Characteristics of surface mechanomyogram are dependent on development of fusion of motor units in humans

YASUHIDE YOSHITAKE,1 MINORU SHINOHARA,2 HIDETOSHI UE,1 AND TOSHIRO MORITANI1
1Laboratory of Applied Physiology, Graduate School of Human and Environmental Studies, Kyoto University, Sakyoku, Kyoto 606-8501, Japan; and 2Department of Kinesiology, The Pennsylvania State University, University Park, Pennsylvania 16802

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Yoshitake, Yasuhide, Minoru Shinohara, Hidetoshi Ue, and Toshio Moritani. Characteristics of surface mechanomyogram are dependent on development of fusion of motor units in humans. J Appl Physiol 93: 1744–1752, 2002.—The purpose of this study was to test whether surface mechanomyogram (MMG) recorded on the skin reflects the contractile properties of individual motor units in humans. Eight motor units in the medial gastrocnemius muscle were identified, and trains of stimulation at 5, 10, 15, and 20 Hz were delivered to each isolated motor unit. There was a significant positive correlation between the duration of MMG and twitch duration. MMG amplitude decreased with increasing stimulation frequency. Reductions in MMG amplitude were in parallel with the reductions in force fluctuations, and the rate of change in both was positively correlated across the motor units. Rate of change in MMG amplitude against force was negatively correlated to half relaxation time and twitch duration. Similar negative correlations were found between force fluctuations and contractile properties. These results provide evidence supporting a direct relation between MMG and contractile properties of individual motor units within the gastrocnemius muscle, indicating that surface MMG is dependent on the contractile properties of the activated motor units in humans.

intramuscular microstimulation; force fluctuation; contractile property

THE MECHANOMYOGRAM (MMG) is a recording of the pressure wave produced by lateral expansion of a number of muscle fibers (22). In vitro studies using simple evoked contractions in frog muscles provide evidence that the vibratory signal from the muscle is an expression of the mechanical behavior of the muscle mass, although the main source of the MMG signal is motor unit activity (2, 12). A similar vibratory signal can be recorded easily from the surface of the skin in humans as a muscle contracts (surface MMG) (22), and it is expected that this technique will prove useful for investigating mechanical characteristics of muscle in the fields of physiology, clinical medicine, and rehabilitation. Surface MMG should prove useful if it is possible to ascertain the contributions of isolated motor units to the surface recording in human muscle. As has been extensively studied in the surface electromyogram (EMG), however, surface MMG is the sum of the signals emitted from a number of activated motor units, mediated and modulated by the architecture of the muscle-tendon complex, fat, and skin. To elucidate mechanical characteristics of the muscle from the recorded surface MMG, it is critical to determine how contractile properties and activation characteristics of individual motor units contribute to the surface MMG.

Studies conducted on the gastrocnemius muscle of rats (5–7) and cats (23, 24, 28) have examined the contributions of isolated motor units to the surface MMG signals under well-controlled conditions. Bichler and colleagues (5–7), for example, investigated isolated motor units within the same muscles in vivo, and the contractile properties of the motor units were identified. The amplitude of MMG during repetitive stimulation of isolated motor units was shown to be associated with the amplitude of force oscillation (6, 7). Similar results were also obtained by Orizio et al. (23) in studies examining the medial gastrocnemius muscle of cats in situ. Therefore, evidence exists in mammals that isolated motor units contribute significantly to the surface MMG signal.

In contrast to the research in mammals, there is little evidence supporting a close relation between surface MMG of the whole muscle and contractile properties and activation characteristics of the involved motor units in humans. In maximal twitch contractions evoked by direct whole muscle stimulation, the rising time of MMG (from the onset to the highest peak) was shown to be very similar to the contraction time of the single-twitch force, and it was found to be longer in the soleus muscle than in the vastus lateralis muscle (15). In studies using voluntary contractions, MMG from the soleus muscle contained an increased percentage of low frequencies compared with the biceps brachii muscles (18). Additionally, distinct responses to the increasing force level are observed in the amplitude of surface
MMG between the soleus and medial gastrocnemius muscle (35). It has been further speculated that different contractile properties of motor units, in particular the speed of contraction and relaxation, may affect the development of fusion in relation to the contractile properties and discharge rate of motor units, thus affecting the amplitude of surface MMG (35). In these studies, the response of surface MMG from different muscles was interpreted with the presumption of the following fiber-type compositions: soleus contains the greatest abundance of slow fibers, followed by vastus lateralis (15), biceps brachii (18), and gastrocnemius (35). However, the contractile properties of the involved motor units were not examined. This kind of design is incomplete because it cannot discriminate the possible substantial effects due to slight differences in the setup of the sensor or the architecture of the muscle-tendon complex, fat, and skin (22).

We hypothesized that the characteristics of surface MMG from the whole muscle in humans are largely dependent on the contractile properties of the activated motor units, especially on those features influencing the development of fusion (how fusion is developed in relation to contractile properties and stimulation frequency). This is based on the findings that fusion is developed at lower stimulation frequencies in slow-twitch fibers compared with fast-twitch fibers (10, 31). Thus far, there is no direct evidence to support this hypothesis because previous studies do not identify motor unit activity in vivo (2, 12), were conducted on isolated motor units in other mammals than humans (5–7, 23, 14, 28), or were limited to the comparison between different muscles in humans (15, 18, 35). To test this hypothesis, we compared, in humans, the responses in surface MMG with the controlled intramuscular microstimulation of isolated motor units that belong to the same muscle with a wide range of contractile properties. With the intramuscular microstimulation technique, individual motor units can be isolated and the contractile properties of the stimulated motor units can be identified with regard to contraction time, half relaxation time, and development of fusion (13), thus allowing an accurate assessment of the contribution of individual motor units to the surface MMG in humans.

METHODOLOGY

Subjects. Eight isolated motor units were studied from the medial gastrocnemius muscle of four healthy male subjects. Their age, height, and body mass were 25.8 ± 0.4 (SE) yr, 177.2 ± 2.5 cm, and 68.3 ± 1.9 kg, respectively. The subjects had no medical history or physical signs of neuromuscular disorder. After subjects were fully informed about the nature of the experiment and possible risks involved, written informed consent was obtained from each subject. The protocol was in accordance with the criterion of the ethics committee formed consent was obtained from each subject. The protocol of the experiment and possible risks involved, written in-
band-pass filtered (1–500 Hz) and amplified (model MEG-6100, Nihon Koden). The MMG, EMG, and force signals were displayed on a 20-MHz digital oscilloscope (model 5020A, Kikusui, Yokohama, Japan) and stored on a personal computer at a sampling rate of 2,048 Hz via an analog-to-digital converter (13-bit; TransEra 410, i2net, Tokyo, Japan).

Stimulation procedures. Two sets of fine-wire bipolar electrodes (stainless steel, 100-μm diameter, 5-μm uninsulated area, ~200-μm interelectrode distance) were inserted into the medial gastrocnemius muscle ~1.5–2.0 cm under the skin surface located directly beneath the MMG microphone sensor. Single rectangular electrical pulse waves of 0.5-ms duration were delivered from an electrostimulator (model SEN-7203, Nihon Koden) through a stimulator isolation unit (model SS 102J, Nihon Koden). To verify that only single motor units were stimulated, the position of the intramuscular fine-wire electrodes and the intensity of the stimulus (1–10 V) were carefully adjusted until reproducible all-or-nothing responses were acquired in both signals of EMG and force, simultaneously. The evoked EMG responses were monitored continuously to ensure that the same motor unit was stimulated throughout. Any trials with irregular EMG responses were rejected on-line.

Electrical stimulation and analyses of the data. First, each motor unit was identified by measuring its mechanical properties during single-twitch contractions. The EMG, MMG, and force signals were averaged from 10 single-twitch contractions for each motor unit. Figure 2 shows examples of the averaged EMG, MMG, and force signals from two motor units that exhibited distinctively different mechanical properties. Peak twitch force, contraction time, and half relaxation time were calculated from the averaged force signals by following the methods of our laboratory’s previous studies (19, 35). Contraction time was the time interval between the onset of force and the peak force. The onset of force was defined as the point at which the value exceeded three standard deviations of the baseline noise for three consecutive sampled points. Half relaxation time was defined as the time taken for the force to decline to one-half of the peak force value in the relaxation phase. Half relaxation time was employed for twitch force because it is a standard method to characterize the relaxation phase of motor units. As a measure of twitch contraction duration, contraction time and half relaxation time were summed and termed as “twitch duration” according to its usage in a previous study (8).

MMG duration was measured in the following way from the averaged MMG signals. The MMG duration was defined as the interval between the onset and end of MMG signals produced by single-twitch contractions. In contrast to the analysis of twitch force, the end of MMG signals was employed because the MMG signals do not necessarily decrease monotonically after the peak. In this study, the end of MMG signals was defined as the point at which the rectified MMG declined to three standard deviations of the baseline noise for three consecutive sampled points. Similar to the methods used for force signals, the onset of MMG signals was also defined as the point at which the value exceeded three standard deviations of the baseline noise for three consecutive sampled points.

Second, each individual motor unit was stimulated at 5, 10, 15, and 20 Hz. To exclude the trials that involved stimulation of surrounding motor units, evoked mass action potentials (M wave) were examined to determine whether they remained constant. Each stimulus lasted ~6 s with a 10-min rest period between frequencies to avoid fatigue. Mean force was calculated from the middle 2-s segment of the signal. For further analysis of the force signals, both the DC component and linear trend of the force signals were eliminated by digital filtering to exclude transient responses (filtered force). From these signals, peak-to-peak amplitude of the MMG signals (MMG amplitude) and force signals (force fluctuations) were measured. For further analysis, the obtained MMG amplitude and force fluctuations were then normalized to the respective maximal values in each individual motor unit. Also, frequency analysis (4,096 points, Hamming window, fast Fourier transform) of the filtered force and corresponding MMG signals was performed over the same 2-s window to obtain the mean power frequency as in our laboratory’s previous studies (20, 35). The mean power frequency was defined as the ratio between spectral moments of orders one and zero (20). The mean power frequency of MMG and

Fig. 2. Examples of the surface EMG (A), MMG (B), and force (C) signals averaged for 10 single twitches of a motor unit. For comparison, data from a motor unit with the shortest twitch duration (163.2 ms, MU 1; left) and with the longest twitch duration (220.6 ms, MU 8; right) are shown. Onset of EMG corresponds to 0 ms on x-axis.
force was analyzed to confirm whether their responses matched the stimulation frequency.

Statistics. Descriptive statistics include mean and SE. Statistical analyses were made by using linear correlation coefficients (Bravais-Pearson’s $r$). All values are expressed as means ± SE throughout the text, figures, and table. A probability level of $P < 0.05$ was considered to be statistically significant.

RESULTS

Single-twitch contractions. The investigated motor units possessed a wide range of contractile properties with regard to twitch force, contraction time, half relaxation time, and twitch duration (Table 1). The MMG duration also varied over a wide range. The differences in the contractile properties of the motor units and the corresponding surface MMG signals were obvious when the signals of the two motor units with the shortest and longest twitch duration were compared (Fig. 2). As can readily be seen, the MMG signal lasted for the full duration of the force twitch. The waveforms were not similar to those measured by accelerometers in which the MMG signal was rarely observed during relaxation phase (3, 4, 25). But the waveforms of the present study were similar to those usually obtained by electret condenser microphones (29) or piezoelectric microphones (5). The relations between MMG duration and contraction time, half relaxation time, and twitch duration of all the motor units are reported in Fig. 3. MMG duration was strongly correlated with half relaxation time and twitch duration, but it was not related to contraction time.

Repetitive contractions. In repetitive contractions, the characteristics of MMG and force signals varied, whereas the mean power frequency of MMG and force oscillations approximately matched the stimulation frequency, in all the motor units. The $r$ values were 0.953 ($P < 0.001$) between mean power frequency of MMG and stimulation frequency and 0.980 ($P < 0.001$) between mean power frequency of force and stimulation frequency.

Figure 4 shows two examples of surface MMG and force signals during repetitive stimulations of a motor unit with different stimulation frequencies. DC components of the force signals are removed as described in METHODS, and the motor units with the shortest and longest twitch duration correspond to the two motor units in Fig. 2. In both of the motor units, systematic reductions in the MMG amplitude and force fluctuations were observed concomitantly as the stimulation frequency increased. When the MMG amplitude and force fluctuations were normalized with respect to the maximal values for each individual motor unit, the MMG amplitude appeared to decline linearly in relation to the decrease in force fluctuations as the stimulation frequency increased (Fig. 5A). The change in the MMG amplitude was most pronounced when the stimu-

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Table 1. Contractile properties of motor units and profiles of surface MMG during single-twitch contractions

<table>
<thead>
<tr>
<th></th>
<th>Range</th>
<th>Mean ± SE</th>
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<tbody>
<tr>
<td>Twitch force, mN</td>
<td>0.17–0.50</td>
<td>0.33 ± 0.04</td>
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<tr>
<td>Contraction time, ms</td>
<td>48.6–85.3</td>
<td>62.9 ± 4.2</td>
</tr>
<tr>
<td>Half relaxation time, ms</td>
<td>95.7–172.0</td>
<td>124.1 ± 9.1</td>
</tr>
<tr>
<td>Twitch duration, ms</td>
<td>163.2–220.6</td>
<td>187.0 ± 8.3</td>
</tr>
<tr>
<td>MMG duration, ms</td>
<td>385.5–674.7</td>
<td>535.8 ± 39.6</td>
</tr>
<tr>
<td>MU action potential, μV</td>
<td>120.6–551.3</td>
<td>315.6 ± 50.5</td>
</tr>
</tbody>
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Twitch duration is the sum of contraction time and half relaxation time. MMG, mechanomyogram; MU, motor unit.

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Fig. 3. Relationships between MMG duration and contraction time (A), half relaxation time (B), and twitch duration (C) of all the motor units ($n = 8$). NS, not significant.
ulation frequency increased from 5 to 10 Hz, where a highly significant correlation was exhibited between the changes in the MMG amplitude and force fluctuations (Fig. 5B). These results indicate that the changes in the amplitude of surface MMG signals are significantly related to how fusion is developed in relation to the contractile properties of the activated motor units and stimulation frequency.

In addition, in the two motor units shown in Fig. 4, reductions in the MMG amplitude seem to be more pronounced in the motor unit with the slower contractile properties. In general (10, 34) and also in the present study (data not shown), contractions of slower motor units produce smaller force compared with faster motor units. Practically, mean force is most often related to the MMG signals in the studies utilizing voluntary contractions (26, 30, 35). Therefore, we further tried to identify and present the effects of contractile properties of the activated motor units on the relation between the characteristics of surface MMG and the magnitude of the mean force. Although the available number of motor units was small, four motor units with longer twitch duration (207.2 ± 6.9 ms) formed the “slower motor units” group and the four remaining motor units with shorter twitch duration (166.9 ± 2.0 ms) formed the “faster motor units” group. These groups were formed to ascertain whether any effect of the contractile properties of motor units appear. The MMG amplitude and force fluctuations of each group were investigated in relation to the mean force during repetitive stimulations. It should be noted that the mean force was calculated from the force signals that were not filtered. In Fig. 6, A and B, greater declines in the group of slower motor units were apparent for the MMG amplitude and force fluctuations as mean force increased. Furthermore, we calculated the individual rate of decline in both MMG amplitude and force fluctuation against the increase in the mean force for each individual motor unit. In this calculation, regression analyses were applied to those values obtained at four different stimulation frequencies. Figure 7 shows that the rates of change in MMG amplitude and force fluctuations are significantly related to half relaxation time and twitch duration, with

![Image](https://example.com/image.png)
DISCUSSION

Among numerous attempts to clarify the significance of surface MMG, this is the first study that provides evidence in humans of a direct relation between the characteristics of surface MMG signals from a single whole muscle and the contractile properties of motor units. Major findings of this study were 1) that the duration of surface MMG was strongly correlated with the twitch duration of a motor unit, 2) that the decline in the amplitude of surface MMG was closely related to the decline in force fluctuations generated by increased frequency of contraction, 3) and that fluctuations in surface MMG and force signals were related to the twitch duration and half relaxation time of the activated motor units. These results support the hypothesis that the characteristics of surface MMG are largely dependent on the contractile properties of the activated motor units, especially on those features influencing the development of fusion.

Surface MMG and contractile properties of motor units in twitch contraction. In vitro studies (2, 12) confirm that the main sources of the MMG signals are the pressure waves generated by the gross lateral movement of the muscle fibers that occur during contraction and relaxation of the fibers. It is not clear, however, how these pressure waves can be reflected on MMG signals that are recorded at the skin surface in humans, although studies have tried to relate the characteristics of surface MMG signals to the contractile properties of muscle fibers by comparing different muscles (15, 18). In single-twitch contractions, pressure waves are generated from a simple movement of muscle fibers by a set of contraction and relaxation. Contraction time and relaxation time during single-twitch contractions are mostly related to myosin ATPase activity and reuptake of calcium, respectively, both of which characterize fiber types, and the latter can be acutely impaired by fatigue (11). If surface MMG signals reflect the pressure waves from motor unit activity, then a close correlation should exist between the duration of surface MMG and the required time for the muscle fibers to complete a set of contraction and relaxation. In the present study, the duration for a set of contraction and relaxation of a motor unit was evaluated by the sum of contraction time and half relaxation time (twitch duration). In the motor unit pool of the gastrocnemius muscle in humans, a strong correlation between duration of surface MMG and twitch duration was found (Fig. 3). Within the twitch duration, the duration of MMG was also correlated with half relaxation time but not with contraction time. This may simply be due to the wider range of half relaxation times compared with contraction times. The present results clearly indicate that the duration of surface MMG during twitch contractions depends on the contractile properties of activated motor units and suggest that the time characteristics of the pressure waves in twitch contractions is well reflected on surface MMG signals. The contributions of individual motor units to the surface MMG were examined in the medial gastrocnemius muscle of rats by stimulating isolated motor units (5–7). The close connection between contractile characteristics of motor units and surface MMG signals in rats has been demonstrated by the strong correlation between the MMG amplitude and the twitch tension of a motor unit (5). Together with the present findings on the strong correlation between the time characteristics of MMG and twitch tension in humans, it is likely that surface MMG during twitch contractions is largely dependent on the contractile characteristics of motor units.

Surface MMG in relation to the development of fusion. In tetanic contractions, lateral movement of muscle fibers may depend on the combination of the contractile properties of the muscle fibers and the frequency of the stimulation. Fluctuations of force during tetanic contractions are generated by the oscillation in tension during a series of contraction and relaxation. As a rule, the relative contribution of the relaxation phase to the fluctuations will be smaller as the stimulation frequency increases and fusion is developed. It is also known that the slower the twitch of the muscle, the lower the frequency at which fusion of the evoked mechanical events takes place (10, 31). As a corollary, force fluctuations at a given stimulation frequency would be smaller in motor units that have slower contractile properties. In the present study, this is demonstrated in the gastrocnemius muscle in humans as a greater rate of decline in force fluctuations in the slower motor units (Fig. 6B). It is further supported by a significant correlation between the changes in force fluctuations and twitch duration as well as in the half relaxation time of the motor units (Fig. 7, C and D).

Provided that both the lateral movement of muscle fibers and force fluctuations originate from a common source (2, 12, 22–24), features influencing the development of fusion in the motor units can affect lateral movement of the muscle fibers and the characteristics of surface MMG as a consequence. In this study, the amplitude of MMG decreased in close relation to the force fluctuations produced by the different frequencies of stimuli (Fig. 5A), and the magnitude of these reductions was significantly correlated across the sampled motor units (Fig. 5B). Moreover, the rate of decline in the amplitude of MMG was significantly correlated with twitch duration as well as the half relaxation time of motor units (Fig. 7, A and B). Collectively, these results indicate that the changes in the amplitude of surface MMG during tetanic contractions of the gastrocnemius muscle in humans are largely dependent on the contractile characteristics and the development of fusion in the active motor unit. During unfused tetani with a variable degree of fusion in rats, progressively decreasing fluctuations in tension have been higher r values in those relations to half relaxation time. These results suggest that declines in the amplitude of surface MMG signals with force are more pronounced when the contractile properties of the activated motor unit are slower.
observed with increasing stimulation frequency, and the MMG amplitude and fluctuations in tension have been linearly related (7). This is consistent with the apparently linear decrease in MMG amplitude and force fluctuations with increasing stimulation frequency in humans (Fig. 5). Although the findings of the present study are limited because of the small number of motor units that were studied, previous literature on a rat muscle favors the present results in a human muscle and lends support to the hypothesis that the characteristics of surface MMG are largely dependent on the contractile properties of motor units.

Surface MMG in relation to mean force and EMG during voluntary contractions. On the basis of the present findings and previous literature on MMG during electrically evoked contractions, various characteristics of surface MMG during voluntary contractions may reasonably be explained. Contrary to the tetanic contractions of individual motor units in the present study, voluntary contractions involve a greater number of activated motor units, and the discharge rate of these motor units varies and is generally not synchronized. It is of additional note that the amplitude of surface MMG is proportional to the amplitude of the motor unit action potential (35). The amplitude of MMG is known to increase with force in most muscles during voluntary contractions from low-to-moderate force levels, and the same holds true for the amplitude of EMG (1, 26, 30, 35). In this range of force, newly recruited motor units augment the gross lateral move-
ment of the muscle fibers while the discharge rate of motor units is not yet high enough to attenuate the amplitude of MMG. At higher force levels, declines in the amplitude of MMG with increasing force have been observed, whereas the amplitude of EMG increases continuously because of the additional recruitment of motor units and the increase in their discharge rate (1, 26, 35). The decline in the amplitude of MMG may be attributed to the development of fusion where the high discharge rate of motor units may have greatly reduced the dimensional changes possible in muscle fibers. It is also expected that a muscle with a greater percentage of slow motor units is more likely to have a reduced amplitude of MMG (35).

During voluntary contractions at a submaximal force level, the deficit in force of motor units during a fatiguing protocol is compensated for by increases in the discharge rate of already recruited motor units and/or by the additional recruitment of motor units (20). These changes in the activation patterns of motor units are reflected in the increased amplitude of EMG with time, whereas the amplitude of MMG declines in time with fatigue (27, 30). It is known that the relaxation time of muscle is prolonged by fatigue (8). The increased discharge rate of motor units with prolonged relaxation time under fatigue would facilitate the development of fusion and thus would decrease the amplitude of MMG.

Collectively, the EMG-MMG relation during voluntary contractions can exhibit a linear relation under the condition where the positive effects on the amplitude of MMG and EMG by the recruitment of motor units are not substantially counteracted by the negative effects on the amplitude of MMG caused by the development of fusion. The present findings indicate that the influence of the development of fusion on MMG would explain this relation between EMG and MMG. It seems, therefore, that the relation between surface MMG and the force exerted during voluntary contractions of various muscles is dependent on the discharge rate and contractile properties of the activated motor units and on relative proportion of slow motor units in the muscle under investigation. This interpretation may also be applied to characterizing physiological tremor by MMG (17), where unfused tetani may play a role (16).

**Technical consideration.** Lastly, it is relevant to point out some technical considerations about the employed methods and limitations of the obtained results. In previous studies seeking a relation between surface MMG signals and the mechanical characteristics of a single motor unit, the spike-triggered averaging technique has been applied during voluntary contractions (29, 35). This technique is advantageous in that it does not require sophisticated stimulation techniques and voluntary contractions are possible, but it cannot necessarily measure true mechanical activity of a single motor unit because the averaged signals can easily be distorted by partial fusion even when it is discharging at a very low rate (14, 21). The present intramuscular microstimulation technique circumvents this problem (14) because it allows the control of discharge rate of a single motor unit (13, 35).

Analysis or comparison of the recorded signals is further complicated by the types of transducers and by the layers of tissue between the muscle and the transducer (9, 22). With the utilization of an electret condenser microphone in the present study, MMG signals during twitch contraction lasted for the entire duration of the force twitch as in the previous studies that utilized electret condenser microphones (present study; Ref. 29) or piezoelectric microphones (5). In contrast, MMG signals detected by accelerometers have not exceeded the contraction phase of the single twitch with its main oscillations (3, 4, 25). Also, the mean frequency of MMG signals matches the stimulation frequency in the studies with electret condenser microphones (32, 35), whereas the studies with accelerometers tend to have higher mean frequencies of MMG signals than the stimulation frequency (37, 38). From the basic mechanical properties of motor units and the consequent force signals in a single twitch, it is obvious that acceleration measured during the displacement of the muscle is much smaller during the relaxation phase compared with the contraction phase. As a consequence, the second-order derivative of the displacement during the contraction phase will be particularly emphasized in the signals recorded with accelerometers. For these reasons, the waveforms obtained by accelerometers (3, 4, 25) could be different from the ones obtained by electret condenser microphones (present study; Ref. 35) or piezoelectric microphones (5).

The skin and fat tissues beneath the transducer can act as low-pass filters (3, 22), and the occurrence of this is greatly different among subjects and individual muscles. It is true that the number of motor units is limited in the present study because of the major drawback of the electrical stimulation in humans, but many of the possible problems in the nature of the signals may be resolved by employing the intramuscular microstimulation technique on a single motor unit belonging to the same muscle and by utilizing the electret condenser microphones. Despite a limited number of motor units sampled, the mean frequency of MMG matched the stimulation frequency, and the observed range of contractile measures was substantially wide and closely consistent with the literature for the human gastrocnemius muscles (13, 33). This indicates that the effects of the medium are small or consistent and that the sampled motor units are well mixed in contractile properties. Still, the findings should be limited to the present setup for the human gastrocnemius muscles. Further studies on a larger number of motor units within a single muscle from a variety of muscles may extend the present findings.

**Conclusion.** In conclusion, evidence from the present study supports a close relation between the surface MMG and the contractile properties of individual motor units within a single muscle in humans. It is suggested that the major characteristics of surface MMG are largely dependent on the contractile properties, especially on features in the development of fusion, of the activated motor units.
REFERENCES


