Frequency Response of Human Soleus Muscle

P. BAWA AND R. B. STEIN

Department of Physiology, University of Alberta, Edmonton, Canada T6G 2H7

SUMMARY AND CONCLUSIONS

1. The properties of human soleus muscle were studied by systems analysis. Single stimulus pulses and random stimulus pulse trains were applied to a branch of the nerve to soleus muscle and the resultant tension fluctuations were recorded.

2. The frequency-response function between stimulus pulses and tension conforms to that of a second-order, low-pass filter. The parameters of the second-order system, low frequency gain, natural frequency, and damping ratio, varied systematically with the angle of the ankle. As the ankle was flexed (the length of the muscle was increased), the low frequency gain increased, the natural frequency decreased, and the damping ratio was unaffected or increased slightly.

3. These results are discussed in relation to the twitch responses of human soleus muscles and the responses previously observed in cat muscles.

INTRODUCTION

Soleus muscle of the cat has been extensively studied because of its role in posture and locomotion (7, 9–11, 13, 16). The effects of length, stimulus rate, and the number of active motor units all contribute to changes in the contractile and viscoelastic properties of the muscle which manifest themselves as changes in the twitch tension, the time course of the twitch, the fusion rate, etc. The dynamics of the soleus muscle have also been studied in the frequency domain (14, 15, 17). The soleus muscle of the cat behaves like a low-pass filter, following low frequencies efficiently and attenuating the higher frequencies. The low-pass filter characteristics are of second order (2) and can thus be described by three parameters: low frequency gain, natural frequency, and damping ratio. In the frequency-domain changes in length, initial force, and stimulus rate produce systematic changes in these three second-order parameters (3). These viscoelastic properties of muscle are also responsible for the compensation for inertial loads which muscles exhibit at low frequencies (3, 14).

The problems of load compensation and stability of posture are much greater in a bipedal animal such as man, but no studies are available to compare human soleus to that of the cat. The reasons are the obvious difficulties of isolating the soleus muscle in a living human being, but the human soleus differs in that a substantial portion of it lies superficially in the leg. This has enabled us to stimulate the human soleus muscle selectively to study its properties in the time and frequency domains and to compare an intact muscle in a normal human subject to a partially isolated cat muscle. The present study is limited to muscle properties in relaxed, normal subjects, but the methods and results can serve as a basis for comparing the changes in muscle properties that result from voluntary activation in normal subjects. In addition, the changes in various pathological states could be analyzed.

METHODS

Sixteen experiments were conducted on five volunteer subjects, male and female, with ages ranging from 20 to 35 yr. The subject lay prone with his left foot on the pedal carrying the strain gauges for force measurement. The foot was as tightly strapped to the pedal as could be done without occluding the blood supply to the foot. Thus, the measurements were nearly isometric. The subject could observe the mean level and the fluctuations of force on an oscilloscope. Surface EMG electrodes were placed on the midline at the back of the leg at about 20 cm from the bottom of the foot, so as to record mainly from soleus muscle (1), and at about 8 cm (indifferent electrode), as shown schematically in Fig. 1.

Stimulation

To stimulate the soleus muscle independently of the other left leg muscles, a bipolar needle electrode was inserted into the muscle proximal to the motor point. The needle was carefully positioned so as to stimulate a nerve branch supplying a fraction of the muscle maximally.
Schematic diagram of the experimental arrangement. A branch of the nerve to the soleus muscle was stimulated with a bipolar needle electrode. EMG was recorded by surface electrodes, while strain gauges measured the tension output. The angle of the ankle, $\theta$, was measured between the long axes of the leg and that of the foot.

FIG. 1. Schematic diagram of the experimental arrangement. A branch of the nerve to the soleus muscle was stimulated with a bipolar needle electrode. EMG was recorded by surface electrodes, while strain gauges measured the tension output. The angle of the ankle, $\theta$, was measured between the long axes of the leg and that of the foot.

with a minimum amount of current. The stimulus was kept brief (0.05–0.02 ms) so as to favor stimulation of nerve rather than muscle fibers. Once positioned the needle generally remained stable for the remainder of the experiment, and subjects reported less pain than with transcutaneous stimulation of the whole nerve at the popliteal fossa. Also, with stimulation of a small branch, there was often no H-wave in the EMG (8) so the direct effects of stimulating motoneurons could be studied in isolation. The EMG was continuously monitored to insure that the population of motoneurons stimulated did not change with time.

The stimulus pulses were distributed in time according to a gamma distribution of order $P = 4$ (5) since interspike-interval histograms for many nerve cells are well fitted by this distribution (18). The power for such a distribution is high over the range of frequencies studied so that the coherence between input and output is not limited by low power at any frequency in the spectrum. The standard deviation of the interspike intervals for this distribution is half the mean interval. In earlier experiments on cat muscles (12), power at low frequencies (up to 0.4 Hz) was low, which resulted in low coherence values at these low frequencies. W. J. Roberts (personal communication) suggested that the low power at low frequencies could change the parameters of the second-order system, so we repeated a few runs under similar physiological conditions in humans, both with the gamma distribution of pulses and the distribution used for the cat experiments. The computed parameters of the second-order system in both cases were the same to within experimental error.

Stimulus pulses at a rate of one every 3 s or 1/s followed by random stimulation (12) for 1 min were applied through the needle electrode. The mean rate of random stimulation was usually 5/s, for comparison with studies on soleus muscle in the cat (2). However, in a few experiments the effect of varying the rate was studied systematically.

**Force measurement**

The twitch tensions (up to 1.5 kg) indicated that we were stimulating only about 10% of the motor units with the maximal shocks to branches of the nerve to soleus. The force measured by the strain gauges was recorded on an FM tape recorder along with the surface EMG and the stimulus pulses. Force records were obtained at various angles of the ankle ($77^\circ$–$106^\circ$) with the subjects at rest. The transducer was calibrated at each angle using masses placed 15 cm from the axis of rotation of the foot plate. Values are given in grams weight in this paper for ease of comprehension, but can be converted into equivalent torque values in newton-meters by multiplying by $0.15 \times 9.8 \times 10^{-3} = 1.47 \times 10^{-3}$.

**Analysis**

Details of the spectral analysis using random stimulation have been given by Mannard and Stein (12) and French (6). The spectra of the input (stimulus pulses) and the output (tension) were calculated, together with the cross spectrum which depends on both the input and the output. The best-fitting, linear frequency-response function can then be calculated by dividing the cross spectrum by the input spectrum (4). The magnitude of the frequency response function represents the gain of the system as a function of frequency. The gain curves were fitted by curves expected for a linear second-order system. Initial values for the parameters were chosen and a computer algorithm then varied each parameter by a preset increment until the values were found which gave the least mean square deviations from the data points (2). The parameters of the best-fitting second-order system: low frequency gain, natural frequency, and damping ratio, were calculated in this way for each angle of the ankle and each stimulation rate used.

The values of phase as a function of frequency for a second-order system with these parameters can also be easily calculated. The experimental values obtained from the frequency-response function showed additional phase lags. A time delay, for example between the stimulus and the onset of contraction, would introduce a phase lag which increased linearly with frequency, but would not affect
the gain of the system. The linear regression line which best accounted for the extra phase lags in the sense of least mean square deviations was then calculated.

RESULTS

Properties of human soleus muscle under rest conditions

When a subject is completely at rest, the synaptic inputs to motoneurons are not sufficient to cause them to discharge. Even during random stimulation, such as we applied, no EMG activity was observed except that directly evoked by the stimulus. By adjusting the stimulus to be maximal for the nerve branch stimulated, the evoked activity was constant (to within 5%) for each pulse in a train. Under such conditions the stretch reflex loop is effectively opened at the level of the motoneurons. By recording the tension fluctuations in response to random stimulation, the dynamic properties of the muscle could be determined (see METHODS). The muscle properties were studied 1) at various lengths of the muscle by changing the angle of the ankle, and 2) at various mean rates of stimulation by playing back prerecorded stimulus tapes at different speeds. Figure 2 shows an experimentally measured frequency response curve from random stimulation of human soleus muscle with a mean rate of 5/s, together with 95% confidence intervals calculated according to the methods of Bendat and Piersol (4). The gain measures the change in tension (in grams) resulting from modulation of the stimulus rate (in impulses per second) at a given frequency, and thus has the units grams-second per impulse. The phase measures the difference between the modulation in the response and that of the stimulus. In general, the muscle shows a phase lag which increases with frequency. The entire frequency-response curve can be efficiently measured from a single period of random stimulation by spectral analysis because the random signal contains a wide range of stimulus frequencies (12).

The continuous lines in Fig. 2 show the predictions for the best-fitting linear, second-order system. The gain of the muscle is independent of frequency at low frequencies, but declines according to the second power of frequency at high frequencies, as expected for a second-order system. The phase lag of a second-order system approaches 0° at low frequencies and 180° at high frequencies. However, there will be a delay between the time of stimulation and the onset of contraction (excitation-contraction delay) that will produce extra phase lags which increase with frequency. The fitted curve includes a value of delay which, when added to the phase lags of a second-order system, produces the best fit to the data. In addition, the coherence function was measured (4). The values of this function are normalized between 0 and 1 and give information about the linearity of the system. The coherence values for the data of Fig. 2 were generally around 0.8 or 0.9, and always above 0.5 up to 16 Hz. The good fit of the continuous curves and the high coherence values imply that a linear, second-order model accounts quite well for the data over this frequency range.

Figure 3 shows the values of gains at angles of 83°, 88°, and 95°. As the angle of the ankle increases, which is equivalent to decreasing the length of the muscle, the gain decreases. Data for Figs. 2 and 3 have been taken from the same subject. Figure 4 shows the variation of low
The natural frequency represents the frequency at which the gain curves begin to decline sharply with frequency. As can be observed qualitatively, this occurs at higher frequencies with greater ankle angles, and this is confirmed by the quantitative data for the two subjects in Fig. 4. The damping ratio determines the shape of the gain and phase curves in the frequency response, and the tendency for oscillation in the time domain. The damping ratio remained unchanged or increased slightly with increases in muscle length (decreases in angle). Similar trends were shown for plantaris muscle (12) and for soleus muscle (2) in the cat. However, the values of the damping ratio are mostly less than 1 in human soleus muscles, typically between 0.7 and 1.0, whereas for isometric cat muscles these values were mostly greater than 1. The values of natural frequency are around 2 Hz, which are similar though slightly higher than those for soleus in the cat.

To test the effect of stimulus rate, random stimulation at mean rates of 5, 10, and 20/s were applied in a few subjects. For most subjects the gain decreased continually with increase in rate, although in one subject it increased from 5 to 10/s. The natural frequency often decreased with increase in rate and the damping ratio often increased, as for the cat. The responses were largely fused at 20/s, although moments of relaxation were observed (and subjectively felt) whenever intervals in the pulse train were much longer than average. At 10/s, the fluctuations in tension could be felt much more than at 20/s, while with 5/s, periods of complete relaxation occurred between periods of partially fused contractions. The increasingly fused nature of the contraction with increase in rate explains the decrease in low frequency gain under these conditions.
Twitch contractions

To conclude the results, Fig. 5 shows three superimposed twitches at three different angles for the first 400 ms after the stimulus pulse was applied, together with the changes in the contraction times and half-relaxation times of the twitches with changes in length of the muscle. These parameters were measured immediately before and after a period of random stimulation to permit comparison of the responses in the time and frequency domains (see DISCUSSION). There was some tendency for the contraction time to decrease and the relaxation time to increase slightly following a period of random stimulation, but the muscle remained reasonably stationary. Note that the twitches are nonoscillatory although the damping ratios from the frequency-domain data are less than 1. The implications of these results will now be discussed.

**DISCUSSION**

These experiments show that in the absence of voluntary contraction the human soleus muscle behaves like a low-pass filter of second order. The parameters of this second-order system change systematically with length and can be explained by the length-tension properties of the muscle. The twitch tension (Fig. 5) increases markedly with increasing length of the muscle (decreasing angle of the ankle) and can account for the similar changes in the low frequency gain measured in the frequency domain. The time course of the twitch also increases at longer lengths (smaller ankle angles) and accounts for the decrease in the natural frequency under similar conditions. Similar results have been shown for partially isolated cat muscles (2, 15).

Under isometric conditions the best-fitting second-order system for the cat generally had two real time constants, one of which was determined by the viscoelastic properties and the other by the decay of the active state. However, the values of the damping ratio in these human experiments were mostly less than 1 (Fig. 4). Such systems should show damped oscillations and not possess two real time constants, but the twitches under rest conditions were not oscillatory (Fig. 5A).

The apparent conflict between the low damping ratios and nonoscillatory twitches suggests that the soleus muscle is not simply a second-order system. Several explanations can be offered. First, in the intact leg there will inevitably be an effect due to the mass of the foot and the attachment of the muscle to the transducer. The addition of inertial masses converts the second-order system of the muscle to a fourth-order system, although the differences would only be detectable at high frequencies under nearly isometric conditions. The result of these differences will be to reduce the effective damping and, under more extreme conditions, the twitches in the cat did become frankly oscillatory (3). It is difficult to hold the foot rigidly isometric without occluding circulation and the anomalously low values of damping may be due to deviations from isometric conditions. In the frequency-domain analysis (Fig. 2) deviations of data points from second-order fitted curves were seen at higher frequencies, particularly

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**FIG. 5.** Response of human soleus muscle to single stimuli at rest. A: time course of twitches at 83°, 88°, and 95°. As the muscle length increases (angle decreases), the twitches become slower and the twitch tension increases. B: there is a slight decrease in contraction time with decrease in length. • are twitches before and + are twitches after a period of random stimulation. C: there is a large decrease in half-relaxation time with decrease in the length of the muscle.
above 20 Hz. However, we cannot give much weight to these data points due to low coherence values above 20 Hz.

Second, nonlinearities were observed for soleus muscle in the cat using elastic loads (2), which produced low values of the damping ratio in the absence of oscillatory twitches. Furthermore, the best-fitting parameters of the second-order system vary with the rate of stimulation. This would not occur in a purely linear system, and the variation means that results from random stimulation at 51/s cannot be applied immediately to twitches generated once every few seconds. Thus, the discrepancy between the observed twitches and the partially relaxed responses is not too surprising. This discrepancy does serve to point out that, although a linear, second-order model may be useful for a number of purposes, it is obviously a simplification of the complex nature of mammalian muscles.

Typical values for the natural frequency of the human soleus muscle were around 2 Hz, which was somewhat higher than the average value for the cat (2), although in the same range. The contraction times and the half-relaxation times of the twitches for human soleus (60-100 ms) were also similar. In fitting the phase data to a second-order system, time delays which were typically between 15 and 20 ms were calculated. These again were in the range measured for the cat, so mechanically human and cat muscles behave remarkably similarly, despite the obvious differences in bulk and force output.

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