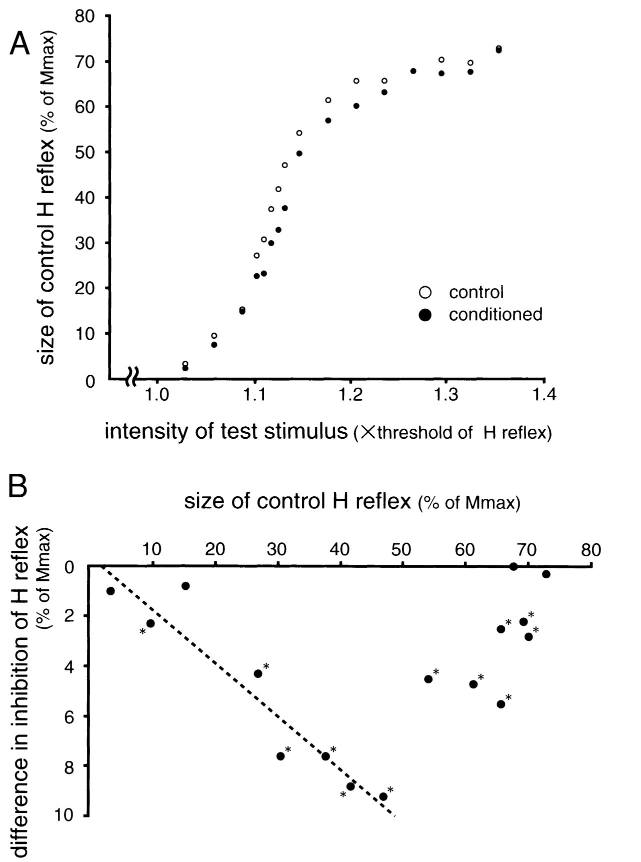

FIG. 9. Relation between magnitude of reciprocal inhibition of soleus H reflex and its amplitude. *A*: stimulus-response curve of soleus H reflex. Abscissa, intensity of test stimulus of tibial nerve; ordinate, amplitude of soleus H reflex in percent of maximum M wave. Open circles, control amplitude; filled circles, amplitude conditioned by stimulation of common peroneal nerve 2.0 ms before test stimulation of tibial nerve. Each circle represents the mean amplitude of 8–12 trials. *B*: changes in magnitude of reciprocal inhibition of soleus H reflex during maximum voluntary teeth clenching, plotted based on the data shown in *A*. Abscissa, amplitude of control soleus H reflex in percent of maximum M wave. Ordinate, decrease in amplitude of soleus H reflex expressed in percent of the maximum M wave; *, significant decrease ($P < 0.05$).

ulation of the sciatic nerve in cats evokes monosynaptic reflex volleys in the tibial nerve consisting of two clearly discernible two, an early and a late (Kubota et al. 1965). The volley recorded from the medial gastrocnemius nerve shows a single peak corresponding with the early peak recorded from the tibial nerve, whereas the volley in the soleus nerve consists of a single peak corresponding to the late peak. It was proposed that the early and late peaks represent efferent volleys conducting in the axons of phasic and tonic motoneurons. It could be assumed that the two component waves of the pretibial H reflex represent EMGs in type I and II muscle fibers evoked by efferent volleys along axons with different conduction velocities in two distinct groups of spinal motoneurons innervating the two groups of the tibialis anterior muscle fibers. Similarly, the same two groups of tibialis anterior motoneurons may be implicated in the two distinct waves in the M wave of the pretibial EMG evoked by stimulation at high intensities.

The common peroneal nerve innervates the extensor digitorum longus and the extensor hallucis longus muscles as well as the tibialis anterior muscle. It is possible therefore that the H reflex recorded from the surface of the belly of the tibialis anterior muscle also includes the H reflexes evoked in these pretibial muscles, which are located in parallel with the tibialis anterior muscle adjacent to one another. The separate waves of the pretibial muscles may represent the EMG activities evoked in these pretibial muscles in addition to the tibialis anterior muscle. We checked whether these pretibial muscles were activated by stimulation of the common peroneal nerve. Although palpation could find no contraction of the extensor digitorum longus muscle, we could not detect whether the extensor hallucis longus muscle was activated, because it was located deep in the pretibial region. Accordingly, we cannot exclude the possibility that the H reflex recorded from the surface of the belly of the tibialis anterior muscle may include the activities evoked in the pretibial muscles other than the tibialis anterior muscle.

The facilitation of the pretibial H reflex started when test stimulation was applied to the common peroneal nerve at 83–124 ms (98.3 ± 15.7 ms, mean ± 1 SD) before the onset of the masseter EMG. The conduction time for the afferent volley evoked by the test stimulation of the common peroneal nerve to reach the pretibial motoneuron pool should be shorter than the difference in latency between the H reflex and M wave (~15 ms). The difference represents the period from the time of test stimulation of the common peroneal nerve to the time of arrival of the reflexively evoked efferent volley of pretibial motoneurons at the point of stimulation of the common peroneal nerve. Because the facilitation of the pretibial H reflex started when test stimulation was applied at 83–124 ms before the onset of the masseter EMG, the excitability of the pretibial monosynaptic reflex must have been elevated ≥68 ms (i.e., 83 − 15 ms) preceding the onset of masseter EMG.

In association with voluntary teeth clenching in monkey, the excitability of the masseter motoneuron pool was reported to start to increase at 25–45 ms preceding onset of masseter EMG (Blair-Thomas and Luschei 1975). With regard to isometric bite task in monkeys, Larson et al. (1981) reported that it was only after the onset of increase in bite force and of the EMG of the temporalis and masseter muscles that afferents from muscle spindles in jaw-closing muscles and periodontal mechanoreceptors started to fire. Accordingly, it is suggested that the command for facilitation of the pretibial H reflex be issued from the cerebral cortex to the spinal cord in parallel with that for excitation of jaw-closing motoneurons. During steady biting, oral-facial afferent impulses induced by biting as well as supraspinal descending impulses may be involved in the facilitation of the pretibial H reflex, as reported with respect to the facilitation of the soleus H reflex in association with voluntary teeth clenching (Miyahara et al. 1996).

Modulation of reciprocal Ia inhibition of soleus H reflex during voluntary teeth clenching

It has been reported that the volleys in the common peroneal nerve exerted a short-latency depressive effect on the soleus H reflex in patients with bilateral athetosis (Mizuno et al. 1971) and during voluntary dorsiflexion of the ankle joint (Tanaka 1972) as well as in resting condition (Tanaka 1974) in normal human subjects. This depression is regarded as the reciprocal Ia inhibition, because the depression is evoked by stimulation of the common peroneal nerve after a disynaptic latency at intensities subthreshold for evoking the M wave in the pretibial muscles (Tanaka 1974).

In the present study the soleus H reflex was depressed by conditioning stimulation of the common peroneal nerve at an intensity subthreshold for evoking the M wave in the pretibial muscles, with the same time course as the reciprocal Ia inhibition of the human soleus H reflex (Tanaka 1983). In addition, the changes in amount of reciprocal inhibition of soleus H reflex in relation to its size in the present study was virtually the same as the reciprocal Ia inhibition of the soleus H reflex reported in humans (Crone et al. 1990). Thus, the depression of the soleus H reflex evoked by stimulation of the common peroneal nerve can reasonably be regarded as the reciprocal Ia inhibition of the soleus H reflex.

The present study has demonstrated that this reciprocal Ia inhibition of the soleus H reflex is reduced during voluntary teeth clenching. It has been reported that the amount of the reciprocal Ia inhibition depends on the amplitude of the soleus H reflex (Crone et al. 1990). The inhibition increases with an increase in amplitude of the test soleus H reflex until it reaches a plateau at the test reflex size of 40–50% of the maximum M wave. In the present study the size of the test soleus H reflex was set ~30% of the maximum M wave and it never exceeded ~45% of the maximum M wave, even during voluntary teeth clenching. In this range the amount of the inhibition should have increased with an increase in amplitude of the test soleus H reflex. As a matter of fact, the amount of inhibition decreased during voluntary teeth clenching even though the amplitude of the test soleus H reflex was increased by teeth clenching. The result indicates that the amount of the reciprocal Ia inhibition of the soleus H reflex was really reduced during voluntary teeth clenching.

Thus, combining the findings in the present study and our previous one, we conclude that in association with voluntary teeth clenching *1*) the H reflexes in the ankle extensor and flexor are nonreciprocally facilitated, and *2*) the reciprocal Ia inhibition from the ankle flexor on the ankle extensor is reduced.

Functional significance of the modulation of the H reflex and reciprocal Ia inhibition of leg muscles in association with teeth clenching

H reflexes in human soleus muscle have been reported to be inhibited during walking (Capaday and Stein 1986; Morin et al. 1982) and running (Capaday and Stein 1987) compared with standing, even when the contraction level of the muscle is the same for the two conditions. The nonreciprocal facilitation of H reflexes of leg muscles in combination with the reduction of their reciprocal Ia inhibition is consistent with an improved control of position required to maintain a stable posture. We propose that voluntary teeth clenching would possibly contribute to stabilization of postural stance rather than smoothness of movement.

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