Signal-handling characteristics of load-moving skeletal muscle\textsuperscript{1,2}

LLOYD D. PARTRIDGE
Department of Physiology and Biophysics, University of Tennessee
Medical Units, Memphis, Tennessee

Considerable information is already available about the effects of the muscle system on signals which it translates from nerve impulses into load position. (Neural signal is considered to involve the whole pattern carried by the nerve rather than referring to the individual pulses of which the signal is composed.) The details of the latent period have been examined in isometric and isotonic conditions (4, 9, 43, 45). The development of force and fusion of the contractions and the effect of stimulus pulse rate on response are quite familiar (10, 26, 31). It is well known that muscle length and initial tension affect the force of contraction (40, 42, 44). Length of muscle also affects the fusion of the tetanic response (12). Abrupt changes of length have been studied both before and during a tetanic stimulus and have been shown to modify response tension (8, 12, 22, 29) and muscle excitation (41). It has been demonstrated that with controlled shortening the force produced by tetanic stimulus varies with the rate of shortening (1, 5, 8, 13, 15, 51). It is further well known that the response to a particular nerve impulse can be modified by the recent excitation history of that pathway, as, for example by posttetanic potentiation (20). Many studies have shown that the force with which a muscle resists passive stretching is dependent on whether the muscle is active or inactive (9, 15). In voluntary, postural, and respiratory activity, it has been demonstrated by electromyography that signals are represented by variation of pulse rate in single units (2, 11, 16, 48), and by changes in the number of units active (6, 16). It appears possible that the pulse rate form of signal is involved in movement whereas the recruiting signal dominates the postural and isometric contraction (11). Isometric responses to transient signals such as the initial stimuli of a train (30), gradually increasing and decreasing pulse rate stimuli (8), sinusoidally modulated pulse rates (35), and tetanic trains with brief discontinuities (32) have also been described.

In spite of this extensive information on details of signal handling by the muscle component, it is not clear how these factors might interact in physiological movement. Thus the response-modifying factors of muscle length, nerve impulse rate, and shortening velocity are all changing simultaneously in muscle movement. The

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Modulated pulse rate signals were used to stimulate circulated cat triceps surae muscle-nerve preparations attached to inertial loads of physiological size. Effects of load size and signal frequency on movement amplitude and timing showed that load position, not muscle force, is the value most nearly represented by nerve pulse rate. This emphasizes the importance of the internal feedback mechanisms of the muscle that makes force output dependent on load movement as well as on stimulus rate. It was also found that once a signaled position is attained, small downward fluctuations of nerve impulse rates have relatively little effect on this position. It was also demonstrated that the dynamic response of muscle introduced signal lags of from slightly below 100 to over 1,000 msec. Further, at higher physiological frequencies, the muscle response to modulation of pulse rate is greatly attenuated. These complex signal-handling characteristics of muscle are of such a magnitude as to be of major importance in the quantitative analysis of motor activity control.

frequency response; dynamics; feedback control; lag; reflex; motor control; load movement; muscle force

Since muscle is interposed between the nervous system and its motor actions, any study of motor control must ultimately examine the contributions and limitations introduced in this control by the muscle component. For this purpose, the muscle need be examined only with respect to its signal-handling role, and not with respect to the energetics or mechanisms involved. The question is asked, "What are the relationships between the signal delivered to the muscle as a nerve impulse pattern and the output signal from the muscle in the form of motor performance?" The present study is particularly directed at extending the available information on this question.
muscle is subjected as well to length changes resulting from the effect of previous activity on the inertial load, and from the action of other muscles and external forces. When tested separately these factors modify muscle response in a nonlinear manner. When acting together, these multidimensional nonlinearities make prediction particularly difficult. Consequently, a direct test of muscle acting in the complex load-moving situation and when subjected to varying input signals is most desirable.

The present study is an analysis of nerve signal controlled movement of physiological-range inertial loads, at speeds and amplitudes comparable to normal responses. The controlling signals were generated by muscle nerve stimulation with pulses delivered at rates that varied in preselected patterns (35-37). The stimulus pulse rates varied within the range found on these nerves in normal function. The relationship between stimulus pattern and response demonstrated under these conditions appears not to have been anticipated.

METHODS

Triceps surae muscle groups have been prepared for recording in pentobarbital-anesthetized cats. The cut Achilles tendons were wired to the recording system and the femurs and tibias were attached rigidly to the system frame by special clamps. The muscle blood supply was carefully preserved and the muscle surface was protected from drying by the overlying skin. In later experiments, the muscle temperature was automatically maintained by using locally measured temperature to control application of radiant heat. Brief supermaximal pulse stimuli were applied to the cut muscle nerve using platinum wire electrodes.

A total of 31 cats, weighing between 1.6 and 4.1 kg, was studied in this series. However, all of the figures shown were derived from experiments on the last three cats; thus, information on each graph can be compared with that on several other graphs without any question of individual variations. All of the conclusions are equally applicable to any of the quite uniform responses in the whole series. To allow the reader to make evaluations in addition to those made in the paper, the cat producing the data of a figure can be identified by the symbol appearing after each figure number. The individual cats are represented by the following symbols: * = 3.5-kg male, muscle length 13.0 cm; 9 = 3.3-kg female, muscle length 12.0 cm; + = 4.1-kg male, muscle length 11.8 cm. (Listed muscle lengths were arbitrarily measured with the joints at approximately midposition.)

Stimulation patterns were generated by conversion of various voltage wave forms to pulse rates proportional to the instantaneous voltage (36). Most of the stimulus patterns used were sinusoidally modulated pulse rates. Each pulse in the pattern was used to trigger a supermaximal stimulus to the nerve. The actual pulse rate was measured instrumentally, pulse by pulse (36), to give a record of the input signal to the muscle (Fig. 1). When repeated tests with identical pulse patterns or complex stimulus patterns were required, the pulse patterns were produced in advance and stored on magnetic tape.

When repeated tests of a standard test sequence showed recognizable changes of response, the experiment was terminated. However, with these circulated muscles the response usually remained stable through stimulation sequences of over $10^6$ pulses and involving several hours of experimentation.

Stimulus pulses, pulse rate, isometric force or acceleration, velocity, and position were recorded in various combinations of an FM magnetic tape recorder for later analysis. The tape-storage step was utilized in spite of the fact that it was an added source of noise. The opportunity to rerun the information had several advantages. Slowed reruns of the tests made plotting on an X-Y recorder possible. The rerun data could be presented in various formats, and records from different parts of an experiment could be recorded superimposed to facilitate analysis and hand measurement. It was also possible to make information originally obtained on sequential runs simultaneously available for analog computation purposes. The greatest advantage came from the simplification of the operations which were necessary at the time of the cat experiment. Since analysis and recording in the final format was postponed, the delays and failures normally associated with these steps were eliminated as causes for experimental failure. In case of an error in these analysis steps, the data were still available for rerun without extending the time of possible deterioration of the cat.

The loads used in the load-moving tests were chosen to correspond with values within the physiological range. A simple gravity load consisting of transducer components and a passive load element was used as the minimum load provided an inertial effect larger than the load seen.
RESULTS AND ANALYSIS

Subjecting loaded muscles to a fluctuating stimulus pulse rate resulted in a fluctuating muscle output, whether measured as force or load position. When the pulse rate of the stimulus was modulated in a periodic manner, the output likewise changed periodically. As has been previously reported, a near-sinusoidal pulse rate modulation results in a roughly sinusoidally varying output tension when measured isometrically (35). In the load-moving tests, sinusoidally modulated pulse rate stimulations similarly produced roughly sinusoidal position change in the load attached to the muscle. For detailed performance analysis of the muscle's translation of pulse rate signals into load position, the response should be examined with respect to at least three factors: amplitude, timing or phase, and over-all linearity.

Amplitude

The response signal amplitude might be expected to vary with input signal amplitude, with input signal frequency, and with the size of the load on the muscle. The effect of each of these three factors on response amplitude was tested separately. For these tests other factors which are known to act on muscle performance were kept as nearly constant as possible.

Frequency-amplitude. The effect of signal frequency on response amplitude can be seen in Fig. 3. All of the cyclic responses shown in this figure were produced by cyclically varying the stimulus pulse rates between 5 and 25 pulses/sec at different cyclic frequencies. At low frequencies the response position varied cyclically but deviated appreciably from the near-sinusoidal predictions. At higher frequencies, the output was less cyclically varied. The effect of varied load size was not considered in these experiments since the load size was held nearly constant during the tests.

FIG. 3. (+) Sample records from frequency response series. Numerals superimposed on each segment of record indicate the signal frequency in that segment (in cycles/sec). Time and mm scales apply to all records of figure. Muscle contraction is shown as upward excursion of line. Pulse rate range of stimulation 5-25 pulses/sec.
The relationship between signal cyclic frequency and muscle response amplitude is summarized in a conventional frequency response graph, plotting log amplitude vs. log frequency (Fig. 4). This graph represents responses to input pulse rate variations from 5 to 35 pulses/sec occurring at cyclic frequencies ranging from 0.04 to 6.3 cycles/sec. Both these pulse rates and cyclic frequencies thus fall within the range of values found for these two parameters in a variety of physiological response measurements (2, 7, 11, 14, 16, 21, 47, 49, 50). Since the input amplitude (pulses/sec) and output amplitude (mm) are measured in different units, the relationship between the two must be expressed in dimensional amplitude ratio units (mm load position movement/pulses per sec stimulus rate variation), instead of the dimensionless ratio "gain." The range of variation of this response ratio between different cats was about 2:1. In all cats this amplitude ratio was essentially independent of stimulus cyclic frequency up to a frequency between 0.6 and 1.2 cycles/sec. Further signal frequency increase was accompanied by markedly decreasing response amplitude ratio. This decreasing response could be measured down to about 2% of the low-frequency amplitude after which the response became lost in the system base-line noise.

This loss of information is specifically located in the upper physiological range of signal frequencies. As a result, the experimental data do not cover the whole range of physiological movement frequencies. The lack of high-frequency information also comes in a range which is important for any attempt to fit an analytical expression to the experimental data. Nevertheless, there has been no attempt to extract more information from the experiments by noise suppression techniques because these same signals which are lost because of noise are also not suitable for analytical use, since at these frequencies the input signals are not adequate, i.e., with the pulse rates found on muscle nerves, it is impossible to produce even a good approximation of a sine wave of 10 cycles/sec in a pulse rate form (37). For analytical purposes, it is essential that the input signal be well defined even though it is unlikely that the physiological signal involved in a high-frequency movement is a smooth signal. For these reasons, the range covered in this and other parts of the study are necessarily less than ideal.

Load—amplitude. In any load-moving system, the Newtonian relationships between forces and movement are well defined. In these experiments, the muscle force is applied to a simple inertial system; thus, for sinusoidal movements, the effectiveness of a given force amplitude, producing cyclic displacement amplitude, changes inversely with the square of the cyclic frequency, as shown in Fig. 5.
by the basic rules of mechanics. In Fig. 4, it was seen that below 1 cycle/sec there is little effect of signal frequency on response amplitude. By contrast, if the inertial load had been driven by a constant amplitude force signal, from 0.04 to 0.4 cycle/sec, the response amplitude would have decreased 100-fold. The fact that the observed response amplitude is frequency independent over this range requires that the force generated by these nerve signals be markedly compensated for this inertial effect. Such compensation should also be demonstrable by other tests.

Measurement of the effect of load inertia on movement amplitude provides such a test. For any particular force pattern the movement amplitudes should be inversely proportional to the load inertia. By repeatedly applying a prerecorded stimulus pattern to a muscle-nerve preparation with different loads on the muscle, a test for inertial compensation in muscle was made. Figure 5 shows records of several cycles of the muscle-determined load position response to the same stimulus pattern with each of six different loads. In these tests, the load varied over a range of 28:1. With a constant force pattern, this load change would result in a response amplitude range of 1:28. The movements of the larger loads predicted on the basis of the observed movement of the smallest load are traced over each of the recorded responses. Although not entirely load independent, the response to this test shows no sequential change with increasing load. This result thus provides a confirmation of the presence of the suspected inertial compensation at least for one test frequency.

To better examine the effect of load on response amplitude, graphs of this effect at several different signal frequencies are combined in Fig. 6. On this plot of log of amplitude against log of load, the inverse relationship of a simple inertial system should appear as a straight line falling with a slope of −1. However, at the three lowest frequencies, the actual data show an almost complete lack of load dependence. (At the highest frequency there may be an actual load dependence with the largest loads.) The constant amplitude movement of different loads could be accomplished only by application of different forces. For this series of test loads, the force generated by the muscle when responding to a particular pulse rate signal on the nerve must have increased almost exactly in proportion to the load.

The simple peak amplitude basis for calculation should be checked by an examination of the detail force pattern through the whole movement cycle. Since acceleration of an inertial load is proportional to applied force, the load-moving force can be determined from accelerometer records. With such records, it was found that the force response to a particular stimulus pattern did change appreciably with load. Figure 7 illustrates the nature of the changes encountered in these tests. This figure shows the pattern of the force response of a single muscle when subjected to two almost identical cycles of stimulation, but when the muscle was operating on two different loads. In one case the load was the minimum load of our test sys-

![Graph](image-url)

**FIG. 6.** (*) Typical effects of load inertia on response amplitude. Each line shows this effect as measured at one cyclic frequency of pulse rate modulation between the limits of 5 and 35 pulses/sec. The signal frequencies represented are $\circ = 0.04$ cycles/sec; $\bullet = 0.25$ cycles/sec; $\oplus = 1.6$ cycles/sec; and $\vee = 6.3$ cycles/sec. If the response amplitudes were inversely proportional to the load, each of these lines would have a slope of minus 1. Since the smallest three values shown on the graph are only about 2% of full scale, they may contain significant error. It is therefore impossible to be sure whether or not a line of slope minus 1 properly describes the movement of the largest loads at 6.3 cycles/sec.

In the other case the muscle was, in effect, operating on an infinite load, i.e., it contracted against an isometric force transducer. The two force responses to the same stimulus pattern were quite different. When scale factor correction is taken into consideration, it is seen that the two responses were similar in magnitude and form only in the period in which the pulse rate was so low that the response to individual pulses appears in the record. Through the remainder of the cycle, the load-moving force was much smaller than the isometric force. Only in tests employing high-frequency signals with very large loads does the load-moving force response to a particular stimulus pattern even approach the response in isometric conditions.

**Phase**

In addition to amplitude relationship, one of the attributes of a system is its effect on the timing or phase of signals which it handles. In muscle, the timing relationship is particularly important for consideration of the operation of muscle in the closed-loop system of the stretch reflex. The relationship between input signal and output signal can be expressed as either a time or phase relationship. If there is no distortion of the signal, a measurement at any point in the cycle can be used to determine the phase relationship. Figure 8 illustrates the
MUSCLE FREQUENCY RESPONSE

FIG. 7. (O) Muscle response to changing stimulus pulse rate with different loads. First and third graphs from the top show cyclic pulse rate of stimulus measured on two separate playbacks of a tape-recorded pulse pattern. Second line from the top shows isometric force response during one of the playbacks. Curved ordinate shows force in newtons (N) and arc of recorder pen. The lowest line shows acceleration in g's on the single unit inertial load moved by the same muscle on the other playback of the stimulus pattern. The ordinate in this graph also shows force calculated from the gravity values and load inertia. Comparison of the second and fourth lines from the top thus reveals some of the load-dependent variation of muscle output to the same stimulus pattern. Scale differences should be noted.

The problem of measurement of phase when either input and/or output curves are not perfect sine waves. The magnitude of the timing difference depends on how measurement is made. Three possible points useful for hand measurement are shown on Fig. 8. The phase-frequency response graph obtained with each of the three measurements is shown in Fig. 9. It appears that an average of the two midamplitude crossing measurements is the best representation of the whole wave that can be derived by convenient hand measurement. This value is also shown in Fig. 9 and is the value used in succeeding phase measurements in this study.

The effects of signal frequency and of load inertia on average phase shift are shown in Fig. 10. At low frequencies and with all loads, the response lags slightly behind the stimulus cycle. This lag increases with frequency. Tests with large loads showed the greatest increase of lag with frequency.

Inertial compensation, if present, should also be demonstrable in a phase measurement. This system might be regarded as two series-connected signal-handling elements: muscle and load. The total phase shift produced by two simple phase-shifting components in a simple series-connected system is the sum of the phase-shifting effects of the two separate components (46). The phase shift introduced between nerve signal and muscle force in isometric conditions has been previously reported (35). The phase-shifting effect of an inertial load can be determined from the laws of mechanics. If there were no other signal paths affecting this system, the phase shift between nerve and load movement should equal the sum of the lag between nerve signal and muscle force plus the inertial lag between force and position. The phase lag between sinusoidally changing force and position of an inertial load is exactly 180° for all frequencies, as can be confirmed by basic Newtonian calculations. (Acceleration is in phase with applied force, velocity cycle lags 90° behind acceleration, and the position cycle lags another 90° behind velocity.) This analytical relationship can be applied to any load-moving problem if the signals are adequately represented by sinusoidal functions.

The lower line in Fig. 10 is the phase shift predicted for load-moving muscle on this analytical basis. Obviously, the experimental results shown in the top six lines do not fit the predictions. The phase lag in the load-moving situation with low-frequency signals shows less phase-lag total than is introduced by the inertial component alone. Except with large loads and with the highest test frequencies, the load-moving response phase lag is less than that predicted by about 180°.

This large difference between measured and predicted values requires a re-examination of the assumptions involved in the prediction. There is no reason to question the applicability of Newton's laws to the load moved. The assumption of signal waveform, however, was an
approximation. Elimination of this assumption is possible by actual calculation of the two integrations between force and position data. After the addition of appropriate values for initial position and initial velocity the movement of a load by a changing force can be calculated. Consequently, the recorded signals from isometric tests were played back into an analog computer circuit for double integration. After suitable adjustment of initial conditions, responses such as illustrated in Fig. 11 were calculated. The computed position curve requires no assumptions about approximate force wave form since it is directly calculated from the recorded isometric force pattern. The phase lag found by this direct prediction (in the illustrated example 220° lag) is in good agreement with that predicted on the crude assumption that the force curve was a true sine wave. The phase difference between the actual movement and the original approximate prediction is thus not explained by the error in the assumption of a sinusoidal force wave form. It can only be concluded that the phase relationship between nerve signal and effective force cycle is quite different in load moving than in isometric conditions. The nature of this difference shows an inertial compensatory action within the muscle.

For discussion of muscle signal-handling characteristics, the expression of the input-output relationships in terms of phase shift is quite convenient. For comparison of these effects with conduction delays and other commonly measured physiological values, it is more convenient to express the information in a time difference form. Figure 12 represents the information of Fig. 10 but in terms of the time lag between input signal and response. It may be seen that the small phase lags associated with the very slow cycles were in fact representative of quite larger time differences in the two cycles. All of the delays were large in terms of the usual neurophysiological delays and ranged between 60 and 1,750 msec. This delay is not seen in terms of response to a single pulse, but only in response to a pulse pattern where it represents the delay of the total cumulative effect of current and past pulses.

**Linearity**

The question of linearity provides the third important specification of the signal-handling characteristics of any system. The application of the simplest system analysis procedures requires that the system under study be linear within the range of interest. More sophisticated techniques can deal with nonlinear systems, but require knowledge of the details of the nonlinearities involved (19).

Several tests can be used to acquire linearity information. These include: the simple graphing of a large amplitude input signal against the resulting response; test of responses to input signals of different amplitudes; and small amplitude signals when superimposed on different input signal bias levels. The responses of load-moving muscles to pulse rate signals have been examined for linearity using each of these techniques.

**Input output graphs.** The stimulus response data, most familiar in the time-based graph form, can be presented in the form of input-output graphs developed as shown in Fig. 13. The input, plotted from a voltage proportional to stimulus pulse rate (38), is shown on the abscissa. The output from a position-determined transducer voltage is simultaneously plotted on the ordinate. The output of a position-determined transducer voltage is simultaneously plotted on the ordinate. By superimposing several cycles of the input-output data, both the individual responses and range of variability can be seen.

![Phase Shift vs Signal Frequency](image_url)
Phase, amplitude, and linearity information can be conveniently obtained from these graphs.

The input-output relationship shown in Fig. 13, although quite reproducible, is also complex. The non-elliptical form of the curve is indicative of factors other than simple phase shift in the signals handled by this system. Response position during the period of increasing pulse rate is roughly proportional to input pulse rate. In this rising curve, deviation from a straight line might be interpreted as either a nonlinearity or a small phase lead (10° at midamplitude crossing point). After the stimulus rate reached its cyclic maximum, the relationship changed markedly. The ensuing pulse rate decrease resulted in only minor changes in response position until the stimulus rate had fallen to a low level. At this point the response position changed rapidly toward the extended position. Because of this late release of the load, the output phase measurement made on the falling limb of the curve shows a large phase lag (57° at midamplitude crossing point).

The ranges of variations of the input-output relationships with frequency and with load are shown in the graphs of Fig. 14. (The input-output relationship in isometric conditions is also shown in this figure.) At the highest frequencies, the response amplitude reduction is so great that details of the curve are obscured in the noise. At moderate frequencies the curve shows a roughly elliptical form, suggesting that a simple phase shift description would fit. At the lowest signal frequencies, the curvature of the rising portion of the graph suggests a simple amplitude-limiting nonlinearity. Together these probably actually represent a combination of phase lag and nonlinearity. At all but the highest frequencies, the delayed relaxation characteristics are clearly demonstrated.

Variable input amplitude. By adjusting the amount of variation of stimulus pulse rate in a cycle, it was possible to compare effects of input signal amplitude on response characteristics. Hysteresis of the response was found in tests at various input amplitudes. (Input amplitude is measured as cyclic difference between maximum and minimum pulse rates) (Fig. 15). Since this “latching effect” occurred with different muscle lengths, it is not dependent on some factor occurring only at a particular muscle length. The pulse rate at the release point was relatively constant in spite of the considerable variations of maximum cyclic pulse rates in the different series. The release pulse rate was also relatively constant over the lower cyclic frequency range. At the higher signal frequencies, the release seems not to occur at all and the amplitude decreased toward a nearly steady position largely determined by the highest pulse rate in the cycle.

As might be expected, the response amplitude was not linearly related to the input amplitude (Fig. 16). The smallest amplitudes of input were most effective in producing output movement. Larger inputs resulted in larger output movements, but with an effectiveness which fell with input size. This nonlinearity was apparent in both slow and fast cyclic tests. Although the curves are suggestive of a logarithmic relationship between input and response, when the data were plotted on a semilog graph, the lines were not straight, but were consistently concave downward. Since the experimental data for analysis of the form of this nonlinearity require small amplitude inputs where accuracy of input signal is poor (37), it was felt improper to attempt a more detailed analysis with the associated need for more precise data.

At all amplitudes tested, the response lagged behind the stimulus cycle and the amplitude decreased with increasing signal frequency. The relationship between signal amplitude and frequency response curves are shown in Fig. 17. The phase lag is essentially independent of frequency at low-signal frequencies, and even at high frequencies the differences associated with signal amplitude appear small and could be related to difficulties of measurement of small signals. The shapes of the different amplitude ratio vs. frequency curves for different signal amplitudes have much in common. All show a relatively large and constant value for low-frequency signals and fall at higher frequencies, breaking at about the same frequency and falling with about the same slope after the
FIG. 12. (*) Effect of signal frequency on lag of muscle load-moving response expressed as time delay. These delay values represent the delay of the cumulative effect of the stimulus pattern and greatly exceed the delay of the initial effect of individual stimulus pulses. Different relative load inertias are represented as $\square = 1$ unit; $\bigcirc = 5.5$ units; $\bullet = 10$ units; $\bigtriangleup = 14.5$ units; $\blacksquare = 19$ units; $\blacktriangledown = 28$ units.

break point. The peaking seen with only the smallest test signal (5-15 pulses/sec), however, did appear repeatedly and may be a specific deviation in these curve forms. The fact that each response amplitude ratio curve is at a different level is in agreement with the amplitude nonlinearity shown in Fig. 16.

Small amplitude tests. The described nonlinearity could be related either to signal level or to peak-to-peak signal amplitude. By using signals of a uniform small amplitude superimposed on various steady bias levels, the effect of signal level can be tested independently of signal amplitude. Time graphs of the response to such tests show a response amplitude that decreases with signal bias. The qualitative observation would be expected if the nonlinearity is dependent on level. Quantitative comparison of the amplitude nonlinearity measured with small and with large signals shows, however, that with these small signals, the amplitude loss is greater at high bias levels than expected.

To further examine this quantitative discrepancy, the small amplitude test data were plotted as input-output graphs. Figure 18 shows the relationship between a sinusoidally varying stimulus pulse rate and response positions as both values were varying within the physiological range. In each test the stimulus pulse rate was varied cyclically around a fixed bias level at the chosen frequency and through a range of ±5 pulses/sec. The bias levels were chosen at 5-pulse/sec intervals between 10 and 50 pulses/sec; thus the input pulse rate ranges of different tests overlapped. Each loop shown on the graph shows 10 cycles of the stable response pattern after the initial transient had subsided.

The response amplitude and pattern of individual loops in Fig. 18 is quite dependent on bias level. In all of the tests, the response lagged behind the stimulus cycle. At low bias levels, the response follows the input with a movement showing lag and nonlinearity, but with an effective movement amplitude. With a bias of 15 pulses/sec, the response continues to have an effective amplitude but the previously noted failure to relax is quite apparent. With a bias of 20 pulses/sec and higher, the cyclic response component almost disappears. After the maximal initial shortening was attained, the muscle stabilized at a position determined by the highest pulse rate in the cycle and did not follow the periodic pulse rate decreases. This insensitivity to decreasing pulse rate contrasted with the still-appreciable response to a similar magnitude pulse rate increment. An appreciable sensitivity to pulse rate decrement occurred only in cycles which involved a decrease of pulse rate to a level below about 10-12 pulses/sec.

These small amplitude tests thus are in agreement with the suggestions based on the large amplitude tests. They show muscle response to be a nonlinear lagging function of rising pulse rates with a hysteresis of response involving a failure to relax until the stimulus pulse rate falls below a critical holding rate.

DISCUSSION

This series of experiments, in addition to accomplishing its rather prosaic goal of quantifying some of the sig-

FIG. 13. (V) Relationship between time-based graphs of input (pulse rate) and output (position) and an input vs. output graph. In this graph, time increases around the loop in a counterclockwise direction indicating an over-all lag of output with respect to input.
nal-handling characteristics of a load-moving muscle, has resulted in the identification of two major, unexpected characteristics of that skeletal muscle. The original descriptive goal led to the provision of previously unavailable information about the response of skeletal muscle to dynamic signals carried on the motor nerve in a pulse rate form. This information is a step toward the quantitative analysis of the various motor systems that involve this muscle. It also suggests the probable form but not the quantitative values for the dynamic response characteristics of other muscles. The two unexpected characteristics found in the study, the inertial compensation in muscle and the difference between the response to increasing and to decreasing pulse rate signals, both require significant change in our view of the role of muscle and neural control of muscle. On the other hand, even though these specific results are new, they have been foreshadowed by many previous studies and might each have been predicted from well-established older observations.

In the descriptive phase of these studies, the observed high-frequency response attenuation was fully expected. This characteristic is closely related to the factor described in tetanus fusion experiments. Since muscle can smooth a discontinuous (pulsatile) input to produce a steady isometric tension or isotonic position, it is reasonable to expect that it would not be able to follow brief discontinuities of input signal. The tests employed here differ from the classical tetanus fusion tests by the fact that instead of single pulses separated by fixed intervals, the stimulus pattern consisted of cyclically varying patterns of pulses. This patterned input was chosen both to allow more convenient quantitative analysis and in the belief that it more nearly resembled physiological nerve signals than did the tetanic train. This study also differed from the usual muscle study in that it employed physiological-range inertial loads so that, as in normal function, the muscle response was measured while both opposing force and muscle length were changing. Even with these considerable procedural differences, the signal frequency (about 1 cycle/sec) at which the cyclic response began to decrease falls in the same order of magnitude as the rate of stimulation at which partial tetanic fusion first appears.

The quantitative values found for frequency-amplitude
effects show that this factor can be of physiological significance. At frequencies below 1 cycle/sec, the amplitude of response is not modified by signal frequency, but examination of sequential photographs of moving cats (34) reveals the fact that this muscle often participates in periodic movements with a period between 1.0 and 0.2 sec. In the corresponding 1- to 5-cycles/sec frequency range, muscle response amplitude was attenuated, reaching values well below 5% of its low-frequency value. It would appear that for such fast movements, this muscle characteristic would introduce definite limitations on the possible amplitude of movement. (It is well to note that tremor studies which show appreciably higher frequency components have generally been accomplished by use of accelerometer measurement (50), a technique which emphasizes those high-frequency components. Such tremor measurements often involve displacements of only a few microns.) The observed high-frequency limitation could be an important factor in restricting the amplitude of high-frequency neural noise or oscillation.

The phase measurement similarly shows a frequency dependence. At low signal frequencies, although the time lag is large, the phase lag is small and only careful measurement reveals its presence. On the other hand, at high signal frequencies, this phase lag becomes a major part of the cycle and should be important in neural control. A previously unexplained lag of this magnitude is, in fact, seen in voluntary movement between the EMG activity and the mechanical response (27).

The present study provides a method of quantitative comparison of the lag introduced by different muscles and by the same muscle under different conditions. If the observed input amplitude independence of phase shift can be shown to apply generally, the comparison would involve only comparison of two graphed lines.

In these experiments, muscle followed a dynamic pulse rate signal with a response which was a nonlinear function of the input pulse rate. This observation was anticipated from the facts that unit firing rate is known to change with movement (2) and muscle response in tetanic tests is nonlinearly related to stimulus rate (8).

For a more concise statement and for convenience in motor-system analysis, it would be desirable to convert the graphic data into an analytical expression. More-
over, frequency response data can quite directly be converted into transfer function equations using standard procedures (46). Such conversion requires the measurement of slopes of portions of the graphed curves and the determination of “break points” in the curve. Unfortunately, suitable input pulse rate signals cannot be generated to extend the data to high enough frequencies to establish the curve slopes accurately (37). It is not possible, for example, to determine which of two previously used muscle response simulations (17, 36) best fits the isometric tests in this experiment. The proper representation of the load-moving data is similarly uncertain. The response nonlinearity further considerably complicates the analysis (19). Because of these problems, it was concluded that at present, graphic presentation of these data was to be preferred to an empirically derived approximate equation.

Even though the development of a descriptive equation is not intended, an analytical examination of the data does yield quite specific information about muscle performance. One might, under the influence of isometric studies, think of muscle as a force-generating machine which is governed by input pulse rate and recruiting signals. If this were the case, the load-motion amplitude would change markedly with both signal frequency and load inertia. If muscle were a force motor, in the 10-fold frequency range between 0.04 and 0.4 and over the 28:1 load range, a total amplitude difference of 2,800:1 should have been expected. Since the maximum measured variation through the whole of these ranges was only 1:3:1, and this did not show any trend (Fig. 4), the prediction was not fulfilled. This discrepancy occurred in the low-frequency range where there was no problem of adequacy of input signals. The discrepancy also occurred with tests involving several different signal amplitudes, thus eliminating the possible artifact of clipping by an overdriven muscle. With a ±5% resolution of measurement, there can be no question that these differences lie in measurement error. It follows that the effect of inertia on the response has been quite effectively compensated by the muscle system. This is further confirmed by the unmistakable absence of the expected 180° additional phase lag due to inertia.

Compensation for the inertia of the load must occur in the muscle. The load was a simple mechanical system in which there is no basis to question the applicability of the rules of Newtonian mechanics. Muscle can act on the load only by the application of force. Thus, to explain the results, the muscle response must depend not only on the input pulse rate signal, but equally on the results of its own activity: the load movement. This was also clearly shown in the comparison of load-moving response with isometric response with respect to both amplitude and phase relationships. In terms of signal handling, such a
dependence of output on output is feedback. The feedback cannot involve a neural reflex loop since it occurs in these tests with cut nerves, although in normal function, it would be entirely within the larger neural feedback loops. The feedback considered here must be within the physical chemical systems of the muscle itself (Fig. 19).

The presence of feedback in muscle has been recognized in previous studies. Both Goodall (18) and Pringle (39) have commented on the presence of feedback in muscle as a result of quite different studies. A factor which probably contributes to this compensation was reported by Hill (25) who stated that feedback was shown by the fact that opposition to muscle contraction results in prolongation of the active state. The old observations that muscle contraction was influenced by both muscle length and contraction velocity although not originally described in those terms is also an example of feedback.

The present study thus does not originate the recognition of intramuscular feedback, but it does place new emphasis on its effect and importance in determining muscle response. It appears that this skeletal muscle acts as a servo-system following a position command on its motor nerve with an appropriate load position, while force used to accomplish this positioning is adjusted as needed by the feedback effect. Like most feedback systems, this performance fails when the load becomes excessive for the compensation.

The observed hysteresis to cyclic input was also unexpected. It has probably generally escaped recognition because its demonstration requires special and somewhat unusual conditions. The hysteresis is not seen except as a result of a stimulus pulse rate which decreases from a higher rate and then only if the pulse rate remains above the release level. Such a procedure has seldom been employed for muscle experiments, although Buchthal (8) did publish one record in which a triangularly modulated pulse rate was used for muscle stimulus in a single-fiber isometric experiment. Close inspection of his records reveals the fact that this failure to release the contraction occurred in his test. The current author also failed to note this effect in a previous isometric study with sinusoidally modulated pulse rates (35). The effect, though present in both of these time-based graphs, is not obvious. When the response force or position is presented as a graph against the stimulus pulse rate, the hysteresis becomes quite clear.

In a retrospective examination of previously available information, there is also indirect evidence to suggest the probable presence of a hysteretic response in muscle. Electromyographic records during movement are characterized by a large burst of activity during the movement which rapidly decreases even though the new posture may be maintained with almost the same force required to resist gravity as was used in the peak of the movement. This pattern could be explained by the observed muscle characteristics. A second basis which might have given warning of the hysteretic behavior is the well-established change of compliance of muscle associated with activity. This change, which would tend to retard the restretching of the muscle, was first called increased viscosity by Gasser and Hill (15). Later, essentially the same effect has been called consolidation (8), change of type of elasticity (23), fused state (28), reversible Vulcanization (24), crystallization (12), and appears as the friction factor in Aubert's equation (3). Although the observations and these terms suggest that muscle may employ this as an economical means of sustaining a contraction, the current studies have not examined the energetics involved. The so-called "catch" or "latch" effect in some invertebrate muscles (28, 33) appears to be a similar phenomenon to that observed here, particularly if the tetanus theory of its production is valid. In addition to the contractile mechanism factors, it is possible that the posttetanic potentiation known in nerve-muscle preparations could contribute to the hysteretic behavior (20).

This examination of muscle as a signal-handling element within the motor control system has emphasized the fact that muscle introduces major modifications into the signals which it handles. That muscle changes the form of the signal from pulse patterns to movement is obvious. The fact that in the process it, like other physical systems, has the tendency to introduce a lag and to show an inability to follow high-frequency signals was also reasonably apparent. The quantification of these effects and the recognition that muscle tends to follow nerve pulse rate as a position signal provide specific working information for the analysis of muscle's role in the total motor system. The hysteretic behavior of muscle adds to the analytical problems introduced by its amplitude nonlinearity, but it is an additional factor that must be considered in any analysis.

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