

THE MECHANISM OF LOW-FREQUENCY SOUND PRODUCTION IN MUSCLE

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ABSTRACT Frog gastrocnemius muscles stimulated isometrically in a saline bath at 20°C were found to produce a single ringing sound event beginning just before the tension record began to rise. The sound event was substantially over by the time the isometric tension began to fall. Results from studies correlating the spatial pattern of the sound, the amplitude and frequency of the sound as a function of the muscle length, and the response of both the passive and active muscle to a transverse pluck were found to be consistent with the conclusion that the sounds in these muscles are caused primarily by transverse resonant vibrations. As the muscle develops force, its lack of cylindrical symmetry gives rise to lateral motions, which are most likely the initiators of the bending vibrations detected as sound.

INTRODUCTION

Human skeletal muscles give rise to sounds when they are active. These sounds may be heard with an ordinary acoustic stethoscope placed on the skin over a large muscle. Upon forcing the muscle to contract isometrically, one can hear a rumbling sound whose frequency changes only modestly with increasing effort, although the amplitude appears to increase monotonically with the mean force level. Some observations of muscle sounds are quite old: for example, Marey (1874) was aware of the sounds produced by his own jaw muscles and said he could change the tone they produced by a fifth (a change in frequency of about 50%) as he clenched his teeth together with more or less vigor. More recently, there has been a renewed interest in muscle sounds (Brozovich and Pollack, 1983), and some exciting clinical applications have been proposed (Barry et al., 1985, 1986).

The purpose of the studies reported here, like those of Barry (1987), is to work toward an understanding of the etiology of muscle sounds through observations of the fluctuating pressures produced by isolated frog gastrocnemius muscles in a saline bath. The muscles were stimulated via the sciatic nerve by a stimulator under computer control. Our first objective was to test the hypothesis that muscles actually do produce low-frequency sound in isolation from the rest of the body. Furthermore, we wished to know: (a) how the amplitude and frequency of the sound changed as a function of the length of the muscle; (b) whether or not the sound depended on the temporal pattern of stimulation of the nerve; (c) what the spatial pattern of the pressure field was like as the muscle produced sound; and (d) how naturally occurring muscle sounds compared with those elicited by plucking the muscle in both active and passive states. Taken together, the results of all these studies point toward the mechanism

by which whole muscles produce and sustain low-frequency sound.

METHODS

Apparatus

A drawing of the muscle bath and instrumentation is shown in Fig. 1. The muscle is held vertically in a rigid stainless-steel jig. The natural frequency of the jig was found to be 428 Hz. This was measured by lightly striking the distal muscle clamp from below when a taut rubber band, simulating a muscle, was in place between the two clamps. Since the frequency of muscle sounds recorded in the experiments was never greater than 150 Hz, the muscle jig was adequately stiff. A force transducer (model 9203; Kistler Instrument Corp., Amherst, NY), mounted on a sliding stage, held the isolated gastrocnemius muscle via a stainless-steel clamp designed to accept the knee joint. A lower clamp of similar design gripped the calcaneus and the distal tendon. Threaded rods extending through the cylindrical clamps could be tightened to prevent either attachment from slipping. The range (0–500 N) and natural frequency (7.7 kHz) of the force transducer (with the proximal muscle clamp attached) were adequate for the measurements.

A Celsco quartz crystal hydrophone (model LC-10; Celsco Transducer Products, Inc., Canoga Park, CA) was suspended in the bath with its tip pointing at the muscle belly as shown, usually 2 mm from the surface of the muscle except in experiments in which it was moved radially away from the muscle to explore the more distant sound field. The sensitivity of the hydrophone was determined by comparing the hydrophone output to the output of a Millar catheter-tip pressure transducer (model PC-380; Millar & Frey Screw Machine Products, South Plainfield, NJ) when both were held next to one another in the far field of a loudspeaker driven by a sinusoidal source over a range of frequencies from 50 to 500 Hz. The Millar pressure transducer had previously been given a static calibration by immersing it to known depths in a water-filled graduated cylinder. The natural frequency and damping ratio of the Millar pressure transducer, established by the ringing response after a light tap was given to it while immersed in saline, were 3,609 Hz and 0.64, respectively. Therefore, the Millar pressure transducer, with its virtually flat frequency response from 0 to 1.0 kHz, was a satisfactory standard against which to compare the Celsco hydrophone over the range 50–500 Hz. The natural frequency of the Celsco hydrophone, established by finding the minimum of its driving-point

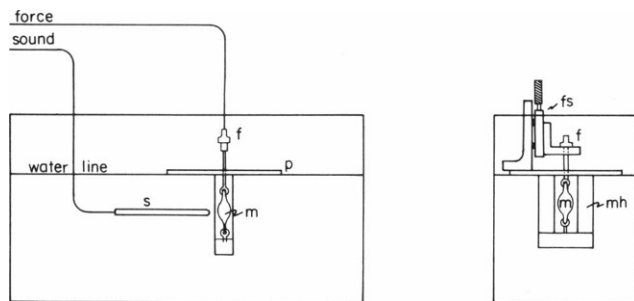


FIGURE 1 Apparatus. Side view (left) and end view (right) of the saline-filled chamber. The hydrophone is shown in place with its tip near the belly of the frog gastrocnemius muscle. *f*, force transducer; *fs*, micrometer stage for force transducer; *mh*, muscle holder; *m*, muscle; *p*, plate at the water line. To avoid clutter, the micrometer does not appear in the side view, nor does the hydrophone appear in the end view.

impedance when it was driven as a sound emitter in saline using a sinusoidal source, was 89 kHz. Therefore, its frequency response was more than adequate to measure the sounds in the range observed in this study. (Although the Millar pressure transducer had an adequate frequency response to allow it to be used as the primary hydrophone in this study, it was not designed to have nearly the sensitivity of the Celsco.)

Surface ripples produced as drops of water were allowed to fall into the tank gave rise to oscillatory pressure transients that could be mistaken for muscle sounds. The effects of ripples were attenuated by fixing a lucite plate at the surface in the vicinity of the muscle and hydrophone. To check that motions of the muscle in the bath were not giving rise to surface ripples, which could be mistaken for sounds, the muscle and force transducer were removed so that a stick with a paddle on the end could be inserted through the force transducer mounting plate into the region of the bath ordinarily occupied by the muscle. When this paddle was agitated, simulating muscle movements during contraction, no pressure events were recorded by the hydrophone. Therefore, we conclude that the water surface must be markedly disturbed, as in a splash, for the hydrophone to detect ripples.

Protocols

A total of 27 frogs (*Rana pipiens*) were used in the experiments. The gastrocnemius muscles were removed from both legs, preserving the sciatic nerve intact along the entire length of the femur. The bath contained a Ringer's solution (100 mM NaCl, 2.5 mM KCl, 1.17 mM NaH_2PO_4 , 1.8 mM CaCl_2 , 1.0 mM $\text{MgCl}_2 \cdot 6\text{H}_2\text{O}$, 5.0 mM glucose, buffered to pH 7.9 using a HEPES buffer) maintained at 20°C (monitored by an Hg thermometer). The cut end of the sciatic nerve was placed into a nerve holder made by machining an L-shaped groove into a lucite block. Electrodes within the nerve holder made contact with the nerve. The nerve was stimulated at a voltage well above that found to produce a twitch of maximum amplitude. The stimulator (Frederick Haer Pulsar 6BP) was operated under software control. Force and sound records were sampled at 1.0 kHz (Data Translation DT-2801-A A/D board) and recorded on a hard disc within an IBM-compatible microcomputer (IBM Instruments, Inc., Danbury, CT).

In 28 muscles, tension and sound were recorded during single isolated twitch stimulations when the muscle was held at a range of lengths from $0.8L_0$ to $1.1L_0$, where L_0 is the length corresponding to maximum developed tension (total peak tension minus passive tension) for twitch stimulation. The muscle length was measured as the distance from one end of the muscle belly to the other, excluding the proximal and distal tendons. In 15 muscles, tension and sound were recorded as the muscle was held near L_{max} , the length where the sound was of greatest amplitude (near $0.94L_0 \pm 0.03L_0$, SD), while the stimulation was varied. The sounds

associated with single spikes, unfused tetani (stimulation frequency, 10 Hz), and fused tetani (30–50 Hz) were recorded.

In five muscles, the preparation was given single stimulations at L_{max} while the hydrophone was moved in 3-mm steps along the axis of the muscle (up and down in the bath), all the while maintaining a 2-mm separation between the hydrophone tip and the surface of the muscle. In these same five muscles, the hydrophone was then positioned 2 mm from the belly of the muscle (point of greatest cross-sectional area), and single stimulations were given as the muscle was rotated in 30° steps through 360°. In two muscles, the hydrophone was withdrawn radially from the muscle to measure the sound at greater distances.

In six muscles, a cylindrical probe 3 mm in diameter with a rounded end was used to pluck the muscle in the way one would pluck a guitar string, pulling the muscle in a direction perpendicular to its long axis and releasing it by allowing the muscle to slide off the rounded end. The probe plucked the muscle at a point ~20% of its length below the proximal clamp (the one holding the knee joint). Muscles were plucked in both the passive state and during a short (500 ms) tetanus.

In five muscles, tension and sound were recorded as the muscle was given a twitch every 10 s over a period of 15 min to investigate the effects of fatigue on the amplitude and frequency of the sounds.

In two muscles, the leg was left intact below the knee except for the removal of skin from the ankle required to hold the muscle in the usual isometric clamp. These muscles were stimulated via the nerve as in all the other experiments to compare the sounds from a muscle in its normal site, in the presence of bone and surrounded by skin, with those from a muscle alone in the bath.

RESULTS

Typical Sound Records

Sound pressure and muscle force records typical of single twitches, partially fused tetani, and fused tetani are shown in *a–c* of Fig. 2. The sound associated with a single twitch (Fig. 2*a*) begins after the stimulus but before the tension begins to rise. At lengths near the plateau of the length–tension curve, there are ordinarily 7–15 half cycles of vibration in the pressure waveform. For most positions of the muscle with respect to the hydrophone, the largest pressure peak is recorded on the second half cycle of vibration, or sometimes on the third or a later half cycle, although, for some particular azimuthal orientations of the muscle with respect to the hydrophone, the largest peak may be reached on the first half cycle. The pressure records from a series of twitches from the same muscle are virtually identical, and no important changes are seen when a rigid baffle is placed in the tank to halve its volume. Fig. 2*b* shows that for a 10-Hz stimulation rate, giving a partially fused tetanus, the first force development elicits the typical sound of a single twitch, but the sounds accompanying subsequent force developments have a smaller initial amplitude and decay in fewer half cycles of vibration than the initial sound. The sound accompanying a fused tetanus (Fig. 2*c*) occurs during the initial force development and decays with substantially the same time course as the sound heard during a single twitch. After the initial sound event, the sound-pressure record of a fused tetanus drops to a level indistinguishable from background noise.

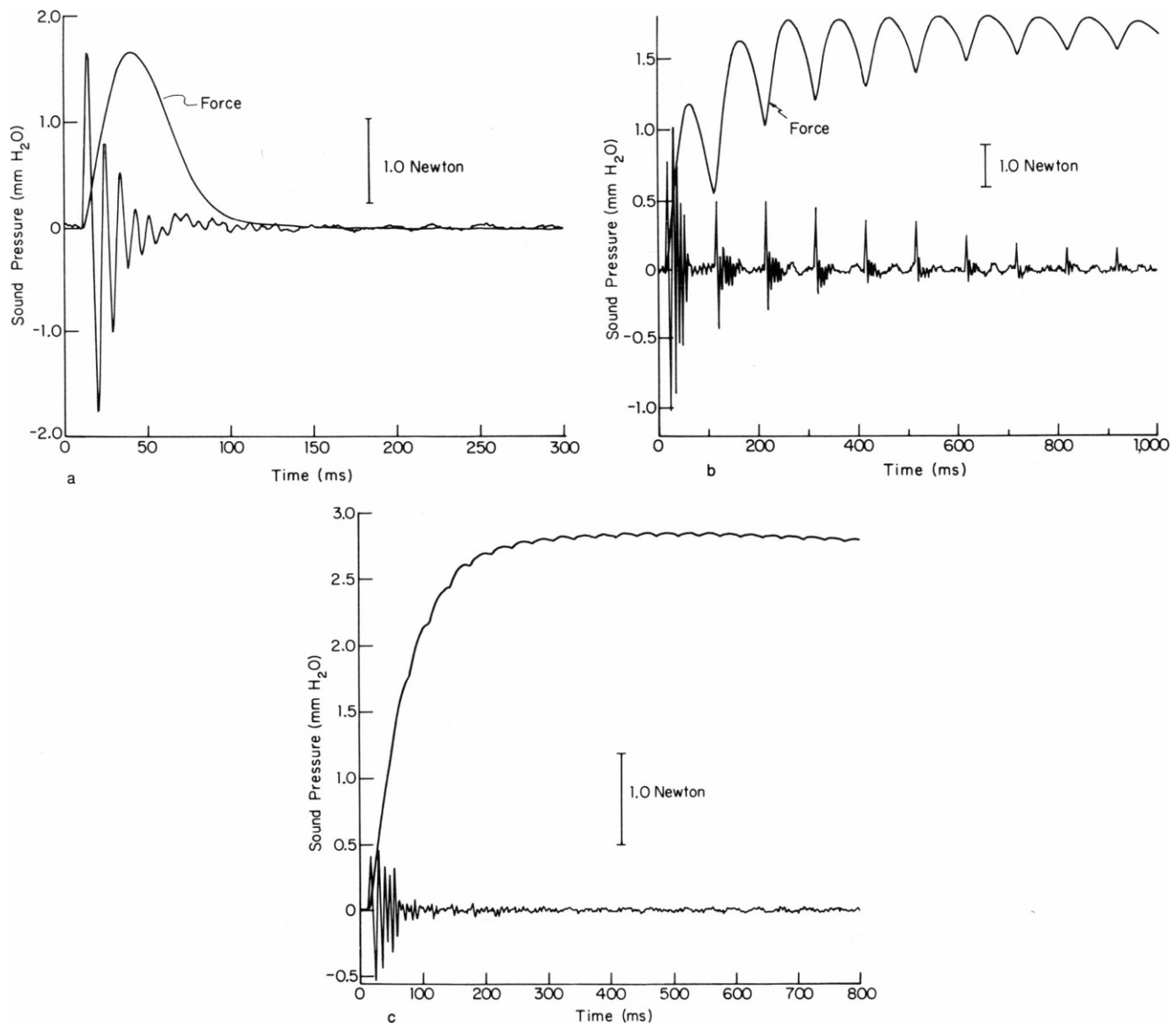


FIGURE 2 Sound and force records. (a) Single twitch. The ringing sound is nearly completed by the time the force has risen to its maximum level. (b) Unfused tetanus. A ringing sound event accompanies each rise of force. The interval between stimuli is 100 ms. (c) Fused tetanus. The only significant sound occurs just before and during the initial rise in force. The interval between stimuli is 30 ms.

Sound Pressure Amplitude and Force Fluctuations

During a partially fused tetanus of the type presented in Fig. 2 b, the amplitude of the sound pressure, measured as the peak-to-peak pressure amplitude during the first cycle of each sound event, increases monotonically with the force increment, measured as the rise in force from the smallest to the greatest value after each stimulation (Fig. 3). The largest sound pressure amplitudes accompany the first few stimulations, i.e., the ones resulting in the largest increases in muscle tension. In the experiments in which muscles were deliberately fatigued by giving closely repeated twitches over long periods, the force increment after each

stimulation declined as the fatigue progressed, and the amplitude of the sound pressure accompanying each force development declined also.

Dependence Upon Length

The variation of sound amplitude, sound frequency, and muscle tension with length during single isometric twitches of the type presented in Fig. 2 a are shown in Fig. 4 for a typical muscle. The tension records, shown as solid curves, describe the passive tension (*P*), the total tension recorded by the tension transducer at the peak of the twitch (*T*), and the developed tension (*D*), defined as the total tension minus the passive tension. Starting at short lengths, the amplitude of the sound increases with increasing muscle

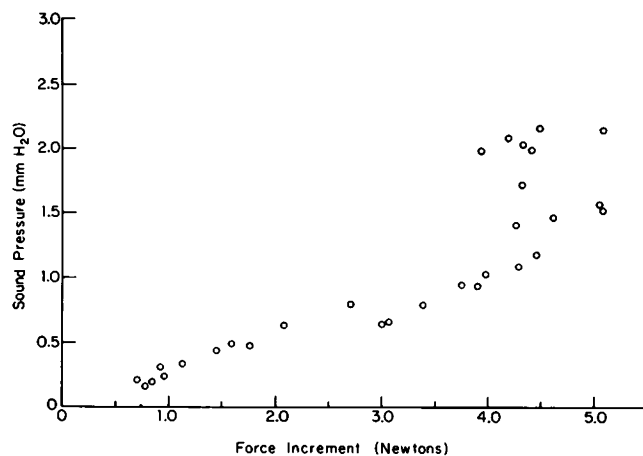


FIGURE 3 Amplitude of sound pressure vs. force increment. In this figure, the peak-to-peak pressure amplitude of the first full cycle of the sound event due to each stimulation is plotted as a function of the change in force after each stimulation. These points represent several intervals of partially fused tetanic stimulations at 5, 7, and 10 Hz. The large sound events accompanying the large force changes (at the upper right of this plot) correspond to the first few stimulations.

length, reaching a maximum in this muscle near $0.95L_0$, before decreasing at the longer lengths. A characteristic frequency of vibration was defined by dividing the first moment of the power spectral density by the area under the power spectral density curve for each sound event accompanying a twitch. As shown in Fig. 4, the characteristic frequency increased slowly with increasing length throughout the intermediate and long range of lengths. At the lower lengths, the frequency increased more rapidly with length.

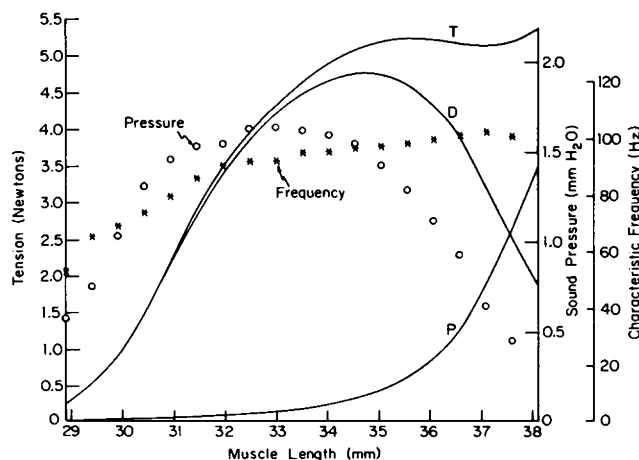


FIGURE 4 Tension-length curves with results describing the sounds accompanying single twitches. Open circles show the sound pressure amplitude during the first cycle of each sound event. The points shown as stars give the characteristic frequency of the whole sound event as obtained from the power spectral density. *P*, passive tension; *T*, total tension; *D*, developed tension. The length corresponding to maximum sound pressure, L_{max} , was always less than the length for maximum developed tension, L_0 .

Pattern of the Pressure Field

Results from the experiments in which the pattern of the pressure field was measured for the sounds accompanying single twitches are given in Fig. 5. In Fig. 5 *a*, the pressure trace is shown for four sequential twitches in which the hydrophone was located a distance of 2, 4, 8, and 20 mm from the surface of the muscle. The axial position of the hydrophone was near the midpoint of the muscle belly in these experiments. In Fig. 5 *b*, the hydrophone was moved along the axis of the muscle. The points show the peak pressure reached on the first half cycle of the sound event. The maximum in the curve corresponds to the central portion of the belly of the muscle. In Fig. 5 *c*, the muscle was rotated with respect to the hydrophone to obtain this record of the peak pressure reached during the first half cycle of the sound event as a function of the azimuth angle. The azimuth angle, defined with an arbitrarily chosen zero, measures the angle in a plane perpendicular to the axis of the muscle. The results show that the first half cycle of the pressure event is maximum positive-going when the azimuth angle is 180° , and maximum negative-going when it is 0° . When the azimuth angle is 90° or 270° , the lines interpolated between the measured points in the figure predict that the amplitude of the pressure in the first half cycle of vibration is near zero, although subsequent half cycles of vibration on the hydrophone record are of finite amplitude.

Plucking

When an unstimulated muscle is given a passive pluck with a blunt probe, the hydrophone measures a ringing pressure transient (Fig. 6 *a*). The frequency of ringing after the pluck of a passive muscle is always less than the characteristic frequency associated with a twitch of the same muscle at the same length. For example, in one experiment typical of many, the frequency of ringing after a pluck was 22.0 Hz while the ringing associated with a twitch stimulated moments later at the same length had a frequency of 95.3 Hz. Muscles plucked while maintained in a state of tetanic activity also showed a ringing response on the hydrophone record. Although the pressure waveform after the pluck of a tetanized muscle was always quite complex (Fig. 6 *b*), the first 7–10 half cycles of vibration always had a frequency higher than that of the same muscle plucked passively at the same length.

Sounds from Intact Lower Legs

Ringling sounds were recorded after twitch stimulations given to muscles in legs with the skin left intact except at the ankle, where the calcaneus was held in the muscle holder. In addition to the ringing sound event accompanying the initial rise in isometric tension, a second ringing event was often present immediately after the peak

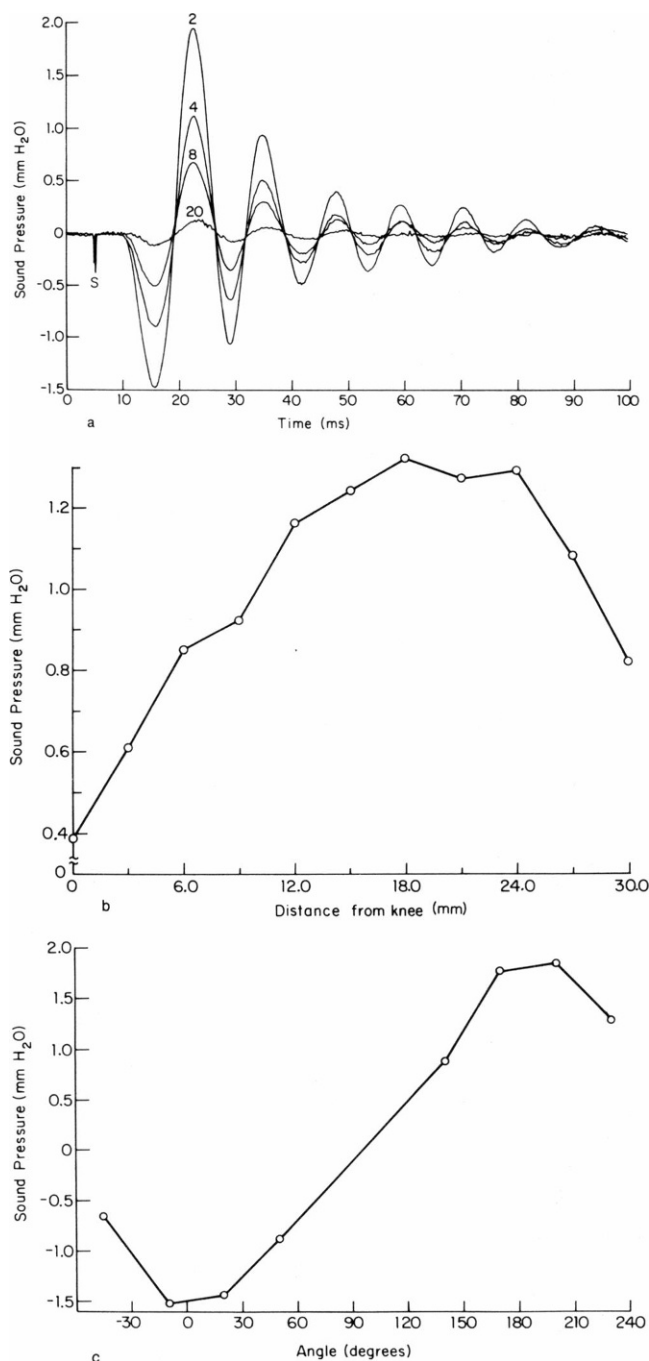


FIGURE 5 Characterizing the pressure field for sounds accompanying twitches. (a) Hydrophone is at the midpoint of the muscle belly but moved radially (at the same depth and azimuth) between stimuli. Records show the sound pressure when the distance between the hydrophone tip and the muscle surface is 2, 4, 8, and 20 mm. S, stimulus artifact. (b) Sound pressure peak as a function of axial distance from the knee. The distance between the tip of the hydrophone and the surface of the muscle was maintained at 2 mm throughout these 11 sequential twitches. (c) Sound pressure recorded on the first half cycle of the sound event vs. azimuth angle. The muscle holder was turned with respect to the fixed tank and hydrophone between each of these eight twitches.

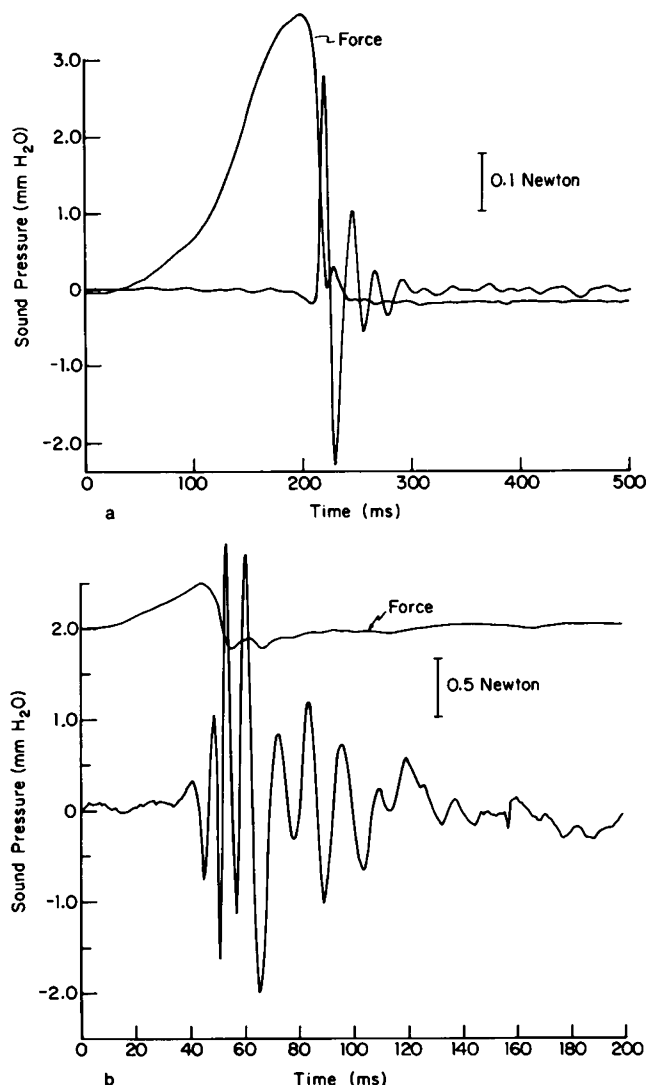


FIGURE 6 Plucking experiments. (a) Passive muscle. (b) Active (tetanized) muscle. The force rises as the muscle is pulled to the side with the blunt-tipped probe, then drops rapidly as the muscle is allowed to slide off the end of the probe. When a passive muscle is plucked, the sound is always a decaying oscillation of one frequency, but the sound after a pluck of an active muscle is much more complex.

of the force record. This second sound event always had a lower peak-to-peak amplitude than the first one.

DISCUSSION

Could the Sounds Be Artifacts?

The first conclusion we wish to draw from this study is the most simple one, that isolated frog muscle produces a low-frequency ringing sound upon each stimulation. We have considered many possible artifactual sources of the ringing pressure fluctuations, including resonances of the muscle holder or of the chamber and the potential role of ripples on the surface of the bath. The following pieces of evidence support the conclusion that the sounds are really

due to the muscle. First, although the muscle holder is capable of resonant vibration, its measured frequency of vibration in the saline bath (428 Hz) is more than three times higher than the frequency of any measured muscle sounds. Second, halving the volume of the chamber did not influence the frequency or amplitude of the sounds. If the chamber were acting as a resonator, halving its volume would increase its resonant frequency, leading to an increase in the frequency of any artifactual sound produced by ringing of the chamber. Third, as shown in Fig. 5 *a*, the amplitude of the sound decreases as the hydrophone is withdrawn (at constant depth in the bath) from the surface of the muscle, but the frequency does not change. If either the muscle holder or the chamber were the real source of vibration, the sound would appear loudest close to the muscle holder or the chamber wall, but instead the sounds were loudest near the muscle. Fig. 5 *a* may also be interpreted as evidence that the presence of the hydrophone did not influence the muscle sound, because the frequency measured was identical at the near and far distances. In a separate experiment, we fixed a large (2.5-cm diam) disc close to the muscle (2 mm from the surface). The result was a reduction in the frequency of vibration accompanying a twitch to about half of the value measured when the disc was not present. This reduction was most likely due to the apparent mass of the flow of saline induced in the narrow gap between the muscle surface and the disc when the muscle moved. The fact that the hydrophone did not cause such a reduction in frequency (even when it was fixed as close to the muscle as the disc had been) supports the assertion that the hydrophone did not interfere with the sound-producing motions of the muscle. Finally, we have presented evidence that surface waves were not creating artifactual sounds. If motions of the muscle were causing disturbances of the surface, which were being detected by the hydrophone, then these pressure fluctuations would not show a maximum amplitude at a depth corresponding to the central region of the muscle belly, as they did in Fig. 5 *b*.

The fact that ringing sounds of the same character were observed in gastrocnemius muscles stimulated within the intact leg is evidence that the low-frequency sounds we observed in isolated muscles have physiological relevance. In light of this result, for example, it is not reasonable to suggest a critical role for the fascia, skin, or long bones of the leg in the generation of muscle sounds since substantially the same early sounds can be recorded whether these elements are present or not.

The Sound Amplitude Depends on the Amplitude of Fluctuations in Tension

Many of the results reported here are in broad agreement with those presented by Barry (1987). We found, as Barry did, that the low-frequency sound produced by isolated frog gastrocnemius muscle has its greatest amplitude when

the muscle is held at a length somewhat less than the length for greatest developed tension; that muscles in partially fused tetanus produce a separate sound on each stimulation; and that a muscle in fused tetanus produces a sound of substantial amplitude only at the beginning of the tetanus (Fig. 2). Furthermore, we found that the pressure fluctuations detected by our hydrophone decreased as the fluctuations in muscle tension associated with each subsequent force development decreased in a partially fused tetanus (Fig. 2 *b*). Thus, Barry's important observation (Barry et al., 1985), that a fatigued human muscle emits less sound than a nonfatigued muscle, is compatible with the fact that the fluctuations in force decline as a muscle fatigues. The sounds heard from human muscles using microphones on the surface of the skin are loudest at the beginning of any activity calling for a sustained partially fused tetanus (Oster and Jaffe, 1980). The results reported here (Figs. 2 *b* and 3) account for why this is so: the largest force fluctuations, and therefore the loudest sounds, occur at the beginning of a partially fused tetanus.

Lateral Motion, Not Thickening, Gives Rise to the Sound

A major conclusion we wish to draw from our work concerns the etiology of the sound. We propose that the sound is excited by a gross lateral movement of the central regions of the muscle, not by a thickening of muscle fibers, as Gordon and Holbourn (1948) suggested, although thickening may well occur, too. The lateral movement is caused by the fact that the muscle is not cylindrically symmetric, so that when activity begins, those regions having larger fractions of contractile tissue shorten more than regions containing sheets of tendon and other noncontractile structures.

We conclude that the first half cycle of the ringing motion is relatively simple. The evidence presented in Fig. 5 *b* shows that the whole muscle begins to move laterally in the same direction at the same time, and the amplitude of the motion is greatest in the middle, as would be the case for a shoelace excited into vibration by starting with it slack and then suddenly pulling it taut. If, instead, the mode of vibration were axially symmetric, with the central regions of the muscle belly bulging as a consequence of shortening, then the initial pressure transient would be expected to be positive-going when measured near the surface in the central regions of the muscle belly and negative-going when measured near the tendinous regions at each end. In all of our measurements, this pattern was never observed.

Further evidence in favor of an initial lateral movement comes from Fig. 5 *c*. If the mode of vibration were axially symmetric, with thickening in the middle, we would expect the initial half cycle of the pressure fluctuations to be positive-going at all points around the azimuth when measured near the central regions of the muscle belly.

Instead, we find the initial half cycle to be positive-going on one side and negative-going with essentially the same amplitude on the other side of the muscle. This is the pattern we would expect to find if the muscle were a cylinder that suddenly began moving at right angles to its axis. In fact, we found we could demonstrate this interpretation on our apparatus. A piece of 1/4-in. diam latex tubing was clamped in the muscle holder where the muscle would ordinarily be. When the rubber tubing was slowly pulled toward the hydrophone and released, the hydrophone recorded a damped ringing vibration. When the tubing was pulled in the opposite direction and released, the first half cycle (and all subsequent half-cycles) was reversed in phase.

Plucking Experiments and Multiple Modes

To learn more about the physical principles by which the vibration is sustained, we may compare the sounds produced in a twitch with those produced by plucking passive and active muscles. The results from Fig. 5 allow us to conclude that the muscle begins vibrating from side to side as the tension rises in an isometric twitch. Therefore, it is reasonable to attempt to excite the same type of vibration by lateral plucking.

In all our records of the sounds produced by passive muscles when plucked, the first half cycle of vibration is the largest, just as would be the case if a taut string were pulled to one side and released. The resonant frequency of a string in its lowest mode of lateral vibration, in which the distance between nodes in the standing wave pattern (a half wavelength) corresponds to the length of the string, is given by (Resnick and Halliday, 1966):

$$f = kT^{1/2}/L, \quad (1)$$

where T is the tension in the string, L is the length of the string between clamps, and k is $1/(2\rho^{1/2})$ for a uniform string of mass per unit length ρ . For the muscle, modeled as a string with a spindle-shaped mass density (i.e., larger in the middle and smaller at the ends), the value of k depends on the actual shape and total mass of the muscle. For a given muscle whose shape and mass are assumed fixed, the frequency would be expected to increase directly as $T^{1/2}/L$. The results given in Fig. 7 *a* show that, to a good approximation, this is just what is found.

Two essential details are different in the results when a muscle is plucked while in a tetanic state. The first is that the ringing pressure event generally grows and then decays, so that the largest pressure peak may occur on the second, third, or even (as it does in Fig. 6 *b*) on the fourth half cycle. The sound trace shows a pattern of beats typical of an oscillation containing more than one frequency. For example, in the decaying phase, a given half cycle is not always followed by a half cycle of lower amplitude. Plots of the early frequency of ringing against $T^{1/2}/L$ did not show

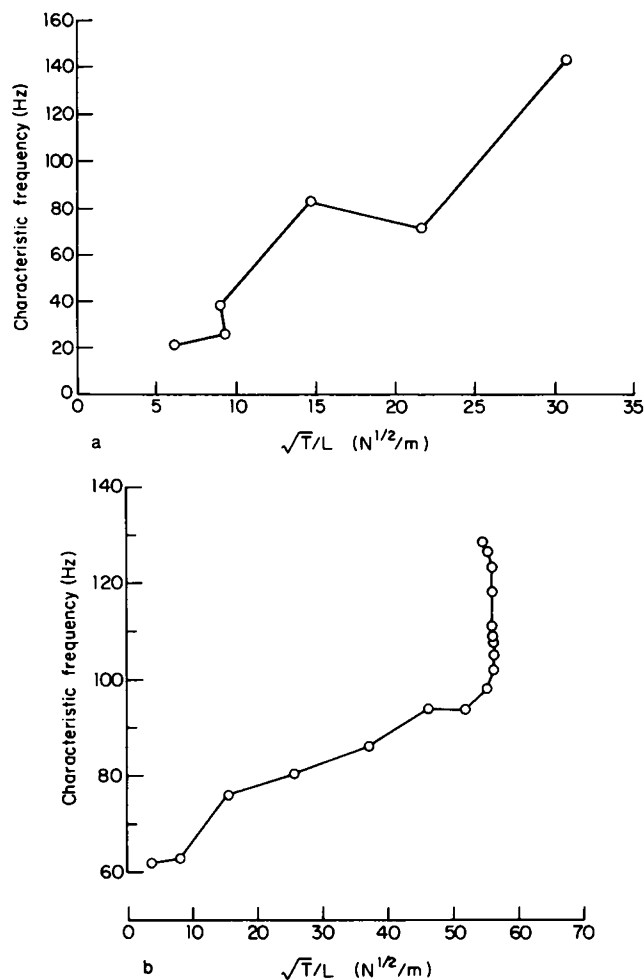


FIGURE 7 Characteristic frequency of ringing vs. $T^{1/2}/L$, where T is the tension and L is the clamp-to-clamp length, including the tendons. (a) Plucks of a passive muscle. (b) The ringing accompanying single isolated twitches. Because its frequency is proportional to $T^{1/2}/L$, the plucked passive muscle may be said to ring like a vibrating string. By contrast, the vibrating string model does not predict the observed relationship between frequency, tension, and length in the muscle excited into ringing by its own twitches.

a direct proportionality for the muscle plucked while in a tetanic state.

Neither did the equivalent plot describing the early ringing of single twitches. As shown for a typical muscle in Fig. 7 *b*, the characteristic frequency of ringing plotted against $T^{1/2}/L$ began at a frequency near 60 Hz even though the tension was near zero (an impossibility for the vibrating string). As the muscle was twitched at a series of greater lengths, both the frequency and the group $T^{1/2}/L$ increase. ($T^{1/2}/L$ increases because $T^{1/2}$ is increasing faster than L ; see, for example, Fig. 4 in the range 29–34 mm.) Beginning just below the plateau in the length-tension curve, the group $T^{1/2}/L$ may no longer increase (for some muscles it actually decreases with increasing length), and yet the experiments showed that the frequency of ringing continued to increase with length. Thus,

the conclusion must be that the muscle ringing while active, excited by either an outside pluck or by its own internal "pluck" during a twitch, is ringing in one or more transverse modes but is using an entirely different physical mechanism for sustaining vibrations, by comparison with the same muscle plucked while passive.

Multiple Frequencies: The Ax-Handle Model

Suppose a long, straight wooden ax handle, having an elliptical shape at each cross-section, is clamped rigidly in a vise. Owing to its greater thickness in one direction than the other, it will have different frequencies of vibration when given plucks (initial displacements) in directions corresponding to the two principal axes. (The same would be true, although the frequencies would be different, if the ax handle were held by tensile loads applied through very stiff springs at either end. In such a case, it would be plucked in the middle.)

Now let the ax handle be plucked in a direction somewhere between the directions of the two principal axes, so that both modes, and therefore both frequencies of decaying vibration, are excited simultaneously. If the ax handle is in water, a hydrophone positioned along the same radial as the direction of the pluck will detect the largest pressure peak in the first half cycle of ringing. If the hydrophone lies at 90° to this direction, it will detect practically nothing during the first half cycle of vibration, but later it will hear both frequencies, since the disturbances due to the two modes cancel each other only at the beginning. When the hydrophone is moved to some other azimuth, beats between the two modes are such that the largest pressure peak is reached on some half cycle later than the first.

Summarizing the Arguments for Likening the Muscle to a String (Passive) or a Beam (Active)

We propose that the muscle plucked passively behaves like a vibrating string. The evidence for this is: (a) the greatest pressure amplitude is always observed on the first half cycle, no matter what azimuthal direction is used for the pluck; (b) the ringing is "pure," with substantially only one frequency; and (c) the frequency is directly proportional to $T^{1/2}/L$, and approaches zero as tension is reduced toward zero.

On the other hand, the muscle plucked while active or excited into ringing by its own force development vibrates like an ax handle, sustaining its transverse vibrations through the interactions of inertia, bending stiffness, and, to a far lesser extent, longitudinal tension. The evidence supporting this conclusion is: (a) the pressure vibrations show beats that cause the greatest pressure to be reached on some half cycle other than the first except when the hydrophone is in one particular azimuthal orientation; (b) the ringing pressure transients, known from the evidence

given in Fig. 5 to be caused by lateral vibrations, can be detected before the tension begins to rise in a twitch, while only vibrations sustained by bending could account for this; and (c) the relationship between frequency, tension, and length in active muscle is not well predicted by a taut string model.

Accounting for L_{\max}

Finally, we may propose an explanation, based on transverse ringing, for the observation that the sounds are loudest at a particular muscle length, L_{\max} . At lengths less than L_{\max} , the velocity of transverse motions is reduced by comparison with those near L_{\max} , due to the reduced developed twitch tension available on the ascending limb of the developed tension-length curve. Above L_{\max} , the twitch tension continues to increase with increasing length, so that lateral vibrations could be sustained if only there were some mechanism to excite them. But this is just what is missing when the muscle is caused to twitch at long lengths, because it is already pulled out nearly straight, so that the lateral motions caused each time the tension rises are relatively weak. At really long lengths, above the plateau in the developed tension-length curve, not only the amplitude but also the velocity of the lateral plucking movement decreases because the developed tension diminishes with increasing length.

Prospects for the Future

Based on the evidence given above, we have concluded that it is primarily the stiffness due to contractile activity, and not the passive stiffness, that sustains the resonant vibrations heard upon each force development. However, an ambiguity remains in what is meant by "stiffness due to contractile activity." A short discussion of this ambiguity may point the way toward some interesting new research directions using muscle sounds.

The stiffness of a steel spring may be measured from the local slope of its static tension-length curve. If the spring is stretched dynamically using a puller which imposes a given sinusoidal displacement, then the stiffness, measured as the amplitude of the force oscillations divided by the amplitude of the length oscillations, is found to be essentially independent of the frequency, provided that the frequency is kept below those values at which the inertial properties of the spring become significant.

Muscle stiffness could be defined in an analogous way as the slope of the total length-tension curve. If this is the definition we adopt, however, an examination of Fig. 4 reveals a large problem, since that slope goes to zero and even becomes negative in the range of lengths around 36 mm for the particular muscle chosen. In that range of lengths, the frequency of muscle sounds does not go to zero but continues to increase with increasing length. Clearly, the stiffness, which makes vibrations possible in active

muscle, is not simply given by the slope of the tension-length curve.

In the future, it will be important to discover just what stiffness, contributed by what elastic structures, is being stretched and relaxed upon each vibration that we hear as muscle sound. Likely candidates for such structures include the crossbridges themselves (although it is important to notice, in Fig. 4, that the frequency of the sound continues to increase at the longer lengths, even as the developed tension, and therefore the stiffness contributed by attached crossbridges, is decreasing with length). The answer to this question promises new insights into the basic mechanical properties of the contractile machinery.

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