LOW FREQUENCY SOUNDS FROM SUSTAINED CONTRACTION OF HUMAN SKELETAL MUSCLE

GERALD OSTER AND JOSHUA S. JAFFE, Graduate School of Biological Sciences, Mount Sinai School of Medicine of the City University of New York, New York 10029 U.S.A.

ABSTRACT Low frequency audible vibrations are produced by human skeletal muscles undergoing sustained contraction. The effect is easily demonstrable with an electronic stethoscope which amplifies sound below 50 Hz. Autocorrelation analysis of the signal shows that it is periodic with a frequency 25 ± 2.5 Hz. The quality of the sound is the same for all the skeletal muscles tested and is unaffected by changes in tension, ambient temperature, and blood flow. Electrically-stimulated contraction produces a sound which is indistinguishable from voluntary contraction. The amplitude of the sound increases linearly with tension. The sound signals are uncorrelated both in frequency and phase with electromyographic signals obtained simultaneously while the muscle is contracted. Arguments are presented to show that the sounds may be an intrinsic property of muscle contraction.

INTRODUCTION

Sounds produced by muscles may easily be demonstrated in the following manner: place the thumbs gently over the ear openings so as to cover the ear canal; with the elbows raised make a fist. The sound perceived, which becomes louder the tighter the fist is made, resembles the rolling of distant thunder. The sound is rich in low frequencies, particularly those at the limit of recognition of tone, ~20 Hz. The present study investigates the rumbling sound associated with the contraction of human skeletal muscle.

The first mention of the subjective experiment described above is that of F. M. Grimaldi (1665, p. 383). Grimaldi, best known for his description of the diffraction of light, was also concerned with acoustics. The subject of muscle sounds was revived by the physicist-chemist W. H. Wollaston in his Croonian lecture (1810). By comparing the sound with that of carriages driven over cobblestones at various speeds, he estimated the frequency to be between 20 and 30 cycles/s. Wollaston employed a rudimentary stethoscope, a stick with a pad for the ear, and found that the contracting muscles of the leg also produced the rumbling sound.

Muscles contracted by electrical stimulation produce the same sound as those contracted voluntarily, as first noted by Herroun and Yoe (1885). These experimenters applied electrical stimuli to a muscle every second and were struck by the resemblance to heart sounds.

Gordon and Holborn (1948) found that a sound accompanies the closing of the eyelids. Using a minute piezoelectric sound detector, they obtained clicks whose frequency increased with the strength of voluntary contraction of the eyelid muscle, *m. orbicularis oculi*. In passing, they noted that muscles of the limbs produce in contraction "a complex rumbling sound" which, for their measurements, constituted a source of interference.

One reason why the phenomenon of muscle sound has been neglected is that body sounds

are usually detected with the mechanical stethoscope. Typically, this instrument is maximally responsive to sounds of 200 Hz but is practically unresponsive to 20 Hz. The newer transistorized stethoscopes, such as the one employed in our work, avoid this difficulty. Another reason why these low frequency sounds have not received attention is that their detection is complicated by confusion with ambient vibrations. These extraneous low frequency sounds from machinery, footsteps, traffic noises, etc.) are considerably more difficult to filter out than are high frequency sounds (e.g., speech, jet whine, sirens). If the signal is periodic, an effective means of extracting it from a noisy background is autocorrelation. In the present study the rumbling sound is analyzed by the autocorrelation technique (see Appendix).

MATERIALS AND METHODS

For the detection and primary amplification of the muscle sounds an Amplitronic transistorized stethoscope (Medelec, Tokyo) was employed. Two transducers were used: the air-coupled microphone supplied with the device, which detects room sounds transmitted through the air, and a contact microphone (pulse transducer, Biocom 1010) which does not register extraneous sounds. Both transducers respond to the low frequency sounds transmitted by the building into the laboratory benches. Either transducer is suitable for the detection of muscle sounds. The contact microphone, although less sensitive, is preferred because of its insensitivity to airborne sounds and its small size.

The spectral response, i.e., gain as a function of frequency, for the transistorized stethoscope was determined using an audio-oscillator (Heathkit Model 1G-18, Heath Co., Benton Harbor, Mich.), the voltage output of which was read from a meter on the device. The generated sine wave was passed into the stethoscope amplifier and the output read on an rms AC voltmeter (Hewlett-Packard Model 400 E, Hewlett Packard Co., Palo Alto, Calif.). The amplifier shows nonlinear characteristics when the input voltage exceeds $\sim 1.5 \times 10^{-4}$ V, but this is considerably higher than that produced in the microphone by the muscle sounds. With the amplifier adjusted to greatest sensitivity (stage 10) and in the high frequency mode (H position) the gain at 25, 250, and 1,000 Hz is 20,000, 2,500, and 125, respectively. In the low frequency mode (L position) the gain at 25, 250, and 1,000 Hz is 18,000, 400, and 3, respectively. As will be shown, the muscle sounds contain no high frequency components. Throughout our studies the stethoscope was maintained at the L position, where the instrument is less responsive to high frequency noises than at the H position. A 25-Hz standard source was not available to us, but using the gain figures for 25 and 250 Hz given above, we calculate that a 25-Hz source operative at 70 dB(SPL) will produce 50 mV in the output of the stethoscope. Apropos, our loudest muscle sounds produced a ~ 50 -mV output.

The spectral response of the transistorized stethoscope was determined independently by Dr. Brian J. Elliott of the Watson Research Center of IBM, Yorktown Heights, N.Y. (B. J. Elliott, personal communication). The approximately free-field response was measured with a sound pressure level meter (General Radio 1565A) as a reference instrument (average level SPL, ~80 dB) with a 4-in spacing between the two transducers. The stethoscope showed no strong resonances in the range 15-50 Hz. The deviations were nowhere >2 dB over this frequency range and hence the spectral response may be considered to be flat.

The air-coupled microphone has a flat frequency response up to at least 1,000 Hz. The same is the case for the contact microphone except that it resonates at 315 Hz, which is too high a frequency to be of importance in the study of muscle sounds. The absolute sensitivity of the microphone-amplifier system was determined using a calibrated sound source (Brüel and Kjoer, Copenhagen, Hearing Aid Test Box, Type 4217). With a sound source of 250 Hz at 90 dB (SPL) the output rms voltage is 50 mV.

For qualitative appreciation of the muscle sounds the earphones supplied with the transistorized stethoscope were employed. Detailed analysis of the waveform of the sounds requires further filtering and amplification of the output of the stethoscope. To remove interference from the electrical mains a 60-Hz elimination filter (Twin-Tee notch filter, K and K Laboratories, Inc., Plainview, N. Y.) was

employed. This elimination is particularly important in the autocorrelation technique where any periodic signal is emphasized. The electrical output was also filtered with a high cutoff filter (Allison Labs, Model 2BR) set to eliminate interferences of frequency >60 Hz.

To display the overall waveform of the output a strip chart recorder (Sanborn Single Channel EKG) was employed. Greater detail of the waveform was obtained with an oscillosope (561B and 3A3 amplifier Tektronix, Inc., Beaverton, Ore.) and photographs were taken of brief intervals. The oscillosope was also used to display electromyograph signals obtained with skin electrodes (Beckman Biopotential Silver electrodes, Beckman Instruments, Inc., Fullerton, Calif.).

The filtered signals from the stethosope output were fed into an autocorrelator (Saicor, SAI 42A). After 2 min the displayed autocorrelation pattern was photographed.

Electrical stimulation of muscles was achieved with a Grass stimulator (Model S-4, Grass Instrument Co., Quincy, Mass.) using silver skin electrodes.

The subjects for this study were two athletic female and six athletic male humans between the ages of 18 and 30 years.

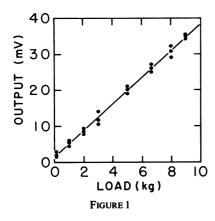
RESULTS

Most of the features of the phenomenon of contracting muscle sounds can be obtained by listening with the earphones to the amplified sound of the transistorized stethoscope. It is particularly convenient to apply the air-coupled microphone to the forearm with the palm turned upward. When the fist is clenched or a weight (lead bricks) of a few kilograms is placed in the hand the rumbling sound is loud. The sound grows louder with increased loading.

At the commencement of the loading the sound is particularly loud but quickly settles to a steady volume. This is seen most clearly in the strip chart recordings (operated at a chart speed of 50 mm/s). On abrupt loading of 2 kg the signal amplitude is about four times that of the steady state signal which is achieved after ~0.5 s. When the load is abruptly removed the signal falls immediately to its base line corresponding to that of the self-supporting but unloaded arm. If loading and unloading is repeatedly carried out the steady state signal during loading becomes progressively larger. This effect occurs concurrently with a trembling associated with fatigue. The trembling and the loud noise is particularly apparent after the weight has been held continuously for 5 min.

It could be argued that the sound is produced by rubbing of the microphone along the skin. Indeed, any microphone including that of the mechanical stethoscope produces a rasping sound when moved along the skin. It is possible that some of the sound from the trembling arm arises in this fashion. The principal rumbling sound, however, is produced by the musculature itself since the sound can be heard when the microphone is not in contact with the skin: the sound is clearly heard and recordable when the arm and the noncontacting microphone are under water. Without touching the walls, subjects fully immers an arm into a plastic tank 1-m long, 0.5-m wide, and 0.5-m deep, filled with water. The air-coupled microphone is placed 1 cm away from the skin. When weights are applied to the palm the rumbling sound is heard but the intensity is less than when the microphone is in contact with the skin. From AC voltmeter readings, the sound intensity at 1-cm separation is about two-thirds that when the microphone is in contact.

The intensity of sound as measured with the AC voltmeter is directly proportional to the weight applied to the hand (Fig. 1). The forearm is kept at ninety degrees to the upper arm, the elbow not touching the trunk with the upward palm maintained parallel to the forearm.



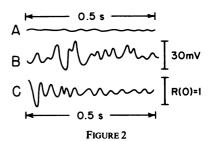


FIGURE 1 Amplified sound signal from the biceps as a function of weight applied to the hand.

FIGURE 2 (A) Amplified steady state sound signal from the flexor carpi radialis with the forearm relaxed and (B) while supporting a 6.6-kg weight. (C) Autocorrelation as a function of delay time for signals from the flexor carpi radialis while the arm is supporting a 6.6-kg weight. The curve is drawn by connecting the 100 statistical points taken at intervals of 5 ms. The data were accumulated for 150 s, thereby allowing 300 summations to be made.

The microphone is strapped over the biceps. In these experiments there is a rest period between trials to avoid effects of fatigue. A weight of ~ 20 kg corresponds to the maximum voluntary tension for our strongest subjects.

The sound intensity produced at the brachialis as a function of elbow angle (the angle between forearm and upper arm) while statically supporting a 2-kg weight in the hand was measured. The intensity is a minimum at 115°. This corresponds to the elbow angle at which the arm can support the greatest weight (Doss and Karpovich, 1965) and hence where the arm exerts the least force to support a given weight.

For other skeletal muscles the sound intensity increases with increasing load. Thus at the gastrocnemius the sound is weak when the subject is prone, increases when the subject is standing normally, and is loud when the subject stands on tiptoe. Indeed, when the subject is straining on tiptoe the measured sound intensity (output ~40 mV) is close to that for the forearm when the subject is holding a 6.6-kg weight.

Sound is also produced when a muscle is contracted by electrical stimulation. Contraction at the forearm was produced by applying over the ulnar nerve a monophasic stimulus of 40 V at 70 Hz with a pulse duration of 0.2 ms. The contact microphone was placed between the stimulating electrodes, which were 4 cm apart; the output from the stethoscope was 20 mV.

The sound of muscle contraction has the same tone quality whether the contraction is produced voluntarily or by electrical stimulation. Furthermore, the tone is independent of the degree of muscle contraction. Thus the typical rumbling sound is produced in the forearm if the load is 0.25 kg or 6.6 kg although the intensity of the sound changes by a factor of about twenty-five. In addition, all of the other readily available skeletal muscles tested (biceps, deltoids, pectoralis major, gastrocnemius, external oblique, and gluteus maximus), when strained, produce the same type of sound.

A typical oscilloscopic tracing of the sound signal from the forearm is shown in Fig. 2. With the hand unloaded a signal is present (Fig. 2 A) but is considerably weaker than that for the

loaded hand (Fig. 2 B). The signal is of variable amplitude but with a quasi-periodicity of frequency ~ 25 Hz.

The output of the stethoscope for the stationary state muscle sound produced at the forearm when loaded was passed through the 60-Hz elimination filter and fed into the autocorrelator to give the curve shown in Fig. 2 C. The curve has a frequency of \sim 25 Hz and the amplitude falls off slowly with a one-half value (relative to zero time) at \sim 0.12 s. As shown in the Appendix, the autocorrelation curve corresponds to a band pass filter centered at 25 Hz with a half width of 5 Hz. The frequency is the same for different loadings in the hand in agreement with the subjective observations of the constancy of the tone.

To ascertain possible contributions to muscle sounds by blood flow, the arteries of the arm were occluded. An inflatable cuff was applied above the elbow. After the subject held the 6.6 kg weight for 1 min the cuff was inflated to 200 mm Hg and remained at that pressure for an additional 2 min. Throughout, the sound detected by the contact microphone and displayed on the strip chart recorder was unchanged both in frequency and amplitude. That blood circulation was arrested by the inflated cuff was evidenced by marked cyanosis of the arm. The subject complained of considerable discomfort while supporting the weight during that time.

The role of ambient temperature on muscle sound was also studied. The signal was recorded while the subject's arm was immersed for several minutes in a water bath while supporting a 6.6 kg weight. The frequency of the sound in the forearm was unchanged over the bath temperature range from 12° to 47°C. The intensity of the sound at the lower temperature was 20% less than that at 25°C.

The electrical potentials (EMG) and sound signals from the gastrocnemius were recorded simultaneously while the subject was standing normally. The EMG, when displayed on the oscilloscope, showed bursts of action potentials occurring roughly ten times a second superposed on a high frequency (200 Hz and higher) background. No synchrony between the amplitude of the sound and the EMG activity was observed.

DISCUSSION

That the rumbling sound associated with muscle contraction arises in the muscles themselves is clearly demonstrated by our experiments. To transmit the sound from the muscles to the microphone requires oscillations of the skin. As seen from the underwater experiments, the sound is not produced by rubbing the microphone surface on the skin. Although some sound intensity is lost by separating the arm and the detector while underwater, water makes a good acoustical coupler between tissue and the microphone. On the other hand, air is not a good acoustical coupler because of its thousandfold lowered density. Hence the muscle sound is not transmitted through air but is reflected back at the tissue-air interface.

The fact that drastic reduction in blood flow through the forearm achieved with the inflated cuff had no effect on the sound indicates that the sound is not of vascular origin. Blood flow in the forearm increases steadily during sustained strong contraction (Humphreys and Lind, 1963) whereas for the gastrocnemius this steady increase is not observed (Barcroft and Dornhorst, 1949). Relaxation of either muscle is immediately followed by a dramatic increase in blood flow (Barcroft and Dornhorst, 1949; Humphreys and Lind, 1963. See also Folkow and Neil, 1971 Ch. 22). We found that for both the muscles of the forearm and the

gastrocnemius the sound intensity remains constant (except for a small increase associated with fatigue) during the sustained contraction and disappears immediately on relaxation. Evidently the sound is not produced by blood movement.

Although filters were employed (namely the L position, the high cut-off filter, and the 60-Hz eliminator) to reduce the interfering background, the unfiltered amplified sound has a deep rumbling character. The dominant frequency is $\sim 25 \pm 2.5$ Hz with or without the filters. As seen in the recordings (see Fig. 2 B) the frequency is in the neighborhood of 25 Hz but there is some shifting of phase or its equivalent, a shifting of frequency. Since autocorrelation does not reveal the phase but only the periodicities, any phase shifting will not appear on the autocorrelation pattern. Thus the curve of Fig. 2 C will persist throughout the duration of the sustained muscle contraction, whereas brief sampling will reveal phase irregularities such as those of Fig. 2 B.

Muscle sounds are difficult to perceive with the unaided ear even though, as we found, they are of a sound pressure level of 60–70 dB. For the human ear the least audible sound pressure at 25 Hz is ~90 dB (Licklider, 1951). Thus the sound produced in the forearm is about one hundredth the intensity that can be heard without an amplifier in the absence of direct coupling to the ear.

Studies of isolated motor units indicate that each individual unit is recruited at a characteristic muscle tension. A newly recruited motor unit has a twitch contraction frequency of 6–8/s and this frequency increases with muscle tension until a complete fusion of twitches occurs at 25–30/s (Henneman, 1974; Allum et al., 1978). At higher levels of force an increased number of motor units are active. EMG signals from intact muscles confirm that with increased loading there is both an acceleration of the rate of firing of individual motor units and the recruitment of additional units (Goodgold and Eberstein, 1972; Lenman and Ritchie, 1970; Lippold et al., 1957). As a consequence, the integrated EMG signal increases with load even though the electrical potential of the individual motor units remains constant (Lippold, 1952). The integrated EMG is linear with the degree of contraction presumably because of smoothly increasing rates of firing and random spatial recruitment of motor units (Lippold, 1952; Taylor, 1962).

The normal tremor ("physiological tremor") observed in human limbs during isometric maintenance of force has been attributed to irregular forcing by the asynchronous activity of unfused twitch contractions of motor units (Allum et al., 1978). The limb behaves as a second order underdamped system driven by those motor units which actively twitch between recruitment and fusion frequencies at the given load (Rietz and Stiles, 1974). The amplitude of physiological tremor is linearly related to isometric force (Allum et al., 1978). This observation can be explained by a linear relationship between twitch tension of motor units and the isometric force at which they are recruited (Milner-Brown et al., 1973). The power spectrum peaks between 6 and 8/s and decreases in amplitude -43 dB/decade toward the high frequency side, with measurable amplitudes above 25 Hz at all force levels. These motions may be propagated as sound waves through the tissue medium to the skin surface. Response characteristics of the complex medium could account for the sound phenomenon which we describe. Against this view are data that show correlation between EMG signals and tremor under some circumstances (Mori, 1973; Stiles, 1973). Furthermore, the pattern of motor unit discharge is most probably very different when the muscle is stimulated

electrically, yet the sound produced is the same. It is difficult to imagine that the tremor frequencies propagated as sound waves would be restricted to a 5-Hz band centered around 25 Hz. The fact that the frequency of the muscle sound does not depend on ambient temperature would rule out any explanation linking the frequency to velocity of nerve conduction since that velocity is temperature dependent.

The increased sound frequency with contraction observed in the eyelid (Gordon and Holbourn, 1948) differs strikingly from our results with different skeletal muscles because of the unique musculature of the eyelid (Moses, 1970). The palpebral portion of *m. orbicularis oculi* has a structural similarity with the extraocular muscles in that the innervation ratio is low, about ten in comparison to 2,000 for the gastrocnemius. Furthermore, the individual muscle units which lie close to the skin can be contacted with a fine microphone (a piezoelectric crystal pickup) through the eyelid. As a consequence, one can follow the involvement of the individual motor units whereas with the larger skeletal muscles only the averaging effects of large numbers of units can be determined.

If the sound associated with muscle contraction is an intrinsic property of muscle tissue then muscle preparations should produce mechanical vibrations during contraction. Diffraction patterns produced by passing monochromatic light through a frog sartorius muscle preparation show oscillations in the mean sarcomere length during tetanic isometric contraction (Larson et al., 1968) although the fluctuation among sarcomeres appears random (Bonner and Carlson, 1975). Vibration ("dither") of the diffraction pattern of chick latissimus dorsi muscle has also been reported (Goldspink, 1970). Examination of Fig. 2 of this latter work shows that the vibrations (shortening of ~4% in the mean length of the sarcomere) have a frequency of ~20 Hz. There are 20 peaks of displacement of the diffraction pattern for 60 frames of their moving picture film, each frame being of 1/60 s duration. The vibration taking place in the muscle preparation seen by the optical technique has an acoustical manifestation. Such vibratory motions may conceivably arise from the making and breaking of cross links (for review, see Fuchs, 1974). Cleworth and Edman (1972) examined the laser diffraction pattern of isolated frog semitendinosous muscle fibers during isometric contraction. They observed no fluctuations of line spacings and concluded that synchronous oscillations of sarcomeres did not occur within the resolution of their method, 50 Å. In any case, lack of synchrony in the oscillation of the sarcomeres would not rule them out as the site of origin of the sound waves.

At any instant during an isometric contraction a number of cross bridges in each sarcomere are not attached (Podolsky and Nolan, 1973). The energy expenditure required for such a contraction may be explained in part by the successive attachment and detachment of cross bridges. It can be inferred from mechanical transient responses to sudden changes in load and length that the time required for this process is ~50 ms (Huxley, 1974). Studies on the biochemical kinetics of cross-bridge movement in vitro indicate that the rate limiting step in the reactions of the cross-bridge cycle is the dissociation of the hydrolytic products of ATP from myosin. Measurement of the maximum rate of the hydrolysis show that it is ~20 s⁻¹ (Taylor and Lymn, 1972). The rate of cross-bridge turnover during an isometric contraction can be calculated by in vivo measurements of ATP consumption, knowing the number of cross bridges per gram of muscle. This method gives the same order of magnitude as the inferred values from the mechanical transient experiments and the studies in vitro of enzyme kinetics

(Curtin et al., 1974). It may be significant that the sound frequencies we report are close to the frequency of cross bridge cycling as determined by these three independent methods.

Regardless of the ultimate origin of muscle sounds, the phenomenon can be of use in physiology and medicine. The intensity of the sound is a noninvasive measure of the force exerted by underlying muscles. The muscles involved in a given task can be identified to the degree that the sound can be localized. The fact that the muscle sound can be measured concurrently with high voltage electrical stimulation eliminates the need for alternately pulsing stimuli and measuring EMG signals from a muscle.

APPENDIX

Autocorrelation

In the evaluation of a randomly fluctuating signal it is convenient to define the autocorrelation function $R(\tau)$. Suppose the time variation of a stationary random signal is x(t). At time τ later it is $x(t + \tau)$. $R(\tau)$ is defined (Schwartz, 1959) as the average over a long time T of the product of x(t) and $x(t + \tau)$ or,

$$R(\tau) = \lim_{T \to \infty} \frac{1}{2T} \int_{-T}^{T} x(t) x(t+\tau) dt.$$

Qualitatively, the autocorrelation is a measure of the regularity of a "random" process. For large values of τ , $R(\infty) = 0$ since the value of x(t) at one time bears no relation to its value at some much later time. The correlation is the greatest when comparing the signal simultaneously (i.e., $\tau = 0$) with itself. As seen from the integral above, at $\tau = 0$ R(0) is the mean square value of x(t) which in Fig. 2 C is normalized for convenience. For white noise, that is when all frequencies are present so the spectrum is flat, $R(\tau)$ is finite at $\tau = 0$ but zero elsewhere. For a periodic signal $\sin(2\pi ft + \phi)$ the $R(\tau)$ is periodic with the same frequency f as the signal but the phase ϕ is lost. Thus the autocorrelation extracts weak periodic signals from the background at the expense of phase information.

As seen from the definition of $R(\tau)$, the computation of autocorrelation requires shifting the signal in time, multiplying it by its previous value and adding the product with other shifted values. The sum is then averaged over a long period of time. There are many electronic devices which can carry out autocorrelations (Lange, 1962, Ch. 2; Kam et al., 1975). More recent systems such as the one we employed carry out the calculations extremely rapidly but information about amplitude of the signals is lost.

Our autocorrelation trace, Fig. 2 C, with its oscillations which diminish with increasing τ suggest band-limited white noise with oscillations about some frequency f_0 . If the band width is Δf then the above integral yields (Schwartz, 1959):

$$R(\tau) = R(0) \frac{\sin(2\pi\Delta f \tau)}{(2\pi\Delta f \tau)} \cos 2\pi f_0 \tau.$$

The envelope, $\sin \alpha/\alpha$, of the oscillating function (of frequency f_0) has a half value when $\alpha = 1.89$. In Fig. 2 C the amplitude is half that at $\tau = 0$ when τ is ~ 0.06 s. So $\Delta f = (1.89)/2\pi(0.06) = 5$ Hz. Hence, the muscle sound signal frequency is 25 ± 2.5 Hz.

This work was supported by Ford Foundation grant 690-0106. J. S. Jaffe was a Student Trainee on this program. Received for publication 9 March 1979 and in revised form 21 December 1979.

REFERENCES

- ALLUM, J. H. J., V. DIETZ, and H. J. FREUND. Neuronal mechanisms underlying physiological tremor. J. Neurophysiol. 1978. 41:557-571.
- BARCROFT, H., and A. C. DORNHORST. 1949. The blood flow through the human calf during rhythmic exercise. J. Physiol. (Lond.) 109:402-411.
- BONNER, R. F., and F. D. CARLSON, 1975. Structural dynamics of frog muscle during isometric contraction. *J. Gen. Physiol.* 65:555-581.
- CLEWORTH, D. R., and K. A. P. EDMAN. 1972. Changes in sarcomere length during isometric tension development in frog skeletal muscle. *J. Physiol. (Lond.).* 227:1-17.
- CURTIN, A. C., C. GILBERT, K. M. KRETZSCHMAR, and D. R. WILKIE. 1974. The effect of the performance of work on total energy output and metabolism during muscular contraction. J. Physiol. (Lond.). 238:455-472.
- Doss, W. S., and P. V. KARPOVICH, 1965. A comparison of concentric, eccentric and isometric strength at elbow flexors. J. Appl. Physiol. 20:351-353.
- FOLKOW, B., and E. NEIL, 1971. Circulation. Oxford University Press, London.
- FUCHS, F. Striated muscle. 1974. Ann. Rev. Physiol. 36:461-502.
- GOLDSPINK, G., R. E. LARSON and R. E. DAVIES, 1970. Fluctuations in sarcomere length in the chick anterior and posterior latissimus dorsi muscles during isometric contraction. *Experientia*. 26:16–18.
- GOODGOLD, J., and A. EBERSTEIN. 1972. Electrodiagnosis in Neuromuscular Diseases. Williams and Wilkins.
- GORDON, G. and A. H. S. HOBOURN. 1948. The sounds from single motor units in a contracting muscle. *J. Physiol.* (Lond.). 107:456-464.
- GRIMALDI, F. M. Physicomathesis de Lumine. Bologna: Author, 1665.
- HENNEMAN, E. 1974. Peripheral mechanisms involved in the control of muscle. *In* Medical Physiology. V. B. Mountcastle, editor. C. V. Mosby, St. Louis. 617-635.
- HERROUN, E. F., and G. F. Yoe, 1885. Note on the sound accompanying the single contraction of skeletal muscle. J. Physiol. (Lond.). 6:287-292.
- HUMPHREYS, P. W., and A. R. LIND. 1963. The blood flow through active and inactive muscles of the forearm during sustained hand-grip contractions. J. Physiol. (Lond.). 166:120-135.
- HUXLEY, A. F. 1974. Muscular contraction. J. Physiol. (Lond.). 243:1-43.
- KAM, Z., H. B. SHORE, and G. FEHER. 1975. Simple schemes for measuring autocorrelation functions. *Rev. Sci. Instrum.* 46:269–277.
- LANGE, F. H. 1967. Correlation Technique. Iliffe Books, London.
- LARSON, R. E., M. J. KUSHMERICK, D. H. HAYNES, and R. E. DAVIES. 1968. Internal work during maintained tension of isometric tetanus. *Biophys. Soc. Abstr.* 11th Annual Meeting, A-8.
- LENMAN, J. A. R., and A. E. RITCHIE. 1970. Clinical Electromyography. J. B. Lippincott, Philadelphia.
- LICKLIDER, J. C. R. 1951. Handbook of Experimental Psychology. S. S. Stevens, editor. John Wiley & Sons, New York. Chap. 25.
- LIPPOLD, O. C. J. 1952. The relation between integrated action potentials in a human muscle and its isometric tension. *J. Physiol. (Lond.)*. 117:492–499.
- LIPPOLD, O. C. J., J. W. T. REDFEARN, and J. VUCO. 1957. The rhythmical activity of groups of motor units in the voluntary contraction of muscle. *J. Physiol. (Lond.).* 137:473-487.
- MILNER-BROWN, H. S., R. B. STEIN, and R. YEMM. 1973. The orderly recruitment of human motor units during voluntary isometric contractions. J. Physiol. (Lond.). 230:359-370.
- MORI, S. 1973. Discharge patterns of soleus motor units with associated changes in force exerted by foot during quiet stance in man. J. Neurophysiol. 36:458–471.
- Moses, R. A. 1970. Adler's Physiology of the Eye. C. V. Mosby, St. Louis. Chap. 1.
- PODOLSKY, R. J., and A. C. NOLAN. 1973. The mechanism of muscle contraction. *Cold Spring Harbor Symp. Quant. Biol.* 37:661-668.
- RIETZ, R. R., and R. N. STILES. 1974. A viscoelastic-mass mechanism as a basis for normal postural tremor. *J. Appl. Physiol.* 37:852–860.
- SCHWARTZ, M. 1959. Information Transmission, Modulation and Noise. McGraw Hill, New York.
 - STILES, R. N. 1973. Reciprocal innervation: phase analysis of demodulated EMGs from antagonistic muscles. *J. Appl. Physiol.* 34:294–298.
- TAYLOR, A. 1962. The significance of grouping of motor unit activity. J. Physiol. (Lond.). 162:259-269.
- Taylor, E. W., and R. W. Lymn. 1972. Enzyme kinetics and the mechanism of muscle contraction. *In Muscle Biology Vol.* 1. R. G. Cassens, editor. Dekker, New York. 47–69.
- WOLLASTON, W. H. 1810. On the duration of muscle action. Philos. Trans. R. Soc. 1-5.