

# A Quantitative Evaluation of the Frequency-Response Characteristics of Active Human Skeletal Muscle In Vivo

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*This paper describes an investigation of the frequency-response characteristics of active human skeletal muscle in vivo over the frequency range 1 Hz to 15 Hz. The applied force, forearm position, and surface electromyograms (from biceps, triceps, and brachioradialis) were recorded simultaneously in four normal adult male subjects for small oscillations of the forearm about a mean position of 90 deg flexion. Two modes of oscillatory behavior are discussed: externally forced oscillations under constant muscle force and voluntary oscillations against an elastic resistance. The observed amplitude and phase relations are presented herein and are compared to the response predicted by a simple model for neuromuscular dynamics. It appears that the small amplitude frequency response of normal skeletal muscle in vivo can be represented by a second order model. The main muscle parameters of this model are a muscular stiffness  $K$ , two time constants  $\tau_1$  and  $\tau_2$  associated with contraction dynamics, and a time delay  $\tau$ : typical values of these parameters at moderate contraction levels (approximately 20 percent of maximum voluntary effort) are  $K = 100 \text{ N}\cdot\text{m}/\text{rad}$ ,  $\tau_1$  and  $\tau_2 = 50 \text{ ms}$ , and  $\tau = 10 \text{ ms}$ . Reflex feedback under forced-oscillation conditions was also examined and may be characterized by a gain parameter  $(\Delta E/\Delta\theta)$ , the ratio of the surface EMG amplitude to the angular displacement of the forearm, and the phase by which the EMG leads muscle stretch. The reflex EMG is observed to lead muscle stretch at all frequencies between 1 Hz and 15 Hz. The muscle stiffness  $K$  and the reflex gain parameter  $(\Delta E/\Delta\theta)$  are approximately proportional to the average force of contraction.*

## Introduction

The mechanical behavior of skeletal muscle in the body is of great interest not only from the fundamental viewpoint of physiology and anatomy: it is also of major importance in many biomechanical and clinical applications. Thus quantitative information on the dynamics of the integrated neuro-musculo-skeletal system is vital for the design and evaluation of sophisticated modern limb prostheses [1, 2]. Efforts are also underway to develop measurements of mechanical response into useful quantitative tools for the diagnosis of neuro-muscular disorders and the evaluation of therapy [3, 4]. From a fundamental point of view, measurements of in-vivo musculo-skeletal dynamics provide quantitative indications of how the various isolated elements of the neuro-muscular system — the motor units, spindles, tendon organs, reflex circuits, and other structures which have been studied intensely by biologists in recent

years — are integrated to serve their function of producing force and motion.

In spite of the great advances made recently by physiologists in identifying the mechanisms of contraction at the microscopic level, useful phenomenological descriptions of muscle mechanics are still based largely on A. V. Hill's [5] conceptual model of muscle as consisting of an elastic element and a contractile element. While Hill's original schema was based on very restricted experimental conditions (constant maximal activation, and constant shortening velocities) these restrictions have been removed in more recent experiments on isolated muscle which employ submaximal, time-varying activation more representative of the actual operating conditions of muscle in vivo [6, 7, 8].

As the mechanical properties of muscle depend on its level of neural activation, any investigation of in-vivo muscle mechanics must seek quantitative relations between mechanical response and some appropriate measure of neural activation. The only readily available measure of activation is the surface electromyogram (EMG). In previous work [9, 10, 11, 12] the quantitative relations between EMG and mechanical parameters have been examined under static and isotonic conditions.

Contributed by the Bioengineering Division for publication in the JOURNAL OF BIOMECHANICAL ENGINEERING. Manuscript received at ASME Headquarters, July 25, 1978.

In order to examine the mechanics of skeletal muscle under more general conditions we studied the mechanical and electrical response associated with small-amplitude oscillations of the forearm in four adult, normal male subjects under a varying oscillatory conditions. For each subject two distinct modes of oscillatory behavior were examined: forced oscillations and voluntary oscillations. The extensive data obtained in these experiments exhibit the neuromuscular response of each subject under quite different but related experimental conditions and provide important information for characterizing muscle mechanics qualitatively and quantitatively. Preliminary reports of this work are available in [13, 14]; the purpose of this paper is to present a summary of the experimental results, to analyze these results in terms of a quantitative model for muscle dynamics, to provide numerical estimates for the values of the system parameters, and to relate these findings to other work on isolated and in-vivo muscle. The Appendix provides a formal derivation of the second-order muscle model used in this paper from a generalization of the Hill model, and furnishes a rationale for interpreting the frequency-response data.

Frequency-response measurements are a standard tool of engineering analysis and have been applied by many investigators to elucidate the dynamics of muscle. Partridge [6, 15] studied the mechanical response of isolated cat triceps surae to sinusoidally modulated stimulating pulse trains. Rack [16] and Rack and Westbury [17] applied sinusoidal displacement inputs to passive and tetanized cat muscle and measured the force response, and Jansen and Rack [18], again using sinusoidal displacement inputs, measured both force and EMG outputs in decerebrate cat preparations. Rosenthal, et al. [19] have performed a very comprehensive frequency-response analysis of the various components contributing to the stretch reflex in cat triceps surae. Using random nerve stimulation Mannard and Stein [8] have investigated the transfer function between stimulation and force for isometric cat soleus. In-vivo studies employing frequency-response techniques have also been extensive. In addition to their obvious applications to prosthetics experiments involving external electrical stimulation of human muscle, either through surface electrodes (Crochetiere, et al. [20], Trnkoczy, et al. [21]) or through stimulation of the motor nerve fibers (Aaron and Stein [2]), provide useful information about the normal function of muscle in the body. Frequency-response studies of normally activated human skeletal muscle have included voluntary oscillations of isometric muscle (Soechting and Roberts [22]) and forced oscillations of steadily contracting muscle (Berthoz and Metral [23], Nielson [24], Joyce, et al. [25], Agarwal and Gottlieb [26, 27]). In this paper we will describe the force-position-activation frequency response of the forearm flexors and extensors in two different modes of oscillation for each of four subjects, show that the observed frequency response can be represented reasonably well by a second-order model for muscle (which leads to a fourth-order model for the limb), and provide numerical estimates for the neuromuscular parameters appearing in the model.

## Apparatus and Procedure

The apparatus used in this experiment is basically similar to that described in previous publications [12, 28] and only a brief account will be given here; a schematic diagram of the experimental arrangement is shown in Fig. 1. The subjects were comfortably seated in specially designed subject chairs, which were adjusted to their body dimensions, with their upper arms horizontal and their forearms clamped in a "clam-shell" fixture consisting of a molded fiberglass sheath and an aluminum surgical splint. This fixture permitted the forearm to rotate about the elbow joint in a sagittal plane. Oscillatory perturbations were applied to the wrist by an electro-mechanical oscillator which permitted a continuous variation of frequency

between 1 and 15 Hz: two driving displacement amplitudes were employed: 0.15 cm and 0.32 cm. Four channels of information were acquired during each test run: force at the wrist (measured by a load cell mounting four semi-conductor strain gages), angular position of the forearm (measured by a capacitive angular displacement transducer), one channel of raw extensor EMG, and one channel of raw flexor EMG (biceps and brachioradialis on alternate runs under identical conditions). The raw EMG's were the instantaneous potential differences between pairs of paste-filled silver surface electrodes placed approximately 3 cm apart over the belly of each muscle. These EMG's were amplified by Grass wide-band differential amplifiers which have a flat response from approximately 10 Hz to 10 KHz; amplification is the only analog processing to which the EMG's were subjected. These four signals were digitized and stored in a Biomation 1015 Waveform Recorder; this unit acquired 1028 samples per channel during each run, at sampling intervals of 0.5, 1.0, or 2.0 ms. The stored information was subsequently recorded on magnetic tape and passed to a computer for digital processing and analysis. A graphical display of typical digitized data acquired during a single experimental run is shown in Fig. 2.

Four normal, adult, male subjects (20 - 36 yr old) participated in this experiment: their heights, weights and forearm properties are listed in Table 1. Each subject underwent a training session plus two full days of testing: the object of the training session was to familiarize the subject with the apparatus and to train him to oscillate his forearm against a fixed elastic resistance with prescribed frequencies, average loads, and load amplitudes. The load (that is, the force at the wrist) was measured by the load cell described in the foregoing and was displayed on an oscilloscope screen. The subject used this display to adjust his performance in a Voluntary Oscillation Test (VOT) in accordance with the experimenter's instructions. These VOT's were conducted on the first day of testing. The elastic resistance consisted of a steel coil spring at the wrist: the effective stiffness of this spring and supporting structures was  $103 \text{ N-cm}^{-1}$ . Each subject was instructed to oscillate his forearm at frequencies of 2, 4, 6 and 8 Hz, with average external loads of 0,  $\pm 22$ , and  $\pm 44 \text{ N}$  (positive loads are those tending to flex the forearm, while negative loads are those tending to extend), and with load amplitudes of 22, 44, and 66 N. On his second day of testing each subject underwent a Forced Oscillation Test (FOT) in which he was asked to maintain a constant level of average force at the wrist (the nominal

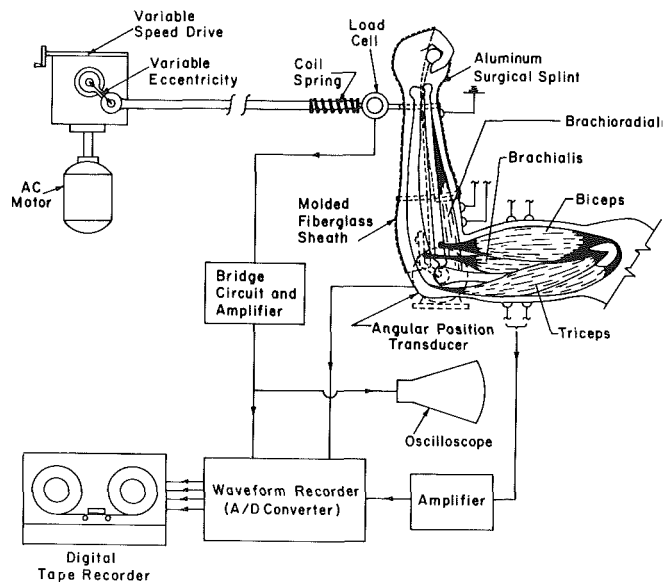
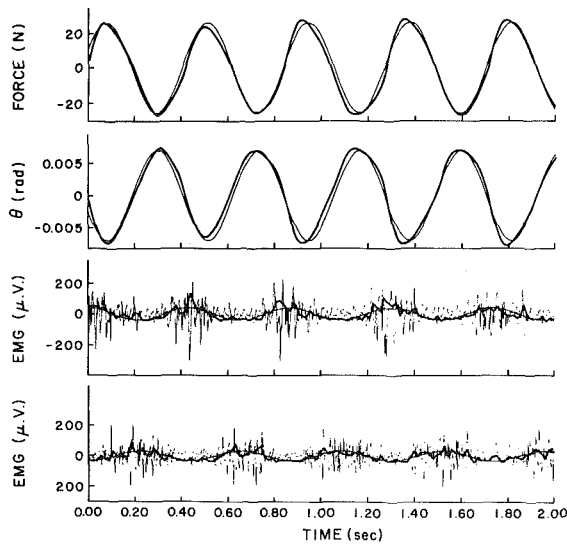


Fig. 1 Schematic diagram of experimental arrangement



**Fig. 2 Typical record from a voluntary oscillation test. Heavy lines: measured force, angle, and standard deviation of EMG (based on 16-ms samples). Channel 3 = triceps, Channel 4 = biceps. Thin lines: least-squares optimum sinusoidal approximations at the driving frequency. Average external moment = 0 N-m.**

**Table 1 Characteristics of subjects**

Subject	Height (m)	Weight (Kg)	Moment arm <sup>(a)</sup> (cm)	Moment of inertia <sup>(b)</sup> (Kg m <sup>2</sup> )	Moment of inertia <sup>(c)</sup> (Kg m <sup>2</sup> )
A	1.78	79.5	27.0	0.113	0.120
B	1.78	75.0	26.0	0.121	0.103
C	1.91	88.5	30.5	0.172	0.165
D	1.76	77.2	27.3	0.116	0.112

(a) From elbow joint to wrist

(b) From measured volume distribution of forearm

(c) From high-frequency amplitude response in a FOT

goals were 0,  $\pm 35$ , and  $\pm 70$  N) while small oscillatory perturbations were applied to the wrist by the oscillator. The subjects experienced no difficulty in maintaining a constant average force at frequencies above 2 Hz when the oscilloscope display become a blurred band with a width proportional to the driving force amplitude: the subject simply centered this band on the appropriate average force level. At the end of second day of testing each subject underwent a Tremor Test in which constant loads were applied to the forearm and the involuntary tremor responses were recorded (the results of these tremor tests and their analysis will be reserved for a separate report, and will not be discussed further here). At the beginning and end of each day of testing the static force-EMG relations were recorded over a range of 0 to 110 N at the wrist.

The data acquired during each experimental run were proc-

essed as follows. A measure of overall muscular activation was first extracted from the raw EMG signal by computing the standard deviation of this signal based on successive 16-ms samples: this produced an essentially positive measure of activation, which in most cases showed reasonably clear periodicity at the driving frequency (the exception occurred in the FOT's at frequencies below 4 Hz). The mean value of the signal in each channel was then computed (the raw EMG's having been replaced by the processed) and was subtracted from the signal itself, yielding the perturbation signal. A least-squares optimum sinusoid at the driving frequency was then fitted to the perturbation signal. The processing program also computed a measure  $\epsilon_i$  of how closely a pure sinusoid at the driving frequency approximated the signal in the  $i$ th channel,  $\epsilon_i = \int_0^T [x_{mi} - x_{ai}]^2 dt / \int_0^T x_{ai}^2 dt$ , where  $x_{mi}$  and  $x_{ai}$  are the measured value and sinusoidal approximation, respectively, and  $T$  is the duration of the run. A sample of the processed EMG's and the sinusoidal approximations to the signals in each channel is shown in Fig. 2.

The frequency response was analyzed in terms of a specific mathematical model for forearm dynamics which is derived in the Appendix. This model relates the perturbations of forearm position about a steady state to those of applied external moment and the flexor and extensor (processed) EMG's. The model is based on a second order model for individual muscle dynamics, so that the system equation becomes fourth order when the forearm inertia is taken into account: the system equation (equation 11) is presented in the following in terms of its Laplace transform in order to facilitate a control systems interpretation.

$$P(s)\delta\bar{\theta} = Q(s)\delta\bar{M} + R(s)\delta\bar{E}_f - T(s)\delta\bar{E}_e \quad (1)$$

where

$$P(s) = [s^2 + (\tau_1^{-1} + \tau_2^{-1})s + \tau_1^{-1}\tau_2^{-1}] (Is^2) + Ks(s + \tau_2^{-1})$$

$$Q(s) = [s^2 + (\tau_1^{-1} + \tau_2^{-1})s + \tau_1^{-1}\tau_2^{-1}]$$

$$R(s) = \tau_1^{-1}\tau_2^{-1}\Gamma_f e^{-s\tau} \text{ and } T(s) = \tau_1^{-1}\tau_2^{-1}\Gamma_e e^{-s\tau}$$

In the foregoing equation  $s$  denotes the Laplace transform variable,  $\delta$  denotes a perturbation about a state of steady contraction, and the horizontal bar above a variable denotes its Laplace transform. The variables  $\theta$ ,  $M$ , and  $E$  represent, respectively, forearm position, external moment and EMG, and subscripts  $f$  and  $e$  denote flexors and extensors, respectively. Seven neuro-muscular parameters appear in equation (1) which must be evaluated from experimental measurements: forearm inertia ( $I$ ), muscle stiffness ( $K$ ), two time constants associated with contraction dynamics ( $\tau_1$  and  $\tau_2$ ), a transport time delay  $\tau$ , and the two  $\Gamma$ 's which represent the contractile moment generated per unit EMG under static conditions. As the system being investigated is nonlinear these parameters can depend on mean activation level. Dimensionless damping ratios are defined as  $\zeta_1 = \tau_1 \sqrt{K/I} / 2$  and  $\zeta_2 = \tau_2 \sqrt{K/I} / 2$ . This model can be specialized for specific experimental situations such as the FOT and the VOT. For example in a FOT where only one of the muscle groups is significantly active (either flexors or extensors) and the EMG fluctuation can be attributed to

**Table 2 Model parameters characterizing frequency response in forced and voluntary oscillation tests**

Subject	$K_0$ (N-m)	$\tau_0 = (C_0/K_0)$ (ms)	$\tau_1$ (ms)			$\tau_2$ (ms)			$\tau$ (ms)			$(\Gamma_e)_{dyn}$ (N-m/ $\mu V$ )	$(\Gamma_e)_{stat}$ (N-m/ $\mu V$ )
			TR	BC	BR	TR	BC	BR	TR	BC	BR		
A	23	77	59	64	106	60	53	49	12	7	8	0.18	0.10
B	14	79	48	78	60	48	44	31	12	6	9	0.14	0.10
C	22	51	40	101	56	41	54	57	24	7	0*	0.14	0.12
D	10	62	141	73	115	15	75	18	25*	6	14	0.51	0.33

reflex origin, the frequency response is given by equation (14); this equation also contains the feedback parameter  $p = \Gamma|\delta E/\delta\theta|/K$  which is a measure of the reflex contractile moment generated per unit forearm rotation. The Appendix should be consulted for details.

All amplitude and phase comparisons employed in analyzing the frequency response were based on the amplitudes and phases of the approximating sinusoids. The several parameters of the above model were determined by comparing various aspects of the model response to the corresponding measured response, using a nonlinear least-squares algorithm. The program (BMDX 85) used for parameter identification was taken from the University of California Biomedical Computer Programs library. This algorithm employs a gradient method to search for a minimum of the cost function and requires starting guesses and bounds on the parameter values. It is not possible, or indeed very informative, to document fully the constraints which were imposed in running this program, but if a parameter was identified to be equal to one of the imposed bounds on that parameter then this fact is noted by an asterisk next to its value listed in Table 2. Identification procedures for individual parameters are discussed in the following sections.

## Results

(a) **Forced Oscillation Tests (FOT's).** The major results of the FOT's are summarized in Figs. 3 and 4. Fig. 3 shows a Bode plot of angular position output versus external moment input at three different levels of average load. These data are quite representative of both the flexors and the extensors of all four subjects. The high-frequency amplitude response is linear with a slope of  $-2$ , indicating that the response is dominated by forearm inertia at the higher frequencies. A linear regressions analysis of the unloaded amplitude response above 4 Hz provides an estimate of the forearm moment of inertia  $I$  which compares quite well with the values of  $I$  calculated from a direct measurement of forearm volume distribution by a water-immersion technique [28]. In the latter case the moment

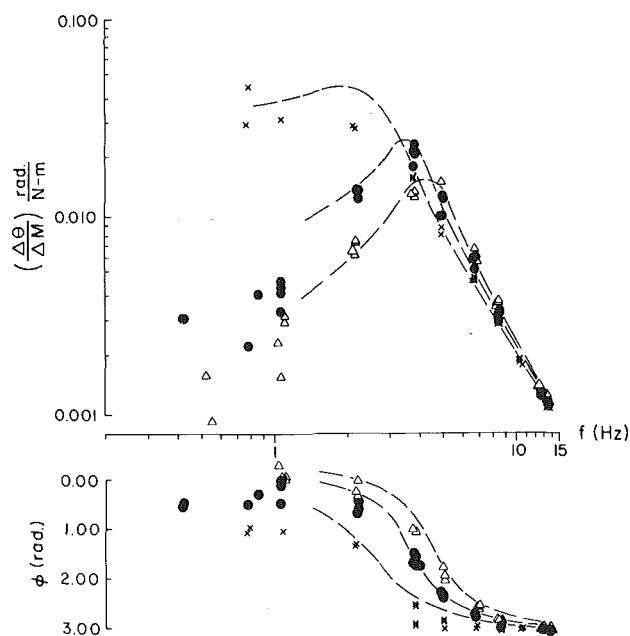


Fig. 3 (Angle/applied moment) amplitude ratio, and phase lag of angle behind applied moment in a forced oscillation test (Subject A). Symbols indicate different values of average external moment: Crosses = 0.1 N-m (relaxed). Filled circles = -10.6 N-m. Open triangles = -19.1 N-m. Curves represent model response according to equation (14) (see text for parameter values).

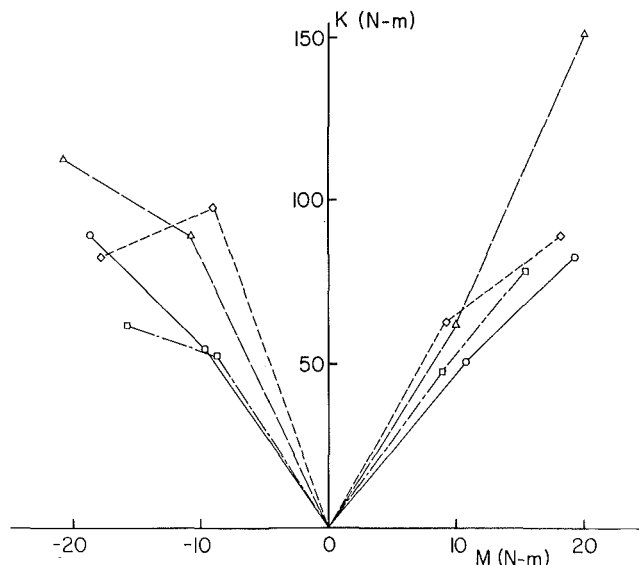


Fig. 4 Angular stiffness of flexors and extensors based on resonant frequency in the forced oscillation tests, as a function of applied moment. Circles = Subject A. Triangles = Subject B. Squares = Subject C. Diamonds = Subject D.

of inertia was computed using  $1.13 \text{ Kg l}^{-1}$  as an average value of forearm density, and this value is compared to that determined from frequency response in columns 5 and 6 of Table 1. The zero-load (relaxed) response resembles that of an over-damped oscillator and the passive stiffness and damping,  $K_0$  and  $C_0$ , parameters were evaluated by fitting equation (15) to the observed data as described in the previous section. It should be emphasized that under zero-load, relaxed conditions there was no measurable EMG (in contrast to the electrical activity which was clearly evident under even light loads), so that purely passive properties of the muscle and loading apparatus were being measured. The values of these parameters are listed for each subject in columns 2 and 3 of Table 2 and the corresponding response curves are shown in Fig. 3. (The values listed are the averages of these parameters determined from the amplitude and phase response separately.)

The remaining curves showing the response of actively contracting muscle exhibit clear resonance characteristics, showing both an amplitude peak and a phase inversion. The most striking feature of this response is that the resonant frequency increases with the average contractile force, indicating an increase in muscle stiffness. The values of the resonant frequency were determined by fitting equation (14), with  $p$  set equal to zero, to the phase data: this amounts to ignoring feedback at this stage of analysis. The passive parameters  $K_0$  and  $C_0$  were set at the values listed in Table 2 and the identification procedure yielded the resonant frequency  $f_n$  and the damping ratio  $\zeta_1$ . Parameter sensitivity studies of our model under FOT conditions, equation (14), show that the magnitude of the resonant frequency  $f_n$  (the frequency at the amplitude peak on the associated phase inflection) is determined primarily by the muscle stiffness  $K$  for fixed inertia  $I$ . For example, a change of 40 percent in the value of  $K$  will result in a change of approximately 100 percent in the value of the resonant frequency, whereas a change of 100 percent in any of the other parameters rarely produces a change as large as 10 percent in the resonant frequency. On the other hand the shape of the response curves is strongly influenced by the values of  $\zeta_1$ ,  $\zeta_2$ , and  $p$  and the effect of each of these parameters is comparable to that of the others. The curves shown in Fig. 3 display the theoretical model response in a FOT with some feedback ( $p \neq 0$ ) equation (14). As these curves were constructed using some parameter values identified from voluntary oscillation test data,

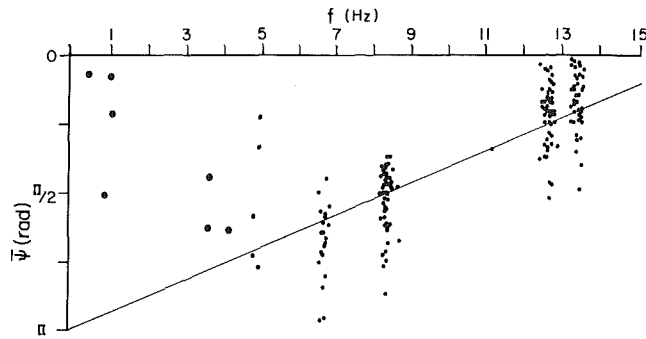


Fig. 5 Phase lead of EMG on muscle stretch for loaded muscles in the forced oscillation tests. Pooled data for all four subjects with  $\epsilon_{3,4} < 2.5$ .

they will be discussed after the latter identification has been described. Values of muscular stiffness were calculated from  $K = 4\pi^2 I f_n^2$ : these are displayed in Fig. 4 as a function of the average muscle moment for both flexors (negative moments) and extensors (positive moments). It can be seen clearly that this stiffness increases with the contraction level of the muscle. A graph of the total stiffness, including the effects of passive tissues and the loading fixture, is obtained by displacing upward the curve for each subject by the appropriate  $K_0$  listed in Table 2.

The FOT's also provided information about the phase and amplitude of the reflex EMG feedback response to sinusoidal forcing. Periodic fluctuations in the surface EMG's become clearly evident only at frequencies above 4 Hz; at lower frequencies the small amplitude EMG perturbations were hard to distinguish from the large amplitude steady background signal. Thus the EMG error measures  $\epsilon_{3,4}$  were high, and the amplitudes and phases exhibited considerable scatter at low frequencies. However, the following trends were reasonably clear. Fig. 5 shows the phase lead of EMG on muscle stretch for loaded muscles in a FOT: the figure shows pooled data for all four subjects and all three muscles as no clear differences between these were evident. To reduce the scatter only data points with small error measures,  $\epsilon_{3,4} < 2.5$ , are shown. Few measurements below 4 Hz, but almost all above 4 Hz, satisfied this criterion. This figure shows that the peak in the reflex EMG leads muscle stretch by a phase angle that seems to increase from 0 at low frequencies, but clearly decreases again at frequencies above 4 Hz. The phase variation from 6 - 13 Hz is reasonably well represented by a straight line through  $\pi$  on the phase axis with a slope corresponding to a pure time delay of 30 ms, which is approximately equal to the conduction time delay of neural signals in the spinal reflex loop (as measured, for example, by the time to the onset of the "silent period" in a quick-release test).

The strength of the reflex feedback in the FOT's was measured by the ratio of EMG amplitude of forearm angle amplitude ( $\Delta E / \Delta \theta$ ) for each muscle. As noted in the foregoing the values of this ratio exhibited considerable scatter and a linear regression analysis did not reveal any consistent variation with frequency. However, an examination of the feedback strength did exhibit one feature rather clearly: the average value of ( $\Delta E / \Delta \theta$ ) over the frequency range 4 - 15 Hz (the frequencies range where EMG fluctuations were clearly evident) increases with the contractile force in a muscle. This is shown in Fig. 6 for both the flexors and extensors.

(b) **Voluntary Oscillation Tests (VOT's).** All the variables measured in the VOT's, including the EMG's showed very clear periodic fluctuations and low error measures, as shown in the typical data of Fig. 2. The results of these tests provided information about the relations between contractile force and

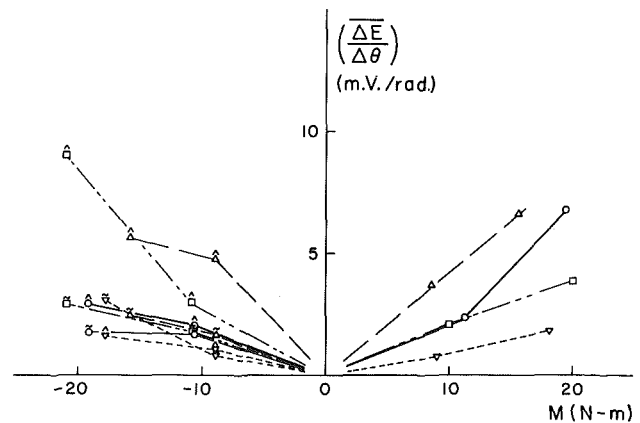


Fig. 6 Mean value of the (EMG/angle) amplitude ratio (over the frequency range 4 Hz to 14 Hz) for loaded muscles in forced oscillation tests, as a function of applied moment. Circles = Subject A. Triangles = Subject B. Squares = Subject C. Inverted triangles = Subject D. Symbols alone indicate the triceps, (^) indicates the biceps, and (~) indicates the brachioradialis.

activation under dynamic conditions. An examination of the data from the biceps and brachioradialis showed that on the average both the mean values and oscillation amplitudes of the EMG's were positively correlated under the conditions of our experiment (fixed degree of supination-pronation, small displacements about the vertical position): This tends to support the assumption of proportional activation in synergistic muscles, which was made in developing the model of the Appendix. In these VOT's the subjects oscillated their forearms against a fixed undamped elastic resistance so that the maximum moment generated by the muscles coincided with the maximum angular displacement. Fig. 7 shows the phase lag of extension (that is, maximal extensor contraction) behind extensor EMG for all four subjects: these data are pooled for all values of the mean external load as there was no clearly discernible influence of the load on the phase response. The phase tends toward zero at low frequencies (EMG in phase with muscle force) and increases to more than 180 deg at 10 Hz. The phase response of the flexors was similar except that the phase was observed to exceed 180 deg at the higher frequencies only rarely. The phase of the biceps and brachioradialis coincided in three subjects, and showed a small displacement in the fourth. Using the phase response for flexors and extensors of each subject together with the values of  $f_n$ ,  $K_0$ , and  $C_0$  which had already been identified from the FOT's, the identification algorithm with equation (13) was applied to estimate  $\zeta_1$ ,  $\zeta_2$ , and  $\tau$ : the values of  $f_n$  used in this procedure were the averages of the values identified at nominal loads of 35 and 70 N. A second-order linear model alone is incapable of producing phase lags greater than 180 deg, so that the time delay  $\tau$  is needed to match the observed phase response. In this stage of identification an upper limit of 25 ms was set on the parameter  $\tau$ , based on an estimate for an upper limit for the time delay which could be associated with muscle action potential conduction from the motor end plate to the end of the muscle. The identification scheme went to this limit in only one case (Subject D, triceps). The identified values  $\zeta_1$  and  $\zeta_2$  were converted to the associated values of the time constant  $\tau_1$  and  $\tau_2$  and these are listed, together with the time delay  $\tau$ , in Table 2. The curve included in Fig. 7 shows the theoretical model response according to equation (13) for the average parameter values listed.

At this stage in the data analysis all the muscle parameters had been determined except the  $\Gamma$ 's (the ratio of "isometric" moment to EMG) of equation (13) which affect the amplitude, but not the phase response in a VOT. Equation (13) with all parameters except the  $\Gamma$ 's fixed at their previously identified

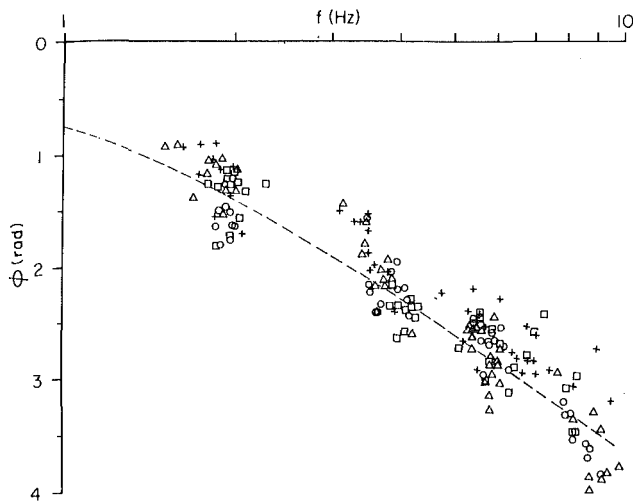


Fig. 7 Phase lag of muscle moment with respect to triceps EMG in the voluntary oscillation tests. Squares = Subject A, pluses = Subject V, triangles = Subject C, circles = Subject D. Pooled data for all values of non-negative mean external load. The dashed curve represents the model response, equation (13) with the following representative parameter values:  $(f_n, \zeta_1, \zeta_2, \tau^*, \gamma, \beta_{01}, \zeta_0) = (4.0 \text{ Hz}, 0.65, 0.65, 0.4, 3.0, 0.4, 0.2)$ .

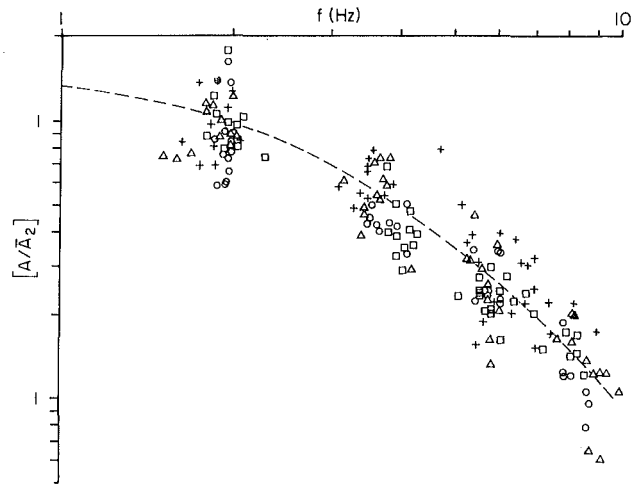


Fig. 8 Amplitude ratio of muscle moment to triceps EMG in the voluntary oscillation tests. Squares = Subject A, pluses = Subject B, triangles = Subject C, circles = Subject D. For each subject the data are normalized with respect to the average value of the amplitude ratio at 2 Hz,  $\bar{A}_2$ , in two external load ranges:  $(-17, 17)$  (nominally "zero" external load), and  $(>17)$  N at the wrist. The dashed curve represents the model response equation (13), with the same representative parameter values as are used in Fig. 7.

values was compared to the measured ratio of muscle moment to EMG in order to identify these parameters. The average values of the  $\Gamma$ 's are listed for the extensors in Table 2 together with corresponding values of the average (muscle moment/EMG) ratio determined from static tests over the load range 0 to 25 N-m; values for the flexors are similar and are omitted. Fig. 8 shows the normalized (muscle moment/EMG) amplitude response in a VOT. The muscle moment is computed as the measured external moment minus the inertial moment of the forearm. Pooled data for the extensors of all four subjects are shown together with the theoretical response predicted by equation (13) for the typical parameter values listed.

## Discussion

The frequency-response characteristics which were measured in these experiments have been interpreted in terms of a second-order model for muscle dynamics, and the results have been reported by evaluating the parameters of this model. While many features of the response could be adequately represented by a first-order model (equivalent to setting  $\tau_2 = 0$ ) for example [29], this model is not appropriate for our present results. The major shortcomings of a first-order model are, first, that it requires rather large values for the time constants ( $\tau_1 \cong 150$  ms and  $\tau \cong 35$  ms) in order to match the phase response in a VOT and, second, that a first-order model produces an amplitude decrease with a slope of  $-1$  in a log-log representation of the VOT amplitude response (see Fig. 8) at the higher frequencies, rather than the consistently observed slope of approximately  $-2$  associated with a second-order model with  $\tau_1$  and  $\tau_2$  of the same order of magnitude (these slopes characterize the model response until  $\nu$  becomes nearly equal to  $\gamma$ : see equation (13)). Further there is a growing body of evidence, both from in-vivo [2, 22] and isolated muscle experiments [8], that the small-amplitude frequency-response of skeletal muscle is represented very well by a second-order model with parameters which are functions of contractile state. Such a model can be derived from a generalization of Hill's model (see Appendix).

Fig. 4 confirms that human muscle in-vivo has a stiffness which increases with level of contraction. This property is well established in isolated muscle preparations, where some

experiments [7] show that the stiffness is almost proportional to muscle force from zero force to tetanus. This "hard spring" behavior seems to be characteristic of most biological materials [30], passive as well as active. However, it must be emphasized that the parameter  $K$  measures the force-dependent stiffness of active muscle; the combined stiffness of relaxed muscles and surrounding tissues is very small by comparison [31], certainly less than 4 N-m/rad. To the extent that comparison is possible the stiffness values which we have measured here by frequency-response techniques agree reasonably well with values reported in the literature [28, 32, 33] measured by different experimental methods.

In spite of the high degree of variability in the reflex EMG's measured during the FOT's, Figs. 5 and 6 indicate some reasonably clear trends. The phase lead of EMG on muscle stretch (Fig. 5) appears to increase from 0 at the low frequencies: this is what one would expect if the EMG were generated by stretch receptors sensitive to stretch and rate of stretch. From 4 Hz on the EMG phase decreases approximately linearly with frequency: this is the phase variation which would result if an excitatory signal were generated at the muscle in phase with stretch acceleration (derivative of stretch velocity) and returned to the muscle, amplified, after a transport time delay in the spinal reflex loop. As indicated on Fig. 5 a straight line through  $(0, \pi)$  with a slope corresponding to a time delay of 30 ms, which is approximately the value of the reflex time delay, fits the data above 6 Hz reasonably well. Although it is attractively simple to attribute the higher-frequency phase variation to a time delay in the reflex loop, an indication that this may not be the underlying mechanism is provided by the results of Jansen and Rack [18], who found a phase variation essentially identical to that shown in Fig. 5 in the soleus of a decerebrate cat preparation, where transport time delays should be much shorter. The high scatter in the (EMG/angle) ratios masked any variation of reflex gain with frequency at constant load. Nevertheless, Fig. 6 clearly shows that on the average reflex gain as measured by  $(\Delta E/\Delta \theta)$  increased with load. One could speculate that this is simply a gross manifestation of the principle of  $\alpha$ - $\gamma$  co-activation [34]; with the higher  $\alpha$ -motoneuron activity required to generate higher contractile forces, the concurrent increase in  $\gamma$ -motoneuron activity makes the spindles more sensitive.

It is difficult to interpret the results of the FOT's in purely mechanistic terms at low frequencies because in this case the subjects could intervene voluntarily and the response depended to some extent on their subjective interpretation of the instruction to "maintain a constant average force level." While some level of reflex feedback and/or periodic voluntary inputs very probably did exist, as stated previously the manifestation of these inputs as fluctuations in the surface EMG was not clearly measurable by the techniques used in this experiment at frequencies below 4 Hz. The theoretical curves for the two loaded cases shown in Fig. 3 were constructed using equation (14) with  $p \neq 0$  — that is, allowing for some feedback. In particular these curves were constructed using the parameters  $(\zeta_1, \zeta_2, \tau^*, K_0, C_0) = (1.2, 0.8, 0.2, 30 \text{ N-m}, 1.5 \text{ N-m-s})$ , and the values of the resonant frequency  $f_n$  were taken as 2.8 Hz and 3.5 Hz for the  $-10.6 \text{ N-m}$  and  $-19.1 \text{ N-m}$  curves, respectively: these numbers are typical of the parameter values identified for Subject A and listed in Table 2. The phase of the EMG  $\bar{\psi}$  was represented by the empirical equation  $\bar{\psi} = \arctan[f/(1.0 - 0.30 f^2)] - 0.175f$ , as an approximation to the phase variation shown in Fig. 5. Constant values of the feedback parameter  $p$  were chosen to produce a good fit of both amplitude and phase response for frequencies higher than 2 Hz: the values chosen were  $p = 3.5$  at  $-10.6 \text{ N-m}$  and  $p = 5.5$  at  $-19.1 \text{ N-m}$ . The shape of the response curves in the FOT, but not the location of the resonance peak, is quite sensitive to the values of the system parameters other than  $K$  and  $I$ . The theoretical curves in Fig. 3 are included to show that the response in the FOT's can be reproduced using parameters identified from the VOT response if moderate levels of feedback are admitted. However a more precise resolution of the effects of reflex feedback at low frequencies will require improvements in our current methods of EMG processing. At frequencies below 2 Hz in the FOT's the subject's voluntary inputs may be more important than any involuntary reflex contribution.

The two time constants,  $\tau_1$  and  $\tau_2$  were identified from the VOT's to have values of approximately 50 ms (see Table 2). This is consistent with the results obtained for human forearm flexors and extensors in vivo by Soechting and Roberts [22] (voluntary oscillation tests) and Aaron and Stein [2] (direct electrical stimulation of the musculo-cutaneous nerve supplying the biceps). Cogshall and Bekey [35] identified the time constants of a second-order muscle model for two subjects performing voluntary isometric contractions of the triceps: the values were 11 and 189 ms for one subject and 22 and 167 ms for the other. Our time constants are considerably smaller than Cogshall and Bekey's dominant (larger) time constant, and they are also smaller than the value of 105 ms used by Gottlieb and Agarwal [36] for both time constants of a second order model of the ankle flexors. In studies of isolated, isometric cat soleus Mannard and Stein found that the frequency response over the range 0 – 30 Hz was very well represented by a second-order model with parameters depending on level of activation. The results reported by these investigators indicate that one of the time constants had a value of 10–30 ms and was relatively insensitive to activation level while the other increased from 30–40 ms at low activation to 200–300 ms at tetanus. Our experiments were conducted at low loads (up to about 30 percent maximal voluntary effort) and our results did not permit us to detect the influence of activation level on the time constants. While one could speculate about the microscopic physical and chemical events which are the source of these time constants (Mannard and Stein conjecture that they are connected with rate-limiting processes which govern the generation and decay of contractile force, respectively), for our present purposes we will simply regard them as parameters which characterize the macroscopic behavior of muscle: on the basis of the development in the Appendix we could refer to  $\tau_1$  as the "viscoelastic" time constant and  $\tau_2$  as the "con-

traction" time constant.

Soechting, et al. [28] reported typical values of 100 ms for the single time constant of a first-order muscle model, based on the measured response of six normal male subjects in quick-release tests. These values are approximately equal to the sum of the two time constants,  $\tau_1$ , and  $\tau_2$ , our second-order model. Another comparison is possible between the values of our "viscoelastic" time constant  $\tau_1$  and values for the ratio of apparent internal friction moment to the angular velocity of the forearm measured in a constant-velocity test, as reported in [12]: this ratio was found to have a typical value of 4.4 N-m-s for the flexors of six male athlete subjects at low levels of activation. If one assumes 75 N-m as a representative value of muscle stiffness in the VOT's, then the foregoing apparent internal friction corresponds to a time constant of 59 ms, which agrees reasonably well with the values of  $\tau_1$  listed in Table 2.

The time delay  $\tau$  was introduced to provide an adequate fit to the VOT phase data, and such a small time delay has been introduced by other investigators for similar reasons [2, 8]. This time delay can probably be associated to some extent with the spread of electrical excitation prior to the mobilization of the muscle's contractile machinery, and as such it would be expected to vary with the placement of the recording electrodes with respect to the innervation zone, and could vary from one muscle to another. If one takes 4 m/s as a typical muscle action-potential propagation velocity, then values of  $\tau$  above 25 ms are implausible.

The values of the parameters  $\Gamma_f$  and  $\Gamma_e$  of equation (13) which measure the ratio of "isometric" moment to activation, of course depend strongly on the details of the procedures used to measure and process the EMG, and in principle these should be determined anew for each re-application of the electrodes. Average values of the  $\Gamma$ 's for the extensors of our four subjects are listed in the next-to-last column of Table 2: these values were determined by fitting equation (13) to the observed amplitude response in the VOT's (see Fig. 8). For comparison values of the average (moment/EMG) ratio measured in static tests at the beginning and end of the first day of testing are listed in the last column of Table 2. It is seen that the static values are somewhat lower than the dynamic values. The variation of the force-activation relation of skeletal muscle during the transition from a truly isometric state to states of motion, albeit at low velocities, requires further investigation, as both in-vivo [12] and isolated-muscle [7] experiments indicate that rather abrupt changes in behavior may occur in passing between these states.

## Conclusions

The frequency-response technique seems well suited to the investigation of human skeletal muscle in vivo. By measuring frequency-response in several modes of oscillation quantitative information can be obtained about limb inertia, muscle stiffness, apparent internal friction, time constants characterizing contraction dynamics, and reflex feedback: when coupled with appropriate modeling and data-analysis procedures, the observed response characteristics yield numerical measures of these various aspects of muscular behavior. Specific conclusions which can be drawn from this study involving four normal adult male subjects, frequencies between 1 and 15 Hz and loads up to approximately 30 percent of maximum voluntary effort are:

- 1 Under external forcing of the forearm the response is dominated by inertia at frequencies above 6 Hz. Further the motion of the forearm shows resonance characteristics. The muscle stiffness may be calculated from measurements of the resonant frequency: this stiffness increases with average activation and attains a value on the order of 100 N-m at a muscle moment of 20 N-m for both the flexors and extensors.

2 In response to external forcing of the forearm, the reflex activation (EMG) leads the stretch in a loaded muscle at all frequencies between 2 and 15 Hz by a phase angle that varies between approximately 0 and  $\pi/2$  (attaining a maximum at a frequency of approximately 4 Hz). The strength of the reflex feedback as measured by the (EMG/angle) perturbation amplitude ratio increases with the activation.

3 The phase lead of activation on muscle force in a voluntary oscillation increases from 0 to  $\pi$  (more than  $\pi$  for the extensors) as the frequency increased from zero to 9 Hz. The amplitude ratio of muscle moment to EMG decreases continuously as the frequency increases. Thus in the Voluntary Oscillation Tests skeletal muscle exhibits the response characteristics of a low-pass filter, or alternately, it exhibits the behavior which would result from the presence of an apparent internal friction.

4 The frequency-response observed in these tests can be represented reasonably well by a second-order quasi-linear model for muscle, containing a small time delay, with parameters that depend on activation level. The two time constants of this model are each of the order of 50 ms, and the time delay is of the order of 10 ms.

## Acknowledgment

This work was supported by the National Science Foundation under Grants GK-43356-61 and ENG 76-80316.

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## APPENDIX

### Formal Derivation of a Model for Forearm Dynamics From a Generalized Hill Equation

In this Appendix we develop a mathematical model to rep-



resent the response of the forearm in our frequency-response experiments, starting with a generalization of A. V. Hill's classic description of whole-muscle mechanics. While a model could be postulated directly, it is instructive to show how the one adopted can be derived from Hill's paradigm, thus providing a connection to the physiological work on isolated muscle.

In his well-known 1939 paper [5] Hill proposed that from a phenomenological point of view, skeletal muscle could be regarded as a series combination of an undamped elastic element, the "Series Elastic Element," (the SE) and a "Contractile Element" (the CE) which represented the active force-generating properties of the muscle. This schema was based largely on the results of isotonic quick-release experiments with tetanized frog muscle which was allowed to shorten (but not lengthen). Further Hill proposed that the relation between the force across the hypothetical CE and its rate of shortening,  $V$ , be taken as the experimentally observed isotonic force-velocity relation. These assumptions lead directly to the following equation relating the muscle length  $x$ , and the force across the muscle  $P$

$$\dot{x} = C(P)\dot{P} - V(P) \quad (2)$$

where the  $(\dot{\phantom{x}})$  denotes differentiation with respect to time,  $V(P)$  is the aforementioned isotonic shortening velocity as a function of muscle force, and  $C(P)$  is the compliance of the SE which is measured in quick-release tests. Based on an analysis of heat and work relations in the isotonic tests, Hill proposed his well-known equation for  $V$

$$V(P, P_o) = b(P_o - P)/(a + P) \quad (3)$$

The constants  $P_o$ ,  $a$ , and  $b$  are assumed to characterize the mechanics of muscle in a given state. Under isometric conditions when  $\dot{x} = \dot{P} = 0$ , the force  $P = P_o$  which satisfies the equation  $V(P_o, P_o) = 0$  is called the "isometric force" and may be taken as a measure of the contractile state of the muscle. This model may be generalized to include time-varying, submaximal activation and lengthening as well as shortening muscle by postulating

$$\dot{x} = C(P, P_o)\dot{P} - V(P, P_o) \quad \text{and} \quad \dot{P}_o + \Phi[P_o, E(t-\tau)] = 0 \quad (4)$$

The generalization consists of the following:

- (a) Both  $C$  and  $V$  are now assumed to depend on the level of activation as measured by the isometric force  $P_o$ ,
- (b)  $P_o$  itself is assumed to depend on a measurable index of activation level  $E$ .

For example in an experiment on isolated muscle,  $E$  can be chosen as the stimulus rate, whereas in an experiment on in-vivo muscle,  $E$  can be chosen as the rms value of the EMG measured with a given recording configuration. To account for the fact that excitation-contraction coupling involves electrical and chemical processes which proceed at a finite rate, the relation between  $P_o$  and  $E$  is postulated in the form of a differential equation (assumed first-order as an initial approximation); this equation contains a time delay  $\tau$  to represent the spread of neural excitation with a definite propagation velocity. Under isotonic conditions  $\dot{x}$ ,  $E$ ,  $P$ , and  $P_o$  are constant and one recovers the usual relation  $\dot{x} = -V(P, P_o)$ , with the Isometric Force given as a function of activation by  $\Phi(P_o, E) = 0$ ; thus  $V(P, P_o)$  can be determined from the results of isotonic experiments carried out at constant, submaximal activation, for example [7]. In the generalized Hill model equations (4), the isometric force  $P_o$  plays a role analogous to that of an "internal" thermodynamic variable. Note that  $V(P_o, P_o) = 0$  for any  $P_o$ , from the definition of isometric force.

With Hill's model thus generalized to include submaximal activation it is a relatively straightforward matter to develop

a model for the dynamics of the forearm undergoing small perturbations about a steady state. Consider such a steady equilibrium state  $P = P^*$ ,  $P_o = P_o^*$ ,  $E = E^*$ ,  $x = x^*$ , and let perturbations about this state be denoted by

$$P = P^* + \delta P, P_o = P_o^* + \delta P_o, E = E^* + \delta E, \text{ and } x = x^* + \delta x$$

Then with appropriate smoothness assumptions, we have

$$C(P, P_o) = C + \left(\frac{\partial C}{\partial P}\right)\delta P + \left(\frac{\partial C}{\partial P_o}\right)\delta P_o + \dots$$

$$V(P, P_o) = V + \left(\frac{\partial V}{\partial P}\right)\delta P + \left(\frac{\partial V}{\partial P_o}\right)\delta P_o + \dots \quad (5)$$

$$\Phi(P_o, E(t-\tau)) = \Phi + \left(\frac{\partial \Phi}{\partial P_o}\right)\delta P_o + \left(\frac{\partial \Phi}{\partial E}\right)\delta E(t-\tau) + \dots$$

where all functions and derivatives on the right-hand sides of the foregoing equations are evaluated at the steady state. Combining equations (5) and (4) and noting that  $V(P_o^*, P_o^*) = 0$  and  $\Phi(P_o^*, E^*) = 0$  we obtain the perturbation equations

$$\delta \dot{x} = C\delta \dot{P} - \left(\frac{\partial V}{\partial P}\right)\delta P - \left(\frac{\partial V}{\partial P_o}\right)\delta P_o$$

$$\text{and} \quad \delta \dot{P}_o + \left(\frac{\partial \Phi}{\partial P_o}\right)\delta P_o + \left(\frac{\partial \Phi}{\partial E}\right)\delta E(t-\tau) = 0$$

Because  $V(P, P_o)$  vanishes when  $P = P_o$  it follows that  $(\partial V/\partial P) = -(\partial V/\partial P_o)$  whenever  $P = P_o$ . If we define

$$k = C^{-1}, \text{ the muscle stiffness}$$

$$c^{-1} = (\partial V/\partial P_o) = -(\partial V/\partial P), \text{ the reciprocal of the damping coefficient} \quad (6)$$

$$\tau_2 = (\partial \Phi/\partial P_o)^{-1}, \text{ the contraction time constant, and}$$

$$g = -(\partial \Phi/\partial E)\tau_2, \text{ the incremental change in isometric force per unit change in activation,}$$

then the perturbation equations become

$$\delta \dot{P} + \left(\frac{k}{c}\right)\delta P = k\delta \dot{x} + \left(\frac{k}{c}\right)\delta P_o \quad (7)$$

$$\delta \dot{P}_o + \left(\frac{1}{\tau_2}\right)\delta P_o = \left(\frac{g}{\tau_2}\right)\delta E(t-\tau)$$

Equations (7) model the dynamics of the muscle when it is subjected to small perturbations about a steady equilibrium state. Note that all the parameters must, in general, be considered functions of the contractile state  $P_o^*$  or  $E^*$ . The "internal" variable  $\delta P_o$  can be eliminated from equations (7) to yield a single second-order model for muscle dynamics

$$L\delta P = \left\{ \frac{d^2}{dt^2} + (\tau_1^{-1} + \tau_2^{-1}) \frac{d}{dt} + \tau_1^{-1}\tau_2^{-1} \right\} \delta P \\ = k(\delta \dot{x} + \tau_2^{-1} \delta x) + \tau_1^{-1}\tau_2^{-1} g\delta E(t-\tau) \quad (8)$$

( $L$  denotes the differential operator contained in braces.) To proceed from (8) to an equation governing the motion of the whole forearm, additional assumptions are required. For our present purposes we may assume that flexion-extension of the forearm is produced by three muscles, say the biceps, the brachioradialis, and the triceps (the brachialis may be considered lumped with the biceps, and additional muscles can be included in the analysis in an obvious way). These three muscles will be indexed 1, 2 and 3, respectively. Now if  $\theta$  represents the angle of flexion and  $a(\theta)$  is the moment arm of the muscle force about the elbow joint it can be readily shown that  $|dx/d\theta| = a$ .

Noting that  $L\delta M = L\delta(aP) = a^*L\delta P + P^*L\delta a$  equation (5) can be written as

$$I\delta\ddot{\theta} = nK(\delta\ddot{\theta} + \tau_2^{-1}\delta\dot{\theta}) + \tau_1^{-1}\tau_2^{-1}a^*g\delta E(t-\tau) + P^*L\delta a \quad (9)$$

where  $n$  is  $-1$  for the flexors and  $+1$  for the extensors,  $a^*$  is the steady value of the moment arm,  $K = (a^*)^2k$ ,  $\delta\theta$  is the angle perturbation, and  $\tau_1 = (k/c)$ , a "viscoelastic" time constant. It can be shown that the term  $P^*L\delta a$  is rather small under the conditions of our experiment, and it will be neglected for the sake of simplifying the development. Equation (9) may be written for the moment generated by each muscle  $M_i$  and, when combined with the equation of motion

$$I\ddot{\theta} = M - \sum_{i=1}^3 n_i M_i$$

where  $M$  is the resultant moment of nonmuscular origin acting on the forearm, one obtains

$$I(I\delta\ddot{\theta} - \delta M) + K(\delta\ddot{\theta} + \tau_2^{-1}\delta\dot{\theta}) = -\tau_1^{-1}\tau_2^{-1} \sum_{i=1}^3 n_i a_i^* g_i \delta E_i(t-\tau) \quad (10)$$

where  $K = \sum_{i=1}^3 K_i$ , the angular stiffness of the forearm, and it

has been assumed that the time constants are the same for each muscle. This assumption of identical time constants is made primarily in the interest of keeping the model manageable: it is not unreasonable to assume that  $\tau_2$  and  $\tau_1$  are independent of muscle size, and while the time delay  $\tau$  is expected to depend on electrode placement and may vary between muscles, it is expected to be rather small and using an average value will suffice for present purposes. Finally some assumption must be made concerning the distribution of forces in synergistic muscles. It is consistent with previously adopted approximations to assume that synergistic muscles are activated proportionately under the conditions of our experiment (this is at least partially justified by the fact that both the mean values and perturbation amplitudes of the measured EMG's from the biceps and brachioradialis were observed to increase together). Adopting this approximation  $\delta E_2 = r\delta E_1$ , where  $r$  is a constant of proportionality, then if we define  $\Gamma_a = a_1^*g_1 + ra_2^*g_2$ ,  $\Gamma_e = a_3^*g_3$ ,  $\delta E_f = \delta E_1$  and  $\delta E_e = \delta E_2$ , we may write

$$I(I\delta\ddot{\theta} - \delta M) + K(\delta\ddot{\theta} + \tau_2^{-1}\delta\dot{\theta}) = \tau_1^{-1}\tau_2^{-1}[\Gamma_f\delta E_f(t-\tau) - \Gamma_e\delta E_e(t-\tau)] \quad (11)$$

which is an equation containing only the measurable variables  $\delta\theta$ ,  $\delta M$ ,  $\delta E_f$  and  $\delta E_e$ , and the muscle parameters  $K$ ,  $\tau_1$ ,  $\tau_2$ ,  $\tau$ ,  $\Gamma_f$  and  $\Gamma_e$ .

Under experimental conditions the external moment is the sum of the applied moment  $\delta M_a$  and the visco-elastic resistance of the loading apparatus: the latter is characterized by a stiffness  $K_o$  and a damping constant  $C_o$ . Thus

$$\delta M = \delta M_a - K_o\delta\theta - C_o\delta\dot{\theta} \quad (12)$$

The response of the forearm in a Voluntary Oscillation Test (VOT) or Forced Oscillation Test (FOT) can be predicted from equation (11) and a comparison of the predicted and measured responses can be used to identify the muscle parameters.

For the VOT we let  $\delta M_a = -\hat{K}\delta\theta$  where  $\hat{K}$  is the (rotational) stiffness due to the elastic resistance at the wrist, and  $\delta\theta = \Delta\theta e^{i\omega t}$ ,  $\delta E_f = \Delta E_f e^{i(\omega t + \phi)}$ ,  $\delta E_e = \Delta E_e e^{i(\omega t + \phi - \pi)}$  which gives the response function

$$\left\{ \frac{(\hat{K} - I\omega^2)\Delta\theta}{\Gamma_f\Delta E_f + \Gamma_e\Delta E_e} \right\} e^{-i\phi} = \{1 + i2\zeta_1\nu + [i2\zeta_1\nu + \beta_0^2(1 + i2\zeta_2\nu)(1 + i2\zeta_1\nu)]/(\gamma^2 - \nu^2)\}^{-1} \{1 + i2\zeta_2\nu\}^{-1} e^{-i\nu\tau^*} \quad (13)$$

where

$$\omega_n = \sqrt{K/I}, \nu = \omega/\omega_n, \zeta_0 = \tau_0\omega_n/2 = (C_o/K_o)\omega_n/2,$$

$$\zeta_1 = \tau_1\omega_n/2, \zeta_2 = \tau_2\omega_n/2, \beta_0^2 = K_o/K, \gamma^2 = \hat{K}/K, \text{ and } \tau^* = \omega_n\tau$$

As the contributions of the passive resistance is rather small in this case one may interpret the numerator of the expression on the left-hand side of the foregoing equation simply as the amplitude of the muscle moment.

In the FOT at most one muscle group is active (say, the flexors) and we assume

$$\delta\theta = \Delta\theta e^{i\omega t}, \delta E_f = \Delta E_f e^{i(\omega t - \psi)}, \delta E_e = 0, \delta M_a = \Delta M_a e^{i(\omega t + \phi)}$$

and the response function for moment input and angular position output is

$$\left( \frac{K\Delta\theta}{\Delta M_a} \right) e^{-i\phi} = Z_o \{1 + (\beta_0^2 + i2\zeta_0\nu - Z_1 p e^{-i\psi}) Z_o\}^{-1} \quad (14)$$

where

$$Z_o = (1 + i2\zeta_1\nu)\{i2\zeta_1\nu - \nu^2(1 + i2\zeta_1\nu)\}^{-1}$$

$$Z_1 = \{(1 + i2\zeta_1\nu)^{-1}(1 + i2\zeta_2\nu)^{-1}\} e^{-i\nu\tau^*}$$

and  $p = \Gamma_f(\Delta E_f/\Delta\theta)/K$  is a feedback parameter: the ratio of contractile reflex moment generated per unit angular displacement to the muscle stiffness. In the limit of a completely relaxed subject in the FOT,  $K$ ,  $\zeta_1$ ,  $\zeta_2$ ,  $\tau^*$  and  $p$  all go to zero and equation (14) degenerates to the response function for a simple second-order damped oscillator without feedback

$$I\delta\ddot{\theta} + C_o\delta\dot{\theta} + K_o\delta\theta = \delta M_a \quad (15)$$

from which the passive parameters  $K_o$  and  $C_o$  can be determined.