A Recruitment Theory of Force–Time Relations in the Production of Brief Force Pulses: The Parallel Force Unit Model

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A theory, the parallel force unit model, is advanced in which the buildup and decline of force in rapid responses of short duration are assumed to reflect variability in timing of several parallel force units. Response force is conceived of as being a summation of a large number of force units, each acting independently of one another. Force is controlled by either the number of recruited force units or the duration each unit contributes its force. Several predictions are derived on the basis of this theory and are shown to be in qualitative agreement with empirical findings about both the mean and variability of brief force impulses. The model also has consequences for the temporal properties of a response. For example, under certain circumstances, it predicts a reciprocal relation between reaction time and response force. Although the theory is proposed as a psychological account, relations between the assumptions and basic principles in neurophysiology are considered. Possible future applications and generalizations of the theory are discussed.

By developing tension around a joint, muscle develops force against external resistance. If the force produced by the muscle exceeds the external resistance, movement at the joint results. In the study of motor control, psychologists have largely focused on overt movement, for example in asking questions about the speed and accuracy of limb positioning, and have tended to neglect the development of force. Or, if they have referred to force development, it has tended to be as a basis for explaining some aspects of overt movement. Thus, Schmidt, Zelaznik, Hawkins, Frank, and Quinn (1979) proposed that the accuracy of aimed movement be accounted for in terms of variability in the driving impulse provided by the muscles. Although this line of research has served to direct attention toward the determination of a prototypical force impulse function (Meyer, Smith, & Wright, 1982), there has been little effort devoted to theoretical understanding of the form of this function. If, for example, in movements of different amplitudes there is scaling of the force impulse function (Meyer et al., 1982), then how is this achieved? In this article, we consider one possible theoretical account of force impulse production that includes a scaling property. However, the theory's axioms lead to further predictions concerning, for example, the variability of force at each point of time. These predictions lead us to a critical review of data on the development of brief force impulses.

The regulation of force per se is not only of theoretical interest but is an important factor in many everyday actions. Two examples are the grasp force used to prevent an object from slipping under the force of gravity (Westling & Johannson, 1984) and the increase in grip force needed to compensate for the inertial loading during acceleration of a projectile, such as a dart, when thrown. In these cases, force levels are selected and modulated in a manner appropriate to the context; people do not appear, for example, to operate on an all-or-nothing basis, switching between zero and maximum force. And contrasting control styles, which in overt movement have led to the distinction between ballistic and guided movement, are also evident in force production (Cordo, 1987; Desmedt, 1983). People are capable of providing rapid changes in force in a predictive, open-loop fashion or of using feedback to make adjustments tailored to a change in the external situation.

In this article, we review empirical work providing information on the time course of the first of these two classes of force control—the production of brief, ballistic pulses. We do this within a framework provided by a simple theory in which the force produced by a subject is viewed as a summation over multiple parallel output units. Each of these force units is assumed to have identical properties. However, the onset of force in a given unit is subject to a variable delay. As we show later, this temporal variability plays a central role in determining the observed force–time waveform.

In addition to its direct focus on amount of force, our thesis also has implications for another area of interest to psychologists—measurement of the time of a response. Consider, for

example, the use of response latency as an index of cognitive processing (Meyer, Osman, Irwin, & Yantis, 1988; Posner, 1978). The elapsed time between the presentation of a signal to respond and the onset of movement is referred to as *reaction time* (RT). Systematic variation in RT associated with differences in the stimulus is taken to reflect change in afferent delay or decision-processing time. However, time is also taken up by movement preparation and execution. Thus, psychologists take pains to use simple responses that would be expected to minimize variation due to qualitatively different types of movement. Brief force pulses have been advocated for this reason. But even with a stereotyped movement such as a keypress, there can be variation in force, which "is much less often recorded than response time, and it is far less completely studied" (Luce, 1986, p. 51). In the following sections, we demonstrate on theoretical grounds that such force variation in itself is sufficient to affect estimates of the time of response. If force changes systematically with stimulus conditions, this clearly could lead to a potential confounding, a point that has long worried psychologists (e.g., Delabarre, Logan, & Reed, 1897; Woodworth, 1938) and was recently restated by Carlton, Carlton, and Newell (1987). The force–time measure of a response could be an additional dependent variable that might be helpful in interpreting RT data.

Data indicating that there can be a systematic relation between response force and stimulus intensity were reported by Angel (1973). The force used in making a thumb adduction response to an auditory or a visual signal was examined as a function of the amplitude of the signal. On each trial, the full force–time function was recorded. Angel reported that peak force increased with stimulus intensity and that RT decreased with peak force. Inspection of the force–time functions reproduced by Angel reveals an increase in peak force with stimulus intensity (see Figure 1). A more rapid rate of rise in force may be seen with higher forces. There are several ambiguities in Angel's report, including uncertainty about his criterion for measuring RT, that is, whether stimulus onset or some other point was taken as the trigger event. However, Figure 1 suggests that if RT is measured as the time at which the response force first reaches a fixed level, or *threshold,* lower than the lowest of the peak force values, the dependence of the force–time function on stimulus intensity would lead us to expect shorter RT estimates for more intense stimuli. The model that we propose is able to account for force–time relations in simple, brief pulselike responses such as those recorded by Angel. With multiple, temporally noisy output units determining the level of force at any point in time, it is the noise in relation to the number of units that mainly determines the form of the force–time function.

Although the model is proposed as a psychological account of force–time relations, it is no accident that the elements of the model have many similarities to basic principles in muscle neurophysiology. Indeed, part of the motivation for the model is that it may lead to a better understanding of the interface between brain and movement (cf. Bunge & Ardila, 1987, pp. 167–169). The constraints discovered through quantitative modeling help define the control problem for the brain. Our approach is based on a simplified view of muscle activation. The simplifications we adopt are motivated not only by mathematical tractability, but also by the view that progress in understanding the
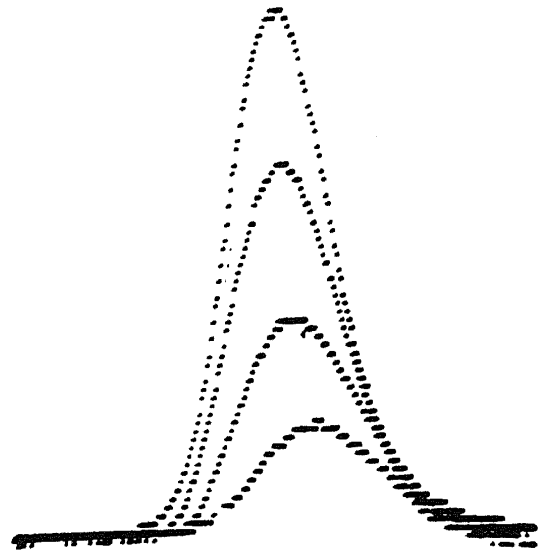

Figure 1. Force functions produced in a simple reaction time task for different intensities of auditory stimulation with relative intensities from bottom to top of 0, 20, 40, and 60 dB. (The length of the record represents 640 ms; no force calibration was indicated in the original. From "Input–Output Relations in Simple Reaction Time Experiments" by A. Angel, 1973, *Quarterly Journal of Experimental Psychology, 25,* p. 196. Copyright 1973 by Erlbaum. Reprinted by permission.)

system is more likely if the system is first described in reduced terms (albeit loosely constrained by available data) and only afterwards complicated by the addition of more structure (Bunge, 1967, chap. 8). Before presenting our model, we first briefly set out certain facts from motor neurophysiology.

The Activation of Skeletal Muscle

Skeletal muscles are composed of a large number of distinct contractile fibers. A brief pulselike change lasting about 1 ms in the electrical polarization of the cell membrane sweeping along the length of a fiber causes changes in the structural arrangement of proteins, and these generate a very small tension (a fraction of a gram[1]) referred to as a *twitch.* Such a twitch typically has a time course spanning 150–300 ms, with the rise in force taking roughly half the time of the decay.

The electrical pulse responsible for the muscle fiber twitch arises in a neuron, the motoneuron located in the spinal cord, and terminates at a motor end plate on the fiber. By means of branching, a given motoneuron makes contact with several muscle fibers. How many fibers are innervated by a given motoneuron depends on the muscle. Figures cited by Burke (1981) give estimates ranging from 15 fibers per motoneuron for the extraocular muscles to 2,000 fibers per motoneuron in the leg muscle medial gastrocnemius, with intermediate values of 100 and 600 for the hand and arm muscles. The term *motor unit* (MU) is used to refer to the motoneuron with its set of muscle fibers. An impulse coming down a motoneuron is propagated simultaneously along all its branches, with the result that the

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[1] The standard unit of force is the newton (N) rather than the kilogram (kg). One kilogram force equals 9.81 N, and hence 1 g force is approximately 1 cN.

twitches in each of the muscle fibers of a given MU are generated in synchrony. Because the fibers ultimately attach to one tendon at each end of the muscle, the individual twitches are mechanically summated. A significant quantity is thus the tension produced in a single fiber twitch summed over the number of fibers in the MU. Depending on the muscle, this may amount to a few grams.

In the performance of everyday tasks, muscle tensions much greater than a few grams are normally required. To generate a tension impulse running into hundreds of grams, activity in many MUs is required. If the twitches in all the MUs occur simultaneously, their mechanical effects will sum, and the resulting tension will increase as more MUs are added or *recruited*. However, there are at least two factors that act to prevent perfect temporal overlap. The first is that, in a group of motoneurons, there is a considerable range of fiber conduction velocities (e.g., see Eccles & Sherrington, 1930). Even though the input to a nerve fiber bundle may be tightly synchronized, the output will be a set of impulses dispersed in time. The amount of the temporal dispersion is a function of the range of fiber conduction velocities and the length of the nerve. This results in a low-pass filtering effect, and an expression for the transfer characteristic of nerve bundles was derived by Williams (1969, 1972). This first factor is deterministic in the sense that a particular MU is always associated with the same conduction delay. A second factor acting to reduce temporal overlap is stochastic in nature; the activation of MUs is not tightly synchronized but is variable. Evidence for this comes from examination of the onset of activity in particular pairs of MUs. Thomas, Ross, and Calancie (1987) studied selected MU pairs in the first dorsal interosseous (the muscle that moves the index finger sideways toward the thumb) during relatively brief (120 ms) ballistic movements associated with the closing phase of using scissors. They documented standard deviations of the interval between the onsets of spike bursts of pairs of MUs in the range of 10–40 ms. Such variability in MU pair onsets might arise in multisynaptic pathways of motor preparation processes. But the important point is that in a brief contraction, such lack of synchronization in the onset of activity across MUs will reduce the overlap of their force contributions.

One means of compensating for the effective drop in tension due to asynchronization in onset times over MUs would be to prolong the contraction time of each MU. Such a prolongation would involve the motoneuron discharging more than once. However, if the spike discharges are closely spaced, not only is the MU contraction duration increased, but the tensions resulting from the later spikes are higher than they would have been in isolation (Partridge & Benton, 1981). Indeed, with contractions extending over a series of MU spikes, firing rate may be used to regulate tension instead of adjusting the number of MUs recruited.[2] However, in maintained contractions at lower levels of tension (up to 50% of the maximum tension that a muscle is capable of), it is thought that the main way of increasing tension is to add more MUs. Only at higher tension levels are increases in firing rate thought to become significant in increasing muscle tension (Freund, 1983).

The neurophysiology just described leads us to view the neuromuscular interface between intention and performance as somewhat uncertain or *noisy*. In producing a brief force pulse, a variable number of units may make their contributions of force, starting at variable points in time and lasting for variable durations. If there is a single point in time at which we would initiate an action, there is clearly going to be a temporal "blurring" in the summated output relative to the underlying punctate command in the brain. A formalization of this idea—albeit directed primarily at a characterization of electromyogram (EMG)—with force treated in incidental fashion, was provided by Meijers, Teulings, and Eijkman (1976). They were interested in understanding the form of the electrical activity of the muscle exhibited in the surface EMG by treating the voltage waveform as the summation of single MU discharges. As their starting point, they assumed the electrical activity of the muscle obtained with direct stimulation of the motor nerve to be a summation, without temporal jitter, of the individual MU electrical waveforms. Using direct stimulation to estimate the single MU waveform, they then took the EMG and, by deconvolution with the MU waveform, obtained an estimate of the distribution of MU onset times, that is, the temporal dispersion of MU activity relative to the central command. On the basis of this onset time distribution (which indicated appreciable temporal jitter similar in magnitude to that documented by Thomas et al., 1987), Meijers et al. then turned to consider how EMG would be expected to accumulate in relation to the number of active motor units.

At the end of their article (Meijers et al., 1976) and in an earlier article (Meijers & Eijkman, 1974), Meijers et al. suggested the applicability of the idea of summation, as used in their modeling of EMG, to the development of force. However, they did not elaborate this idea into specific predictions for the expected form of the overall summated force. Instead, they pointed out how such a model predicts a reduction in temporal uncertainty from the case of the single MU response to the situation where the "response" is defined as the point at which some preset proportion of units have been activated. With an interest in the effects of stimulus intensity on simple RT, Ulrich and Stapf (1984) adopted and extended the proposal of Meijers et al. Assuming the total number of units activated increases with stimulus intensity, Ulrich and Stapf showed that the model predicts a corresponding decrease in both mean and variance of RT (defined in the model as the time to attain a certain number of active units). These predictions were qualitatively in agreement with their data.

In this article, our purpose is to bring all these strands together. We provide a formal statement of a model for the development of brief force impulses. We compare (qualitatively) the model's predictions on force–time relations with published behavioral data. We draw out implications for both future research and future elaboration of the model, particularly where current neurophysiology indicates there are major simplifications that could seriously alter the model's predictions.

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[2] The increase in tension with firing rate is limited by the development of tetanus, when the individual twitches merge into a steady contraction. Normal firing rates are considerably below this level.

The Parallel Force Unit Model

The parallel force unit model[3] (PFUM[4]) is an account of the rise and decay of force with time in tasks where subjects are required to produce brief, ballistic pulse changes in force. The elements of the model are represented in Figure 2. (See Appendix A for a glossary of terms used throughout this article.) Observed force is assumed to depend on the sum of forces developed by a subset of a large number of *force units* (FUs), each acting independently of one another. The behavior of each FU is taken to be a function of the activity of an underlying MU in combination with the mechanical coupling between the MU and the point of measurement of force. We suppose that a brief voluntary contraction involves many FUs and that there is variability in the times and hence in the periods of activity across FUs.

The Assumptions of PFUM

We make the following assumptions, $\mathcal{A}_1$ through $\mathcal{A}_5$, about the production of a force impulse:

$\mathcal{A}_1$. In each trial, a subset of b FUs is recruited from a pool of n units. The units in this subset are identified by the index $i = 1, \ldots, b$.

$\mathcal{A}_2$. The observed force $F_o(t)$ at time t is given as the summation

$$F_o(t) = \sum_{i=1}^{b} F_i(t) \qquad b \leq n, \qquad (1)$$

where $F_i(t)$ is a random variable,[5] which denotes the *force contribution* of unit i at time t.

$\mathcal{A}_3$. Let $t = 0$ be the discrete moment in time at which activation of the FUs underlying an observed force pulse is centrally commanded. Unit i starts to contribute force at time L_i, where the random variable L_i denotes the *latency* of unit i.

$\mathcal{A}_4$. The random nature of $F_i(t)$ is embodied in L_i. We assume that a deterministic nonnegative FU *force–time function* $u_i(\cdot)$ characterizes the time course of force contributed by unit i, once force production is initiated. The trial-to-trial variability of $F_i(t)$ is then generated by random displacement of the function $u_i(\cdot)$ along the time axis by L_i; that is,

$$F_i(t) = \begin{cases} 0 & \text{for } t < L_i, \\ u_i(t - L_i) & \text{for } t \geq L_i. \end{cases} \qquad (2)$$

Figure 3 illustrates Equation 2.

$\mathcal{A}_5$. To enhance the mathematical tractability of PFUM, we assume that all n FUs are identical. Thus, we add two subsidiary assumptions. (a) All force–time functions are identical: $u_i(\cdot) \equiv u(\cdot)$ ($i = 1, \ldots, n$). (b) The latencies $L_i (i = 1, \ldots, n)$ have the identical probability density function (PDF) $f(\cdot)$.

Force development is thus conceived of as a probabilistic process defined over a large set of FUs, each contributing a small fraction to the total output. Although the units are not necessarily assumed to be statistically independent, they are taken to be mechanically distinct, and so the observed force level at any time is the sum of the effects of those units that are currently active.

Predicted Mean Force–Time Function

In this section and the next, we start our formal development of PFUM, using only Assumptions $\mathcal{A}_1$ through $\mathcal{A}_5$. We first obtain a convolution property for brief force pulses. It shows how the observed force–time function $F_o(\cdot)$ depends on the individual force–time function $u(\cdot)$ and on the density $f(\cdot)$.[6]

Figure 2. A stylized example of the development of force during a single trial under the parallel force unit model. (Top five lines: A central command at time $t = 0$ activates after a random delay the force production in a number of single-force units. Bottom line: At each point of time, the force developed in a muscle equals the summed force of all recruited units.)

[3] In this article, the meanings of the terms *theory* and *model* are taken within the framework of the hypotheticodeductive system (cf. Bunge, 1967). In particular, a general theory $\mathcal{T}$, together with specific or subsidiary assumptions $\mathcal{S}$, yields the model $\mathcal{M}$ (cf. Bunge and Ardila, 1987, p. 128). The set $\mathcal{S}$ enables the deduction of consequences (theorems) from $\mathcal{M}$, which would be difficult or even impossible on the basis of $\mathcal{T}$ alone. Hence, strictly speaking, $\mathcal{M}$ entails $\mathcal{T}$; or in other words, $\mathcal{M}$ is a specific version of $\mathcal{T}$. This usage contrasts with an alternate interpretation of the term in which *model* is treated as a synonym of *analogy*. In the latter case, a model is taken, for heuristic or didactic purposes, to be a pictorial representation of a theory (cf. Lachman, 1960; Schmidt, 1988, pp. 36–37).

[4] We encourage the German pronunciation of the acronym, as in P f-erde, and hence P f-um.

[5] We follow the convention of using boldface letters for random variables.

[6] Meijers, Teulings, and Eijkman (1976) derived mathematical expressions for the mean and the variance of EMG signals that in principle could be applied to force–time functions. However, they tailored the variance prediction for multiphasic signals to obtain a mathematically tractable expression, which holds only approximately. Furthermore, the mathematical analysis of their predictions is unnecessarily complex. For these and other reasons, we provide simplified versions of their original proofs, which are better suited for the purpose of this article. The simplified proofs concern Propositions 1 and 5 in our article, which correspond to Expressions 10 and 15, respectively, in the work of Meijers et al. (1976).
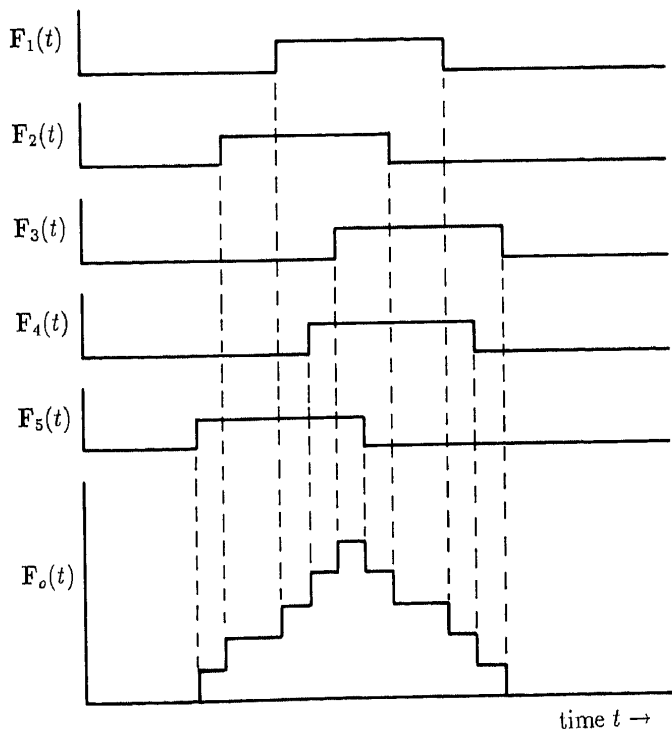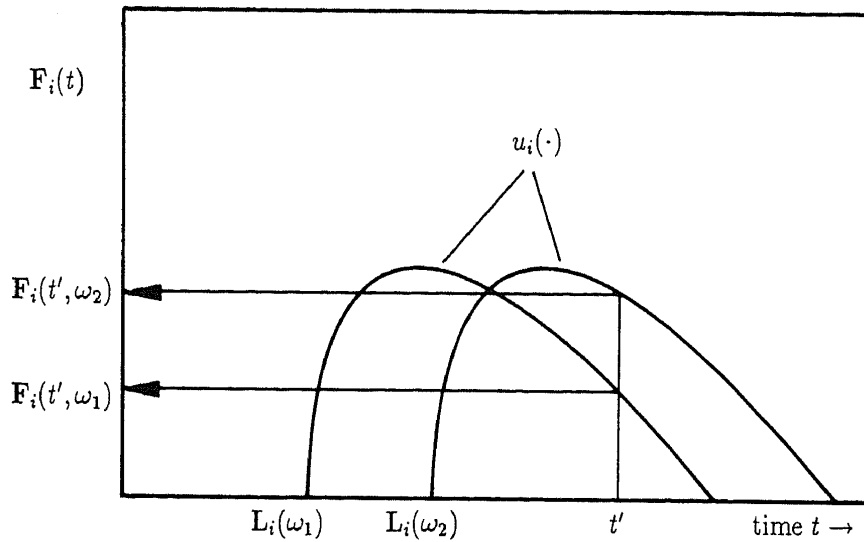
Figure 3. The relation between L_i and $F_i(t)$. [The random variable $F_i(t)$ denotes the force level produced by force unit i at time t. This level changes from trial to trial because the force-time function $u_i(\cdot)$ is randomly displaced along the time axis. The latency L_i causes the random displacement. The two realizations ω_1 and ω_2 illustrate this random displacement of $u_i(\cdot)$ with two different levels of force associated with a particular point t' on the time axis.]

We then show that the obtained force-time function leads to a scaling property for which there are supportive empirical observations. In later sections, we introduce some simplifying assumptions to derive mathematically more tractable expressions for the mean and variance of the observed force-time function.

For the following considerations, some definitions are needed: Let the total area $A = \int_0^\infty u(t)dt$ under $u(\cdot)$ be the *impulse* of an FU, and let $z(\cdot)$ be defined as

$$z(t) \equiv \frac{u(t)}{A} \qquad (3)$$

for $t > 0$. The function $z(\cdot)$ will be called the *normalized FU force-time function.* Note that the area under the normalized function equals 1.

Proposition 1. If Assumptions $\mathcal{A}_1$ through $\mathcal{A}_5$ hold, then the mean force-time function $E[F_o(\cdot)]$ is given for all $t > 0$ by

$$E[F_o(t)] = b \cdot A \cdot h(t), \qquad (4)$$

where b is the number of recruited FUs, A is the impulse of an FU, and $h(t) \equiv \int_0^\infty z(t - t')f(t')dt'$ denotes the convolution of the normalized function $z(\cdot)$ and the PDF $f(\cdot)$ of the latency L.

Proof. Taking the mathematical expectation on both sides of Equation 1 yields

$$E[F_o(t)] = \sum_{i=1}^{b} E[F_i(t)]. \qquad (5)$$

From Equation 2, one obtains

$$E[F_o(t)] = \sum_{i=1}^{b} E[u_i(t - L_i)]. \qquad (6)$$

Simplifying according to Assumption $\mathcal{A}_5$,

$$E[F_o(t)] = b \cdot E[u(t - L)]. \qquad (7)$$

Because $u(t) = A \cdot z(t)$, we have

$$E[F_o(t)] = b \cdot A \cdot E[z(t - L)]. \qquad (8)$$

According to the "law of the unconscious statistician" (cf. Ross, 1980, pp. 39–40), the expectation $E[g(X)]$ of any real-valued

function $g(\cdot)$ of a random variable X with PDF $f(\cdot)$ is given by $E[g(X)] = \int g(x)f(x)dx$. Applying this law to Equation 8 yields

$$E[F_o(t)] = b \cdot A \cdot \int_0^\infty z(t - t')f(t')dt'. \qquad (9)$$

The integral $\int_0^\infty z(t - t')f(t')dt' = (z * f)(t)$ is the so-called convolution of $z(\cdot)$ and $f(\cdot)$. The asterisk is a common abbreviation for the convolution operation. The proof is complete.

Remarks on Proposition 1. Proposition 1 is thus concerned with both the size and the shape of the mean force-time function. The force at any given time $t > 0$ increases with the number b or the impulse A (or both) of the active FUs. The shape of the mean force-time function is determined by both the PDF $f(\cdot)$ of the FU onset latency L and by the normalized FU force-time function $z(\cdot)$. The factor that determines the shape is the convolution term $h(\cdot)$. Because $z(\cdot)$ is nonnegative and the area under it is 1, $z(\cdot)$ can be regarded as a PDF. Let X be a random variable that corresponds to $z(\cdot)$. This random variable does not appear in the assumptions of PFUM. It has the status of a dummy random variable. However, the definition of X is helpful in that it allows the use of familiar concepts of probability theory to interpret the shape of the mean force-time function. Assume that X and L are independent random variables; then, the PDF of the sum $X + L$ is given by the convolution $h(\cdot)$ (cf. Feller, 1971, chap. 1). Therefore, if the variance of L is relatively large compared with the variance of X, then the shape of the mean force-time function is mainly determined by the shape of $f(\cdot)$. However, if the converse is true, then $z(\cdot)$ mainly determines the shape of the mean force-time function. The larger the variance of L, the less $E[F_o(\cdot)]$ resembles the shape of the force-time function $u(\cdot)$ and the more "smeared" is the force impulse.

The smearing of the FU force-time function is not only a feature of the mean force-time function but can be observed in

single trials. This is illustrated in Figure 4 by computer simulations. Each panel shows three realizations of force development under the same set of assumptions and model parameters. In the panels on the top, the underlying FU force–time function is a symmetric triangular function, whereas in the panels on the bottom it is a rectangular function of the same duration. In all four panels, the impulse and the number of recruited FUs is kept constant. The simulations are based on the assumption that the PDF of the onset latencies corresponds to the so-called special Erlangian distribution (discussed later). In each panel, the mean of L is constant. In the right-hand panels, the standard deviation SD[L] is twice that in the left-hand ones. As evidence of smearing, note that none of the simulated functions indicates the shape of the underlying function $u(\cdot)$. Also, note that the smearing effect increases with the variability of L; the summed force functions derived from triangular and rectangular underlying functions are more similar in shape in the right-hand panels, where there is greater variance of L.

The simulation clearly illustrates the dependence of the shape of the overall force–time function on the variability in latency, L, that produces FU onsets of asynchronicity. It is therefore important to ask for evidence that FU-onset standard deviations are as large as the 20- to 40-ms values chosen for the simulation. If FUs in the model are equated[7] with MUs, estimates of the onset variability may be taken from Thomas et al.'s (1987) observations of variability of the interval between the onsets of pairs of independent MUs. Suppose the efferent delays from a single central command to the onset of observable activity in each of a pair of MUs represent identically distributed and independent random variables D_1 and D_2; then the interval between their onsets is $\Delta = D_1 - D_2$. Then, as pointed out by Ulrich and Stapf (1984) for the case of response asynchronies in simultaneous bimanual keypresses, the variance of Δ equals twice the variance of D. Thomas et al. estimated the standard deviation of MU-onset asynchrony as large as 40 ms in some pairs. Assuming the onset delay variance of one MU to be half that of the asynchrony, this estimate would indicate values of standard deviation for the MU delay as large as 28 ms. Moreover, as noted in the introduction, Meijers et al. (1976) estimated a distribution of MU onset times on the basis of EMG data. This estimated distribution spanned about 60 ms, indicating a rather large standard deviation of D. Both findings clearly provide the possibility of a considerable degree of smearing of the single FU force–time function in arriving at the total force function.

Scaling of the Mean Force–Time Function

Given Proposition 1, an important consequence is that, if peak force is controlled by recruiting varying numbers of FUs, mean force–time functions for different levels of peak force should have the same basic form. To demonstrate this, consider the following proposition:

Proposition 2. The area A_o under the mean force–time function is

$$A_o = b \cdot A. \tag{10}$$

Proof. Because $\int_0^\infty h(t)\,dt = 1$ must hold, this proposition follows directly from Proposition 1.

Remark on Proposition 2. The proposition embodied in Equation 10 provides a simple way to test the hypothesis that different mean force–time functions are generated by different recruitment levels. We define a rescaled mean force–time function $r(\cdot)$ for $t > 0$ by

$$r(t) \equiv \frac{E[F_o(t)]}{A_o}. \tag{11}$$

Then all rescaled mean force–time functions of various amplitudes should superimpose if their corresponding force levels were achieved by varying the number of FUs recruited. However, if the rescaled mean force–time functions do not coincide, then we must suppose that a change of normalized function $z(\cdot)$ has occurred.

Empirical observations on scalability. If subjects are asked to produce higher peak forces and they do this by recruiting more units, that is, by increasing b, then according to the model, the form of the force–time function for different force levels will be related. PFUM predicts that after scaling by the area under the curve, the force–time functions will superimpose.

Data from various studies provide support for this scaling property of the model. Referring to Figure 1, we note that the force–time functions reproduced by Angel (1973) look distinctly similar in form. Because the functions with the higher peak values exhibit greater rates of rise of force, the times to peak force are little changed, and the functions might well be expected to superimpose once normalized by their differing areas.

An analysis giving more detailed information about the form of the mean force–time function was provided by Freund and Büdingen (1978). In their experiment, subjects produced brief (rise times around 90 ms) isometric force pulses of up to 100 N with the muscles of the index finger. Two conditions were run. In one, the *target condition*, subjects were expected to produce as fast as possible a peak force within 10% of a target value. In the *nontarget condition*, subjects were simply asked to produce pulses of minimum duration with a range of peak values over trials. The average force was generally a smooth, single-peaked function of time, with more time being taken in the decay phase than in the buildup to the peak force value. The form of the functions (Freund & Büdingen, 1978, p. 6), which were assessed by times for successive thirds of the peak force, did not depend on peak force—a finding consistent with rescalability of the force–time function. This finding suggests that force levels were controlled by changes of b according to PFUM.

The clearest evidence of scaling of the force–time function is to be found in Gordon and Ghez (1987a). Subjects produced elbow flexion force impulses to targets at three different levels, with the highest force being between 40% and 50% of maximum. Instructions emphasized production of a single smooth impulse of force and that, once initiated, responses should not be amended. Trial data aligned at force onset are shown in Figure 5. In Panel B of the figure, the traces normalized by peak force show remarkable constancy. Gordon and Ghez (1987a)

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[7] Further consideration of the relation between the model's axioms and muscle neurophysiology may be found in the Discussion section.
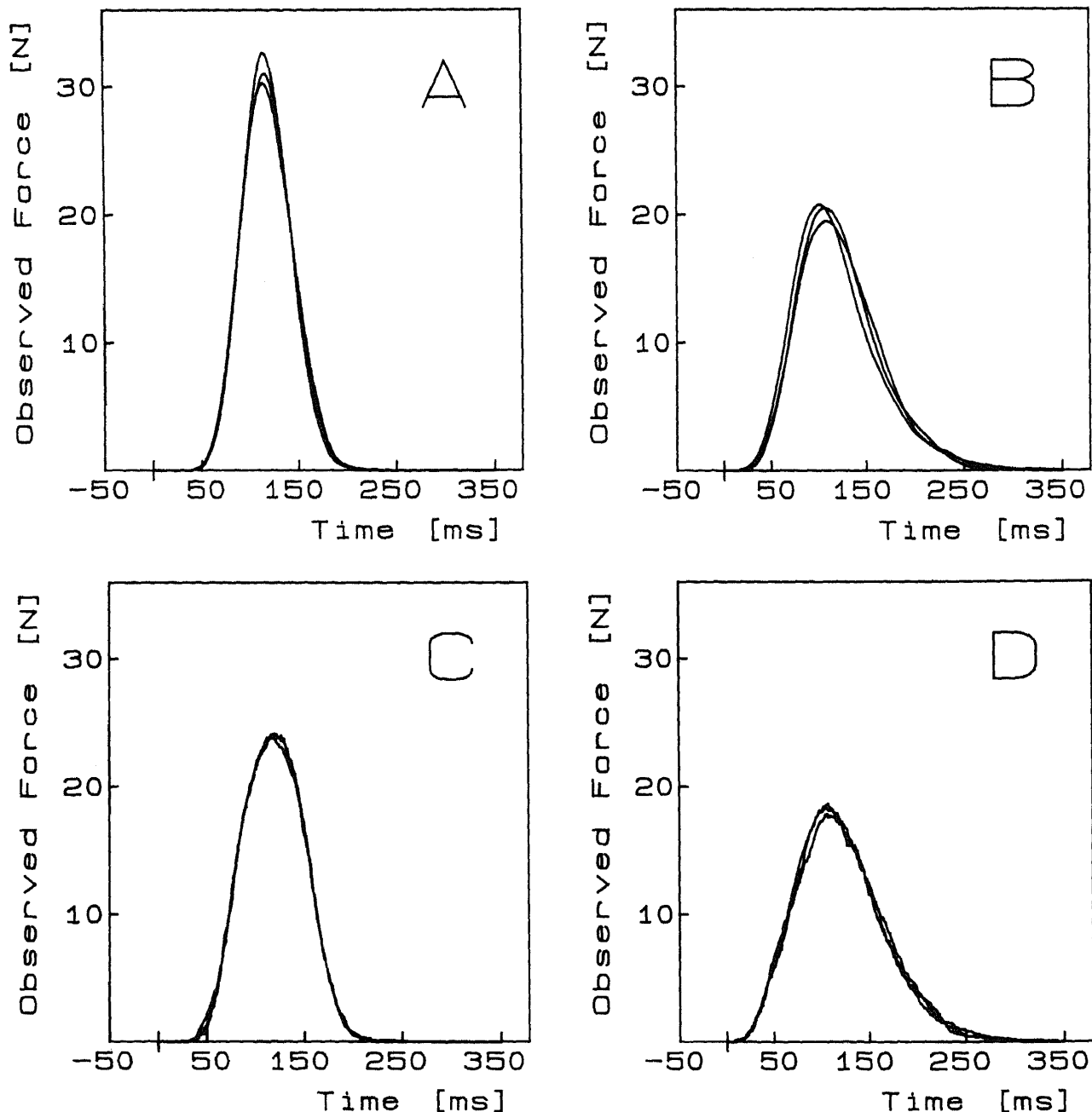
Figure 4. Simulation of force development. (Individual force units [FUs] are activated at random times determined by a special Erlangian distribution with constant mean. The functions represent the overall force summed over the 400 FUs at each point in time, t. The form of the underlying FU force–time function is symmetric triangular on the top [Panels A and B] and rectangular on the bottom [Panels C and D]. In each case, the duration of the FU force–time function is 80 ms, with an impulse of $A = 5$ Nms. The standard deviations of the Erlangian-distributed latencies $L_1, \ldots, L_b$ are 40 ms in the right panels and 20 ms in the left panels. Three simulations are depicted in each panel. Note that the temporal dispersion of the activation times "smears" the shape of the underlying FU force–time functions. Averaging the overall force–time functions would introduce further smearing.)

stated that "trajectories of responses to different targets were scalar multiples of a common waveform" (p. 246).

Rectangular FU Force–Time Function

Note that Propositions 1 and 2 do not require that the latencies $L_1, \ldots, L_n$ be independent random variables. No form of statistical dependence would invalidate Propositions 1 and 2. In Assumption $\mathcal{A}_3$, time was defined relative to an unobservable

central command.[8] However, the definition of time could be extended to an external command such as the imperative signal in a simple RT task. Although inclusion of a signal-detection period in the latency L_i would introduce positive dependence over i, Propositions 1 and 2 would still hold. In this section, to

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[8] We consider the problem of aligning observed force–time functions for averaging in the On the Time to Attain a Predetermined Force Level section.
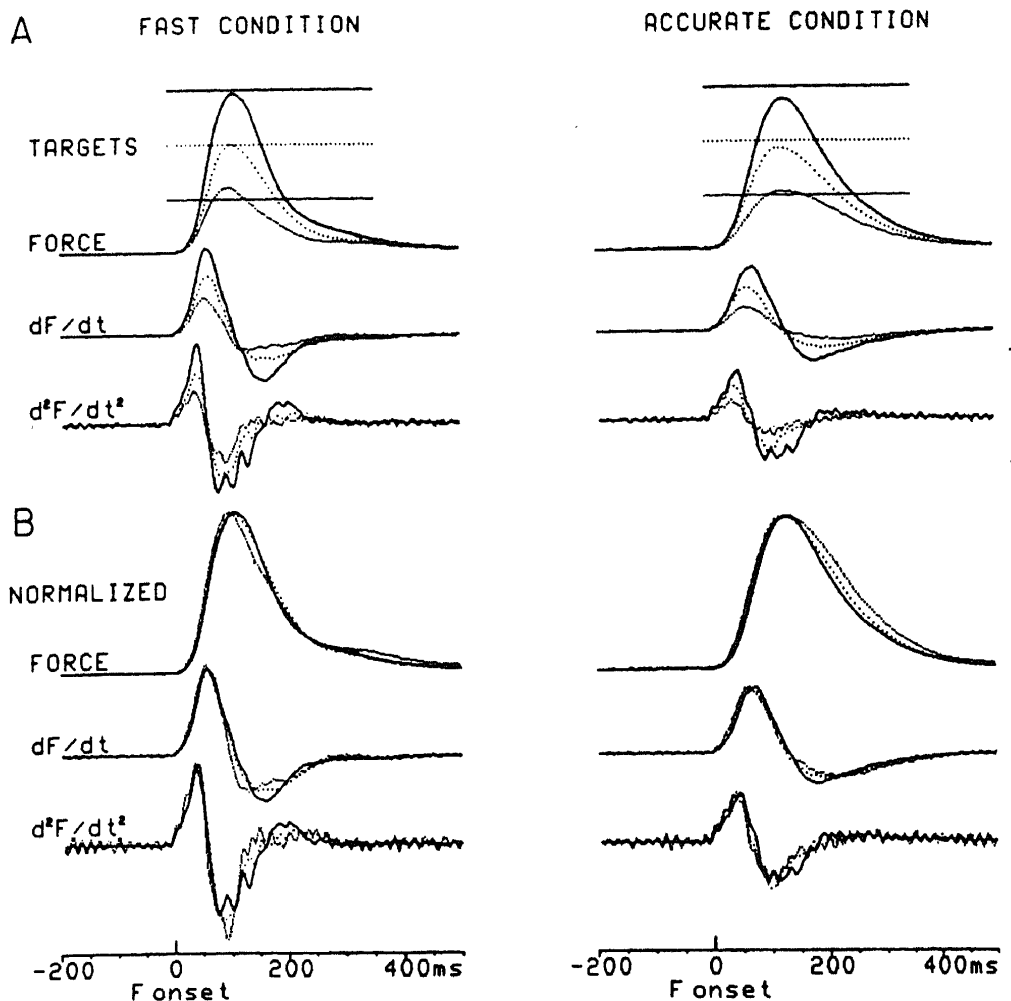
A   FAST CONDITION   ACCURATE CONDITION

TARGETS

FORCE

dF/dt

d²F/dt²

B

NORMALIZED

FORCE

dF/dt

d²F/dt²

-200   0   200   400ms   -200   0   200   400ms
F onset   F onset

Figure 5. A: Mean observed force $\bar{F}_o(t)$, $d\bar{F}_o(t)/dt$, and $d^2\bar{F}_o(t)/dt^2$ functions for responses to three target levels in fast (left) and accurate (right) conditions. B: Same functions as in Panel A, but normalized by peak force. (From "Trajectory Control in Targeted Force Impulses: II. Pulse Height Control" by J. Gordon and C. Ghez, 1987, *Experimental Brain Research, 67*, p. 245. Copyright 1987 by Springer. Reprinted by permission.)

further develop the predictions of PFUM for the mean force–time function, we make an assumption about the form of the single FU force–time function. However, once again, the development does not depend on independence of the separate FU latencies. Only when we turn to predictions for the precision of force–time functions in The Predicted Precision of Brief Force Pulses section do we have to tighten the assumptions to exclude dependence. To demonstrate the usefulness of Proposition 1, we now make the following assumption, $\mathcal{A}_6$, that the FU force–time function can be approximated by a rectangular function (cf. Figure 2). At time L_i following the central command to recruit FU i, a constant force a_i acts for a duration d_i. Thus, assuming all FUs are equivalent ($\mathcal{A}_5$):

$$u(t) = \begin{cases} a, 0 < t < d \\ 0, \text{ else.} \end{cases} \qquad (12)$$

The next proposition follows from Proposition 1.

Proposition 3. *If Assumptions $\mathcal{A}_1$ through $\mathcal{A}_6$ hold, then the mean force–time function is*

$$E[F_o(t)] = b \cdot a \cdot [F(t) - F(t-d)], \qquad (13)$$

where $F(\cdot)$ is the cumulative distribution function (CDF) of L and the constants a and d are defined in Equation 12.

Proof. The area A under the rectangular function given in Equation 12 is $A = d \cdot a$. According to Equation 3, we obtain $z(\cdot)$ by dividing Equation 12 by this area. This yields

$$z(t) = \begin{cases} \dfrac{1}{d}, 0 < t < d \\ 0, \text{ else.} \end{cases} \qquad (14)$$

The convolution $h(\cdot)$ is calculated as

$$h(t) = \int_0^\infty z(t - t') f(t') dt' \qquad (15)$$

$$= \int_{t-d}^t \frac{f(t')}{d} dt' \qquad (16)$$

$$= \frac{1}{d} [F(t) - F(t-d)]. \qquad (17)$$

Inserting $A = a \cdot d$ and Equation 17 into Equation 4 yields Equation 13. The proof is complete.

Two Modes of Peak Force Adjustment

Given the rectangular form of the FU force–time function assumed in the previous section, the resulting expression for the mean force–time function in Equation 13 can be used to demonstrate two contrasting modes of control over peak force, once a particular CDF for L has been specified. We choose the special Erlangian distribution, which is given for $t > 0$ by

$$F(t) = 1 - \sum_{r=0}^{m-1} \frac{e^{-\rho \cdot t}(\rho \cdot t)^r}{r!}, \qquad (18)$$

with scale parameter $\rho > 0$ and shape parameter $m = 1, 2, 3, \dots$ The corresponding PDF is skewed to the right, J shaped for $m = 1$, bell-shaped for $m > 1$, and attains its maximum at $t = (m - 1)/\rho$. The expectation and the variance of an Erlangian distributed random variable L is $E[L] = m/\rho$ and $\mathrm{Var}[L] = m/\rho^2$, respectively. The Erlangian distribution embodied in Equation 18 has been a very popular tool in stochastic modeling of psychological processes (cf. Luce, 1986; Townsend & Ashby, 1983) because it provides a reasonable balance between flexibility and mathematical tractability. Equation 18 was also used by Meijers and Eijkman (1974) and by Ulrich and Stapf (1984) to model the summation of force development in RT tasks. Unless otherwise stated, in the following illustrations, we set the parameters $m = 4$ and $\rho = 0.05$ ms^{-1}, yielding $E[L] = 80$ ms and $SD[L] = 40$ ms.

Proposition 3 offers two modes of increasing peak force in brief impulses: first, recruiting more FUs, that is, increasing b; second, lengthening the duration d of each FU that contributes its constant force a.[9] Figure 6 illustrates the consequences of both control modes, with reasonable choices of the parameters a and d (cf. Desmedt, 1983, p. 228) and b (cf. Buchtal & Schmalbruch, 1980, p. 95). The left side of this figure shows the impact of b on $E[F_0(\cdot)]$ when d is fixed. The greater b is, the larger the area under $E[F_0(\cdot)]$. However, the shape of the function stays the same. Thus, for example, the zero crossings of the first and second derivatives (corresponding to peak force and peak rate of change of force) coincide in time, as may be seen in the bottom rows in the left panel. This time invariance is to be expected for this control mode according to Proposition 1. If the various mean force–time functions on the left side were to be rescaled, then all the functions would coincide. Indeed, this is observed to be the case in the data of Gordon and Ghez (1987a), shown in Figure 5.

The right side of Figure 6 shows the consequences of varying d while b is held constant. Two effects of d on the mean force–time function may be noted. First, an increase of d raises the overall force level. Second, beyond the initial force rise, an increase in d raises $E[F_0(\cdot)]$ at every point in time; that is, the shape of the function varies with d. Thus, for example, the zero crossings of the first and second derivatives shown in the bottom rows in the right panel do not exhibit time invariance. The different functions produced by varying d are not rescalable.

Remarks on the concept of peak force. Before further contrasting the predictions of PFUM with empirical observations, a clarification of the term *peak force* is necessary, because it is not used consistently in the literature. Some researchers (e.g., Freund & Büdingen, 1978), working with averaged data, denote the maximum of the mean force–time function as peak

force. Suppose that this maximum is located at time t_p, indicating time to peak force; their concern would be with estimating the single quantity $E[F_0(t_p)]$. Other researchers (e.g., Newell & Carlton, 1985) have worked in terms of the highest force level achieved in each individual trial. The average of the latter, single-trial measures is then denoted as mean peak force, or confusingly as peak force. Because time to peak force varies from trial to trial, it must be treated as a random variable, say T_p. Thus, the single-trial peak force can be represented as a "double" random variable $F_0(T_p)$ and its average as $E[F_0(T_p)]$. The analytic treatment of $F_0(T_p)$ is complex, and for this reason computer simulations were run to assess the difference between $E[F_0(T_p)]$ and $E[F_0(t_p)]$. The simulations led to the following conclusions: (a) The variance of T_p is negligible if b is large, say $b > 200$. (b) In general, the mean of T_p coincides with t_p; that is, the mean of the times to peak force corresponds to time to the peak of the mean force–time function. Hence, on the basis of PFUM, the difference between $F_0(T_p)$ and $F_0(t_p)$ can be disregarded for our purposes in this article. All analytic results presented in the following were assessed by computer simulations on $F_0(T_p)$. However, because the results were essentially the same, only the analytic results regarding $F_0(t_p)$ are reported herein.

Empirical observations on the invariance of time to peak force. In the experiment by Freund and Büdingen (1978), where subjects produced brief isometric force pulses of up to about 80 N with the index finger, the time to peak was constant over different target peak forces. This invariance held over various directions of finger movement and so was not limited to one particular muscle. Carlton et al. (1987, Experiment 2) asked their subjects to generate peak forces with the index finger to targets in the range between 2 and 9 N in both simple and two-choice RT paradigms. Time to peak force varied only slightly with target force level. Gordon and Ghez (1987a) also reported constancy of rise time in isometric elbow flexion force impulses, particularly when accuracy was emphasized. In a more recent article, Favilla, Hening, and Ghez (1989) studied both flexion and extension of the elbow. Again, constancy of time to peak force was evident despite the different muscle groups involved. Finally, further evidence of the generality of the invariance of the time to peak force comes from a very different task studied by Lee, Michaels, and Pai (1990). Standing subjects had to make abrupt bilateral pulls against a handle to targets from 5% to 95% of their maximum pulling force. Despite the many muscles involved in this task, these authors'

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[9] If FUs are identified with MUs, then on the basis of muscle physiology outlined in The Activation of Skeletal Muscle section, one might argue that the parameters d and a should be positively correlated. Increases in the duration of MU contributions are associated with increases in the number of repetitive motoneuron action potentials. If these discharges are close in time, then there is superposition of these effects on successive twitches, with resulting higher force level. Hence, d and a may not vary independently. However, according to Equation 13, an increase in a would have the same effect on the mean force–time function as an increase of b. We may thus keep a constant and note that this restriction could underestimate the "real" observed force level, although this restriction does not affect the shape of the mean force–time function.
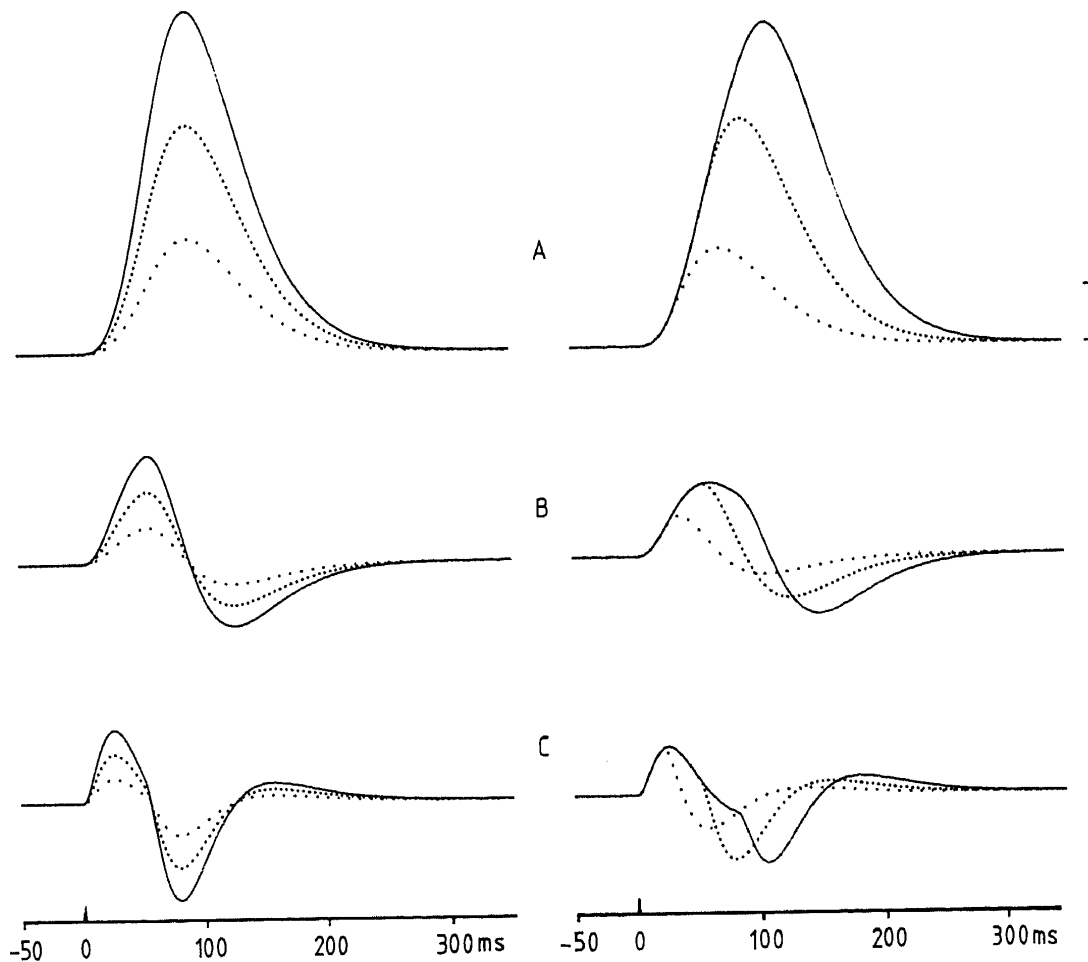
Figure 6. Predicted mean force–time functions (A) along with their first (B) and second (C) derivatives predicted from Equations 13 and 18. (The following parameter values are fixed for all figures: $m = 4$, $\rho = 0.05$ ms^{-1}, and $a = 5$ cN. The vertical calibration bar represents 2.41 N, 163 N/s, and 7,163 N/s^2 in Panels A, B, and C, respectively. Left panels: Changing force by varying the number of force units, b, while their duration, $d = 50$ ms, is fixed. $b = 600$ [solid line], 400 [closely spaced dots], and 200 [widely spaced dots] force units. Right panels: Changing force by varying d while b is fixed at 400 force units and $d = 80$ [solid line], 50 [closely spaced dots], and 20 [widely spaced dots] ms.)

data demonstrate very clear constancy of rise time to peak force. All these studies would suggest within PFUM that subjects met the different target forces primarily by adjusting FU recruitment.

Empirical observations on time to peak force correlated with peak force. So far, we have considered amplitude increases achieved by an increase of b. However, within PFUM, amplitude increases will also occur if there are increases in d. Under these circumstances, changes in peak force will be accompanied by lengthening in time t_p to the peak. Increases in time to peak as a function of peak force were reported by Freund and Büdingen (1978) in their nontarget condition. In that study, the force–time plots presented showed a small but progressive increase in the rise time with peak force. A small increase of rise time with peak force was also reported by Gordon and Ghez (1987a) in a condition where speed rather than accuracy was emphasized. A dependence between force and time to peak force may also be seen in two of three types of movement involving different muscles studied by Desmedt and Godaux (1977).

The first experiment in the study of Carlton et al. (1987) clearly demonstrates that time to peak force and peak force are

positively related as predicted by PFUM if FU duration d is lengthened. Subjects were asked to produce a brief force impulse of a prespecified duration in a range of 150–600 ms while all other dynamic factors were free to vary. Time to peak force increased with impulse duration. Hence, it must be concluded on the basis of PFUM that Carlton et al.'s subjects manipulated FU duration to produce the desired impulse duration. However, if subjects mainly regulated force duration by adjusting FU duration, then one would expect that peak force should increase with required impulse duration, and this is exactly what Carlton et al. observed.

The studies mentioned in this section, indicating a degree of dependence of peak force and time to peak force, all involved normal subjects. In another study, a dependence was reported in subjects with motor disorders in situations where the normal control subjects displayed peak time invariance. Hefter, Homberg, Lange, and Freund (1987) observed that in some cases of Huntington's chorea, the time to peak force increased with force over a 2- to 10-N range. In 1 patient, maximum rate of change of force was remarkably constant, and the duration of the force pulse was lengthened. However, other Huntington's patients exhibited lengthened contraction duration while re-

taining some increase in rate of change of force with peak force. It is interesting to speculate whether progression of the disease implies progressive loss of recruitment, which is compensated by lengthening of duration.

Maximum Effort Peak Force and Time to Maximum Effort Peak Force

In the studies reviewed so far, the forces produced by the subjects were less than the maximum of which they were capable. In contrast, Newell and Carlton (1985) have evaluated isometric force production by the elbow in a task that required the subject to produce as great a force as possible (termed *maximum effort peak force*) with a fixed criterion time to peak force (see also Carlton & Newell, 1987). They reported that maximum effort peak force depends on the the time t_p to peak force. Their findings were that mean maximum effort peak force increases in a negatively accelerated manner with t_p (cf. Newell & Carlton, 1985, Figure 1).

This finding is in accord with PFUM, as may be demonstrated by computing mean maximum effort peak force as a function of t_p. According to PFUM, the value of t_p can be controlled by increasing or decreasing d. If subjects are instructed to produce their maximum possible force while maintaining a prescribed time to maximum effort peak force, they have to adjust d accordingly and recruit all n available FUs. The following proposition shows how d and t_p are related within the framework of PFUM.

Proposition 4. Suppose that $\mathbf{L}_1, \ldots, \mathbf{L}_n$ are distributed according to Equation 18 and that $u(\cdot)$ is a rectangular function given by Equation 12; then the relation between d and t_p is

$$t_p = \frac{d}{1 - \exp\left[-\dfrac{\rho \cdot d}{m-1}\right]}. \tag{19}$$

Proof. At the point t_p where the function $E[\mathbf{F}_o(\cdot)]$ reaches its maximum $E[\mathbf{F}_o(t_p)]$, it becomes at least momentarily flat. Hence, to locate the peak $E[\mathbf{F}_o(t_p)]$, one need only differentiate $E[\mathbf{F}_o(t)]$ with respect to t and set the result equal to 0 and then solve for t_p. Thus, according to Proposition 3,

$$\frac{d}{dt}E[\mathbf{F}_o(t)] = 0 \tag{20}$$

$$\frac{d}{dt}\{a \cdot b \cdot [F(t) - F(t-d)]\} = 0 \tag{21}$$

$$a \cdot b \cdot [f(t) - f(t-d)] = 0 \tag{22}$$

$$f(t) - f(t-d) = 0. \tag{23}$$

Solving the last expression for t yields the desired value, t_p. If $\mathbf{L}$ follows a special Erlangian distribution, then the last expression becomes

$$\rho e^{-\rho \cdot t_p}\frac{(\rho \cdot t_p)^{m-1}}{(m-1)!} - \rho e^{-\rho \cdot (t_p-d)}\frac{[\rho \cdot (t_p-d)]^{m-1}}{(m-1)!} = 0 \tag{24}$$

$$t_p^{m-1} - e^{\rho \cdot d}(t_p - d)^{m-1} = 0. \tag{25}$$

Solving for t_p yields Equation 19. The proof is complete.

An illustration of the predicted relation between t_p and mean maximum effort peak force. Figure 7 shows the relation be-

tween d and t_p, which was computed on the basis of Equation 19. Two properties of this relation are obvious. First, the minimal value of t_p depends on the minimal possible value of d. However, the minimal value of t_p can never be smaller than the mode of the PDF of $\mathbf{L}$. Hence, the two curves shown in the figure do not start at $t_p = 0$ but at $t_p = (m-1)/\rho$, which is the mode of $f(\cdot)$. Second, as d increases, t_p approaches d.

The adjusted d value for a prescribed value of t_p shown in Figure 7 was entered into Equation 13 to establish the desired mean maximum effort force function. The result of this computation is depicted in Figure 8, showing mean force as a function of t_p if all n available FUs are recruited. As one can see, the resulting function increases in a negatively accelerated fashion with t_p. There are four interesting aspects connected with this figure: (a) The curves do not start at the origin ($t_p = 0$) but at the mode of $f(\cdot)$. Note that this nonorigin property seems also to be true for the empirical graphs reported by Newell and Carlton (1985, Figure 2). (b) The smallest possible value of d determines where a graph starts. For example, consider the dotted curve; if the smallest value of d were 36 ms, then the curve would start at $t_p = 80$ ms, with $E[\mathbf{F}_o(80)] = 17.4$ N. (c) The theoretical curves approach the value $n \cdot a = 45$ N as t_p increases. In other words, if d is very large, then all FUs are simultaneously active at time t_p, producing maximum possible force. (d) Mean maximum effort peak force can be more than doubled by an appropriate increase of t_p; this was also reported by Newell and Carlton (1985, p. 235) for their subjects.

The Relation Between Mean Maximum Effort Peak Force and SD[L]

The larger the variability of latency $\mathbf{L}$, the more smeared is the force impulse. This was illustrated in Figure 4. This smear-
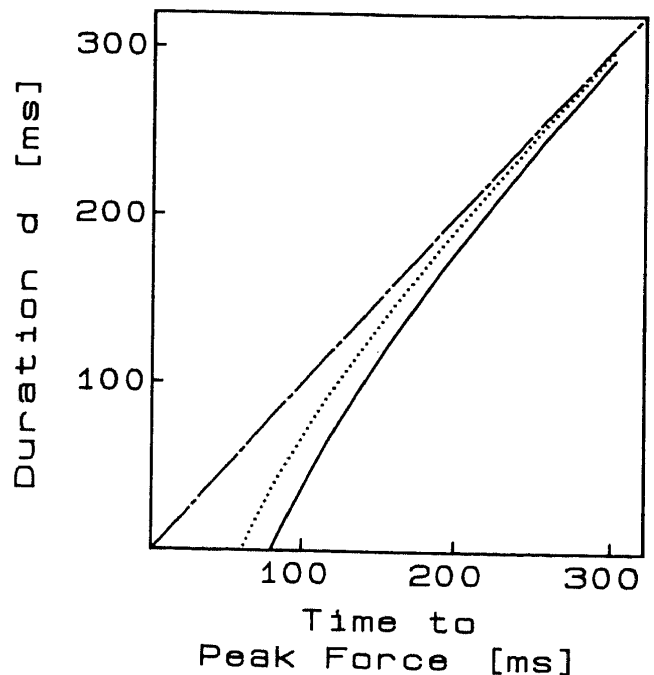

Figure 7. Predicted relation between duration, d, of the force unit force–time function and time t_p to peak force of the observed mean force–time function for two Erlangian latency distributions. (Solid line: $\rho = 0.05$ ms^{-1} and $m = 5$. Dotted line: $\rho = 0.05$ ms^{-1} and $m = 4$. At longer times to peak force, both functions approach the straight line, $d = t_p$.)
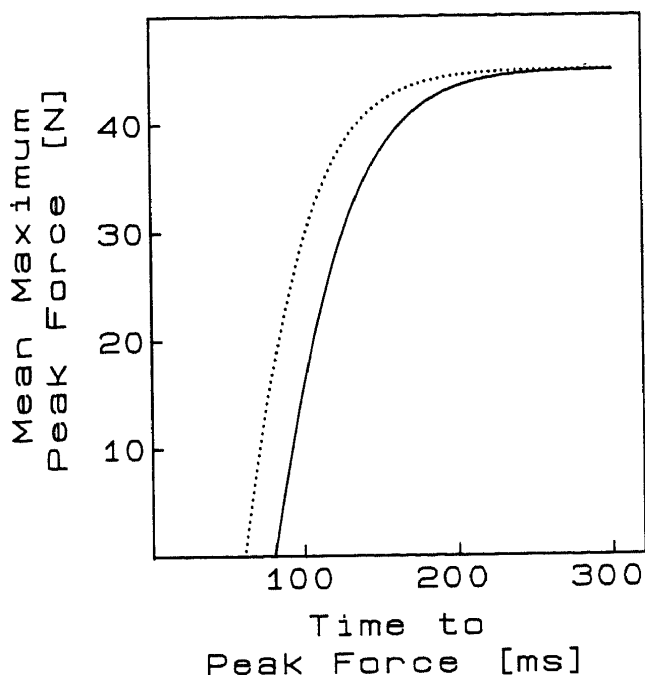
Figure 8. Predicted mean maximum effort peak force as a function of t_p. (For both curves, the parameters are: $\rho = 0.05$ ms^{-1}, $a = 5$ cN, and $b = 900$ force units. The two curves differ with regard to the shape parameter m of the Erlangian distribution. Dotted curve: $m = 4$. Solid curve: $m = 5$.)

ing effect implies that mean maximum effort peak force is attenuated. The number of simultaneously active FUs determines peak force. Therefore, if SD[L] is large, then the probability is small that all FUs are simultaneously active, that is, that their periods of activity overlap in time. Hence, maximum effort peak force decreases with increasing SD[L]. This effect, however, can be counteracted by increasing duration d, because this will increase the likelihood that the periods of activity of several FUs will overlap in time.

To observe how SD[L] attenuates the force output, we computed mean maximum effort peak force $E[F_o(t_p)]$ as a function of SD[L] and d on the basis of Equations 13, 18, and 19. The parameters m and ρ of the Erlangian distribution were varied in such a way that the mean $E[L]$ held constant at 80 ms but SD[L] varied in the range between 0 and 50 ms.[10]

The result of this computation is shown in Figure 9, which relates both SD[L] and d to the mean $E[F_o(t_p)]$ of the maximum effort peak force. The values of this mean are given as percentages of the force output under complete synchronization of FUs (SD[L] = 0). Mean maximum effort peak force decreases monotonically with SD[L]. If d is small, then $E[F_o(t_p)]$ decreases especially fast. Even with moderate values of d, the effect of SD[L] on peak force can be quite dramatic. For example, with $d \doteq 40$ ms, an SD[L] of about 30 ms would already imply a 50% reduction of mean maximum effort peak force. According to PFUM, therefore, SD[L] must be regarded as an important limiting factor in force production.

The Predicted Precision of Brief Force Pulses

The precision of response is often used as an index of the skill of a performer. Hence, several studies (e.g., Gordon & Ghez,

1987a, 1987b; Hening, Vicario, & Ghez, 1988; Jenkins, 1947; Newell & Carlton, 1985, 1988; Noble & Bahrick, 1956; Schmidt et al., 1979; see Newell, Carlton, & Hancock, 1984, for a review) have been devoted to the sources of response variability. Understanding the relative contribution of central and peripheral sources to response variability is a fundamental goal of research (cf. Newell & Carlton, 1985, p. 240). With the goal of shedding light on peripheral contributions, in this section, we investigate the precision of force impulses within the framework of PFUM and contrast the theoretical results with empirical findings on force variability.

The variance $\text{Var}[F_o(t)]$ of force $F_o(t)$ for all $t > 0$ offers a suitable index of response precision. According to PFUM, the source of this variability is entirely due to the variance $\text{Var}[L]$ of the FUs' onset latencies. Surprisingly, this source alone can account for several findings on force variability.

Perhaps the most tractable theoretical result concerning $\text{Var}[F_o(t)]$ for the following analysis can be summarized as follows (cf. Meijers et al., 1976, p. 10):

Proposition 5. If Assumptions $\mathcal{A}_1$ through $\mathcal{A}_5$ hold and the latencies $L_1, \ldots, L_n$ are independent random variables, then the variance of $F_o(t)$ for $t > 0$ is

$$\text{Var}[F_o(t)] = b \cdot A^2 \cdot \{(z^2 * f)(t) - [(z * f)(t)]^2\}, \quad (26)$$

where $(z*f)(\cdot)$ denotes the convolution of $z(\cdot)$ and $f(\cdot)$, $(z^2 * f)(\cdot)$ the convolution of $z^2(\cdot)$ and $f(\cdot)$, A the impulse of a FU, and b the number of recruited FUs.

Proof. Because $L_1, \ldots, L_n$ are assumed to be independent, we can write

$$\text{Var}[F_o(t)] = \sum_{i=1}^{b} \text{Var}[F_i(t)] \quad (27)$$

$$= b \cdot \text{Var}[u(t - L)] \quad (28)$$

$$= b \cdot A^2 \cdot \text{Var}[z(t - L)] \quad (29)$$

$$= b \cdot A^2 \cdot \{E[z^2(t - L)] - (E[z(t - L)])^2\} \quad (30)$$

$$= b \cdot A^2 \cdot \left\{ \int_0^\infty z^2(t - t') f(t') dt' - \left(\int_0^\infty z(t - t') f(t') dt' \right)^2 \right\}. \quad (31)$$

Note that the first and second integrals on the right-hand side are the convolutions $(z^2 * f)(\cdot)$ and $(z * f)(\cdot)$, respectively. The proof is complete.

Remarks on Proposition 5. All other things being equal, $\text{Var}[F_o(t)]$ increases linearly with the number b of recruited FUs and as the square of impulse A. This property is illustrated in Figure 10 by means of computer simulations.

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[10] If latency L follows an Erlangian distribution, then the relation between E[L] and SD[L] is given by SD[L] = E[L]/$\sqrt{m}$. Because the parameter m is restricted to the integer values $m = 1, 2, 3, \ldots$, the standard deviation SD[L] is restricted to the values E[L]/$\sqrt{1}$, E[L]/$\sqrt{2}$, E[L]/$\sqrt{3}, \ldots$ Hence, SD[L] and E[L] cannot vary independently. To bypass this problem, we treat m as a real positive value and thus obtain a natural generalization of the Erlangian distribution, namely, the so-called gamma distribution (cf. Feller, 1971, pp. 47–48).
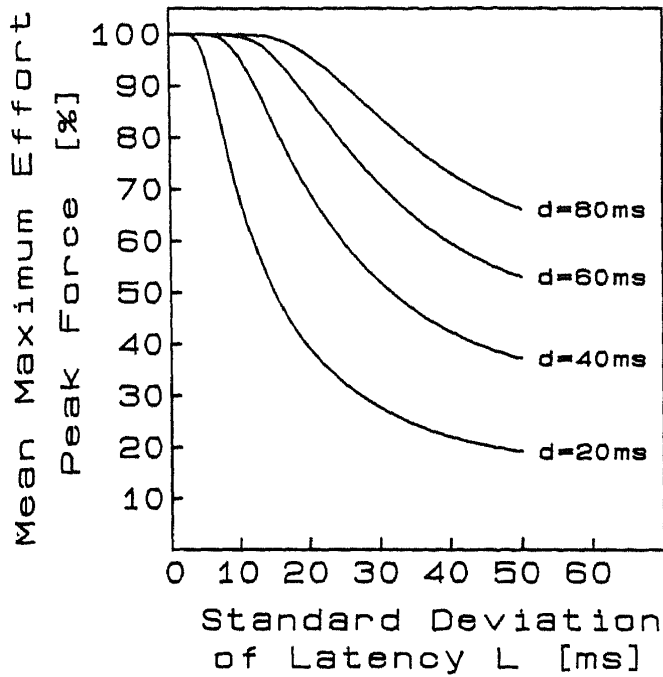
Figure 9. Mean maximum effort peak force $E[F_o(t_p)]$ as a function of standard deviation SD[L] and d. (Maximum effort peak force is expressed as a percentage of the force developed for SD[L] = 0. Latency L is assumed to follow an Erlangian distribution with E[L] fixed at 80 ms.)

Proposition 5 implies an interesting principle of response precision. Suppose that for a given target, force-level force pulses are to be as similar as possible. In other words, the observed force level at time t should on the average be $E[F_o(t)]$,

with minimal $\text{Var}[F_o(t)]$. Within the framework of PFUM, there are two contrasting possibilities for attaining the required force level without affecting the shape of the mean force–time function. First, recruit only a small number of FUs, where each FU contributes a relatively large impulse A. Second, recruit all n available FUs, where each FU contributes only a small A. Would $\text{Var}[F_o(t)]$ be smaller in the first or in the second case? On the basis of Propositions 1 and 5, the second alternative is preferable because larger units give a lower resolution. Therefore, if a precise response is required, according to PFUM, as many FUs as possible should be recruited, with each FU contributing only a small fraction of total force, as illustrated by Figure 10. Increasing the number of units (recruitment) is better than increasing the force of each unit in keeping $\text{Var}[F_o(t)]$ to a minimum and so achieving fine control.

Rectangular FU Force–Time Function and Variability

No specific assumption about $u(\cdot)$ is contained in Proposition 5, and therefore $\text{Var}[F_o(t)]$ cannot be elucidated at this general level. If we proceed again from the idea that $u(\cdot)$ can be approximated by the rectangular function in Equation 12, then a tractable mathematical expression for $\text{Var}[F_o(t)]$ can be derived from Proposition 5.

Proposition 6. If $u(\cdot)$ is defined by Equation 12, then

$$\text{Var}[F_o(t)] = b \cdot a^2 \cdot [F(t) - F(t - d)]$$
$$\times [1 - F(t) + F(t - d)], \qquad (32)$$

where $F(\cdot)$ is the CDF of L and the parameter a is the constant force contribution of a FU with duration d.
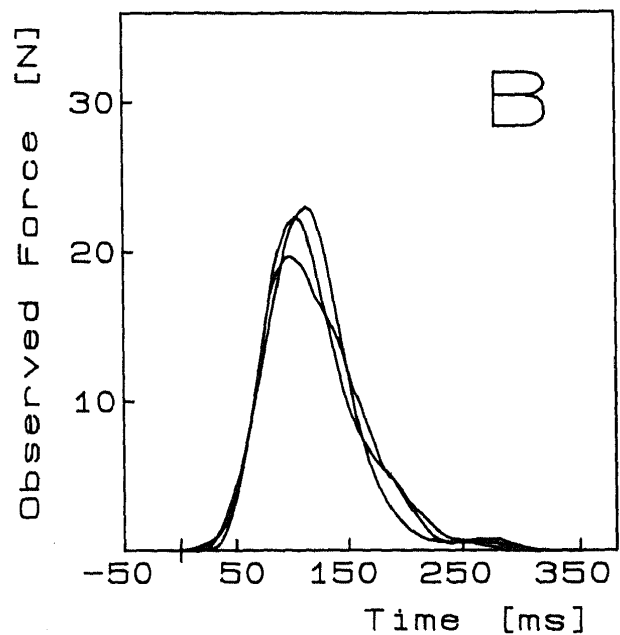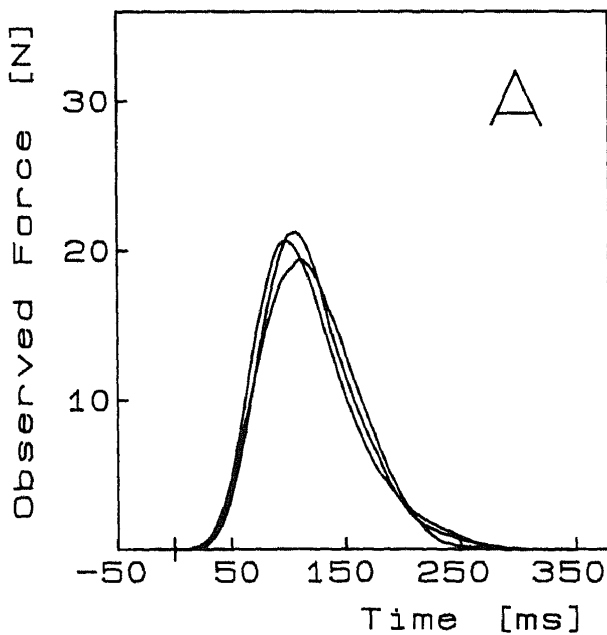
Figure 10. Dependence of variance of the observed force–time function on number and amplitude of the individual force units (FUs). (The simulations in both panels are based on a temporal dispersion of FU onsets that follows a special Erlangian distribution with the mean E[L] = 80 ms and the standard deviation SD[L] = 40 ms. The underlying FU force–time functions are symmetric triangular functions of duration 80 ms. The number of FUs and their impulses differ in the two panels. A: $b = 400$ and $A = 5$ Nms. B: $b = 100$ and $A = 20$ Nms. The curves in Panel B exhibit a larger variability than do those in Panel A. Note, however, under Proposition 1, that the mean force–time functions for both panels would be identical.)

Proof. The convolution $(z^2 * f)(\cdot)$ is calculated as

$$(z^2 * f)(t) = \int_0^\infty z^2(t - t') f(t') dt' \qquad (33)$$

$$= \int_{t-d}^t \frac{f(t')}{d^2} dt' \qquad (34)$$

$$= \frac{1}{d^2} [F(t) - F(t - d)]. \qquad (35)$$

Inserting $A = a \cdot d$ and Equations 17 and 35 into Equation 26 yields the desired result. The proof is complete.

Remarks on Proposition 6. Figure 11 illustrates the predicted variability function of Equation 32 for the case where the CDF of L is the special Erlangian distribution. (All model parameters except d are the same in all panels.) The value of d is 50, 100, and 150 ms in Panels A, B, and C, respectively. An especially interesting feature of the variability function is its local minimum, which becomes more salient as d increases. It can easily be shown that Equation 32 predicts a local minimum $\mathrm{Var}[F_o(t_p)]$ at t_p and a maximum $\mathrm{Var}[F_o(t_m)]$ for all times t_m satisfying the equation $F(t_m) - F(t_m - d) = \frac{1}{2}$.[11] There is an intuitive explanation of this local-minimum feature: Consider the case in which d is infinitely long (relative to onset variability); variability during the force rise phase must drop to zero as force asymptotes at a new steady level. However, we are interested in brief impulses in which FUs only maintain their activity for a brief duration before turning off. Note, then, that an asymptotelike ending to the rise phase is visible in Panel C of Figure 11. This may be related to the degree to which individual FU durations allow their active phases to overlap before their offsets begin to pull the force–time function down again. The increasing overlap of FU activity (which also increases peak force) from Panels A through C in Figure 11 may then be seen to cause the predicted local minimum in variance. The peak in variability during force rise occurs at the first point at which 50% of the FUs become active. This time point corresponds to the median of latency L, which is located at $t = 73$ ms in Figure 11. The second variability peak occurs d ms later as the number of active FUs drops below 50%.

Suppose that force level is controlled only by d and that L follows a special Erlangian distribution; then both t_p and $E[F_o(t_p)]$ increase with d, as was shown earlier (cf. Figures 7 and 8, respectively). How does $\mathrm{Var}[F_o(t_p)]$ behave under this condition? Figure 12 provides the answer, showing $\mathrm{SD}[F_o(t_p)]$ as a function of t_p. This analysis reveals that after an initial fast increase, the variance of peak force diminishes with longer values of d. Note that this prediction contrasts with the case where force is controlled by b only. In the latter case, $\mathrm{SD}[F_o(t_p)]$ increases with b as suggested by Proposition 5.

Empirical observations on the relation of $\mathrm{SD}[F_o(t_p)]$ *and* t_p. We do not know of any study that documents $\mathrm{SD}[F_o(\cdot)]$ as a function of t or as a function of t_p. However, an observation reported by Newell and Carlton (1988, Experiment 4) should be mentioned in this context. They examined the effect of t_p on peak force variability. Subjects were required to produce the same criterion peak force (54 N) for different times to peak force. Mean peak force did not differ significantly across the times to peak force. However, the standard deviations of peak
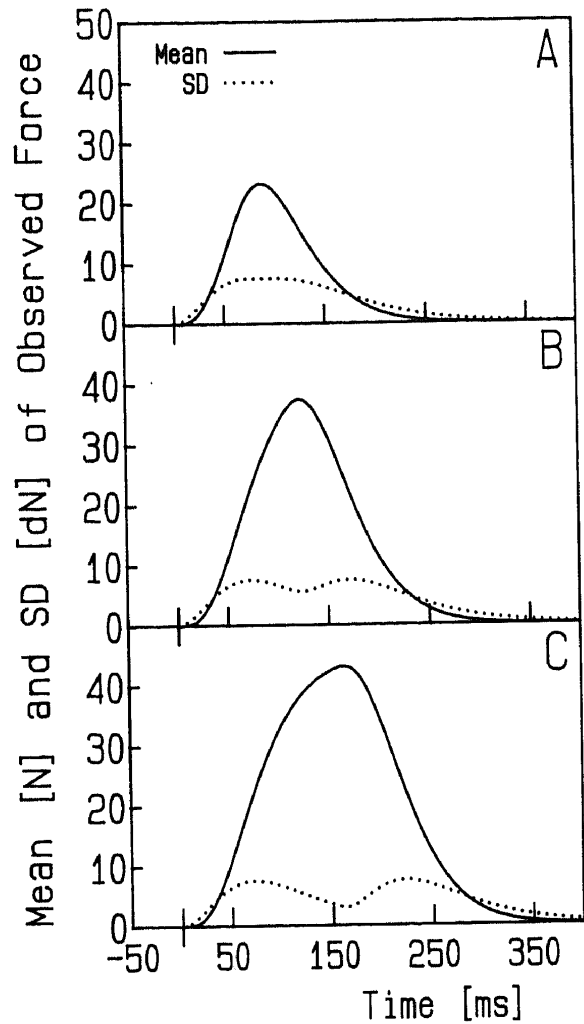

Figure 11. Predicted mean $\dot{E}[F_o(t)]$ and standard deviation $\mathrm{SD}[F_o(t)]$ as a function of time t. (Time point $t = 0$ is marked by a large tick on the t axis. Note that the unit of $\mathrm{SD}[F_o(t)]$ is dN = N/10. In all three panels, the parameters are $m = 4$, $\rho = 0.05\ \mathrm{ms}^{-1}$, $a = 5$ cN, and $b = 900$ force units. A: $d = 50$ ms. Maxima $\mathrm{SD}[F_o(t_m)] = 7.50$ dN are located at $t_m = 80$ and $t_m = 98$ ms. Local minimum $\mathrm{SD}[F_o(t_p)] = 7.496$ dN and maximum $E[F_o(t_p)] = 23.19$ N are located at $t_p = 88$ ms. B: $d = 100$ ms. Maxima $\mathrm{SD}[F_o(t_m)] = 7.50$ dN are located at $t_m = 73$ and $t_m = 171$ ms. Local minimum $\mathrm{SD}[F_o(t_p)] = 5.61$ dN and maximum $E[F_o(t_p)] = 37.44$ N are located at $t_p = 123$ ms. C: $d = 150$ ms. Maxima $\mathrm{SD}[F_o(t_m)] = 7.50$ dN are located at $t_m = 73$ and $t_m = 223$ ms. Local minimum $\mathrm{SD}[F_o(t_p)] = 3.03$ dN and maximum $E[F_o(t_p)] = 43.08$ N are located at $t_p = 163$ ms.)

force decreased significantly as t_p increased. To apply PFUM to such a task, b must be adjusted at each prespecified value of t_p to achieve the required constant criterion peak force.

Table 1 illustrates this point. Suppose the experimental conditions call for a criterion peak force of about 50 N and four prespecified times to peak force of 100, 150, 200, and 250 ms. The table shows the necessary adjustments of d and b to achieve these requirements. The rightmost column contains the standard deviations of $F_o(t_p)$ computed with Equation 32. This standard deviation decreases as t_p increases, and hence this prediction is in qualitative agreement with the observations of Newell

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[11] This conclusion would not apply if $F(t) - F(t - d) < \frac{1}{2}$ is true for all $t > 0$. However, this inequality only holds for small values of d.
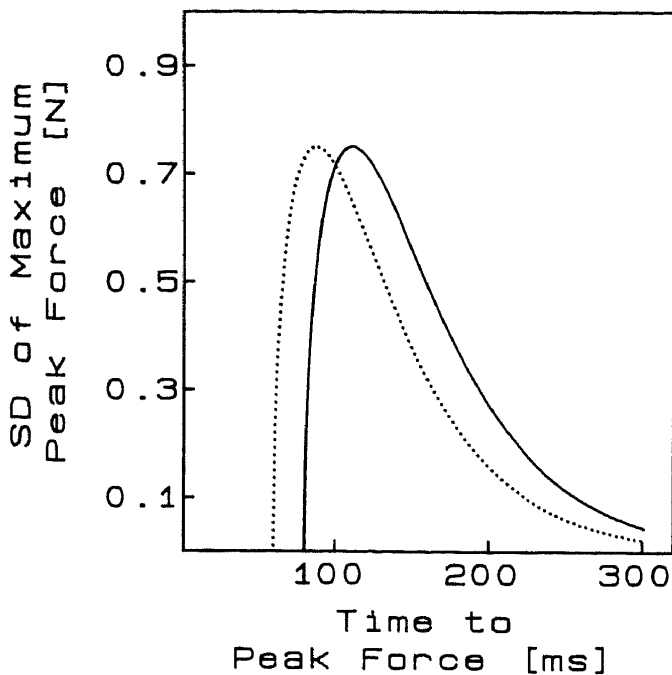
Figure 12. Predicted standard deviation $SD[F_o(t_p)]$ of maximum effort peak force, with adjustment of d determining time to peak force. (For both curves, the parameters are $p = 0.05$ ms^{-1}, $a = 56$ cN, and $b = 900$ force units. Dotted curve: $m = 4$. Solid curve: $m = 5$.)

and Carlton (1988).[12] This prediction of PFUM is intuitively easy to grasp: Short FU durations are necessary when the pulse has to be made within a brief interval, as shown by the second column in Table 1. Under PFUM, with short FU durations giving relatively little overlap, more force units are required for the desired peak force level than if larger durations of FU activation had been possible. Because variability increases with number of FUs, the variance of peak force is higher at short t_p.

To attain a given level of peak force with a range of prespecified values of t_p, adjustment of both d and b is necessary. With two variables to control, one might expect that several practice trials would be required before good performance levels can be achieved. This feature of PFUM may underlie an observation made by Corcos, Agarwal, Flaherty, and Gottlieb (1990). They reported that producing isometric force pulses to a fixed-target force level (50% of maximum voluntary contraction) in different durations was more difficult to perform than producing force pulses of fixed duration to different force targets. Within

Table 1

Duration d, Number b of Force Units, Standard Deviation of $F_o(t_p)$ and Mean of $F_o(t_p)$ as a Function of Time to Peak Force

t_p	d	b	$E[F_o(t_p)]$	$SD[F_o(t_p)]$
100	68	766	50	1.31
150	134	537	50	0.59
200	192	506	50	0.24
250	246	501	50	0.09

Note. Computations are based on $m = 4$, $p = 0.05$ ms^{-1}, and $a = 10$ cN. The unit in the first and second columns is the millisecond. The unit in the fourth and fifth columns is the newton.

PFUM, the former would require simultaneous adjustment of b and d, whereas the latter could be achieved with changes to b alone. Moreover, in a study of saccadic eye movements, Bahill, Hsu, and Stark (1978) concluded that control of the duration of the muscle impulse driving the eye to a new position is more difficult than control over the amplitude (height) of that impulse. This is also consistent with the idea that control of b (impulse height) is easier than the adjustment of both b and d (impulse duration).

Preload Force and Peak Force Variability

As discussed in the Maximum Effort Peak Force and Time to Maximum Effort Peak Force section, Newell and Carlton (1985) investigated peak force produced in elbow flexion pulls ranging between 2% and 90% of maximum force. Using a variant of the original paradigm, Newell and Carlton (1988) examined rapid isometric elbow flexions starting from different resting level forces (preloads). In the first experiment, subjects were asked to produce the same peak force (54 N) starting from different preloads (0, 13.5, 27.0, and 40.5 N). A significant decrease in standard deviation of peak force was observed with increase in preload. In the second experiment, the change in force level (peak force minus preload) was kept constant at 13.5 N, but preload was varied from block to block (0, 13.5, 27.0, and 40.5 N). The standard deviation of peak force decreased with preload, although the observed force increase was approximately constant. In the third preload experiment, the ratio of preload to peak force was kept constant at ½ while varying the absolute levels of preload and peak force. Thus, there were four preloads of 6.75, 13.5, 20.25, and 27.0 N, with the associated criterion peak forces of 13.5, 27.0, 40.5, and 54.0 N, respectively. In this task, the standard deviation of peak force increased with preload.

There is a natural way to apply PFUM to these preload experiments. Suppose that there are two categories of FU. One, the tonic FUs, produces the required preload force level. The other, the phasic FUs, produces the required force increment. At any point in time, observed force $F_o(t)$ is assumed to be equal to the summed forces over both categories. Suppose at time $t = 0$ the tonic FUs are already active. The role of the central command must then include not only activation of the phasic FUs at this time, but also at time $t = d$, a deactivation of the tonic FUs. Thus, there are two time-locked components to the command, and we assume both are subject to random delays with the same PDF. In this way, both phasic and tonic FUs are deactivated on the average simultaneously at time $t = E[L] + d$.

Let $b_T(b_P)$ be the number of tonic (phasic) FUs with $b_T + b_P \leq n$. If $u(\cdot)$ is assumed to be a rectangular function of length d and height a, then the predicted mean force–time function of preload experiments is

$$E[F_o(t)] = a \cdot [b_T + b_P \cdot F(t) - (b_T + b_P) \cdot F(t - d)]. \quad (36)$$

(See Appendix B for proof.) Furthermore, if the latencies L_1, ..., L_n are pairwise independent, then the variance of observed

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[12] However, the decrease is not of the same order as the one reported by Newell and Carlton (1988), and $SD[F_o(t_p)]$ approaches zero as t_p further increases.

force is given by

$$\text{Var}[F_o(t)] = a^2 \cdot \{b_T \cdot [1 - F(t - d)] \cdot F(t - d)$$
$$+ b_P \cdot [F(t) - F(t - d)] \cdot [1 - F(t) + F(t - d)]\}. \quad (37)$$

(See Appendix B for proof.)

Figure 13 exemplifies Equation 36 with the special Erlangian distribution for $F(\cdot)$. The figure shows four mean force–time functions having the same peak force but starting from a different resting level (as in Newell & Carlton's 1988 experiment). The functions differ only with regard to the number of tonic and phasic FUs; that is, it is assumed that force level is controlled only by the number of FUs. The higher the preload force, the less the number b_P of phasic FUs required to achieve the same level of peak force. From the figure it is also evident that t_p decreases somewhat with increasing preload force. Hence, the scaling property of mean force–time functions, as discussed earlier, does not generalize to preload experiments. Newell and Carlton (1988) did not report whether t_p varied with preload condition. However, their Figure 1 (1988, p. 39) shows some example trials in which t_p decreases somewhat with preload force in the manner of Figure 13.

The three examples in Table 2 were modeled according to the preload conditions of Newell and Carlton's (1988) Experiments 1, 2, and 3. The main question is whether the variability predictions of PFUM agree qualitatively with data reported by Newell and Carlton. The computations in Table 2 were based on Equations 36 and 37 with the parameters $m = 4$, $\rho = 0.05$ ms^{-1}, $a = 10$ cN, and $d = 50$ ms. Only the parameters b_P and b_T were varied in such a way that the resulting force–time functions satisfied both the required preload and peak force-level condition of their experiments. However, the intention was not to match the exact
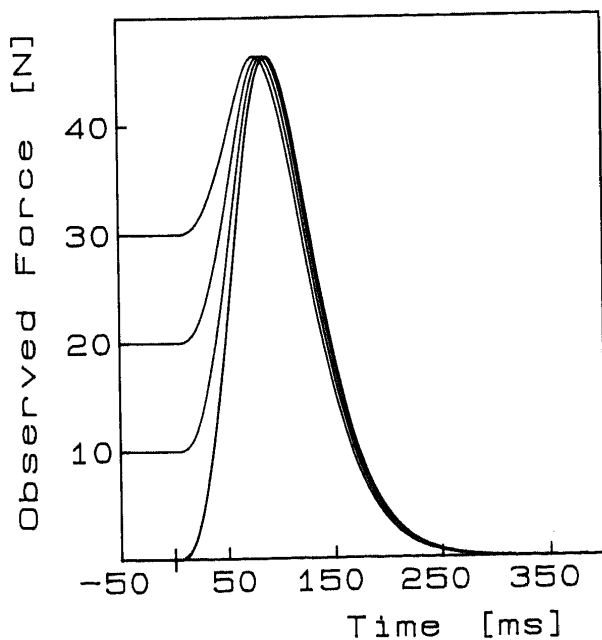
Table 2

Preload Force Level, Mean of $F_o(t_p)$, Standard Deviation of $F_o(t_p)$, and Time to Peak Force t_p as a Function of b_p (Number of Phasic Force Units) and b_T (Number of Tonic Force Units)

b_P	b_T	Preload	$E[F_o(t_p)]$	$SD[F_o(t_p)]$	t_p
		Example 1			
970	0	0	50	1.56	88
799	100	10	50	1.45	86
623	200	20	50	1.31	83
439	300	30	50	1.12	79
		Example 2			
195	0	0	10	0.70	88
213	100	10	20	0.77	81
225	200	20	30	0.81	77
235	300	30	40	0.83	75
		Example 3			
107	50	5	10	0.55	81
213	100	10	20	0.77	81
320	150	15	30	0.95	81
426	200	20	40	1.10	81

Note. Computations are based on $m = 4$, $\rho = 0.05$ ms^{-1}, $d = 50$ ms, and $a = 10$ cN. The unit in the third, fourth, and fifth columns is the newton. The unit in the sixth column is the millisecond.

force values of their study because at this stage of model development, our concern is only with the qualitative adequacy of predictions based on PFUM. In Example 1 it is assumed that the same peak force level (50 N) has to be achieved starting from different preloads (0, 10, 20, and 30 N). Note that the standard deviation of peak force decreases with preload level, and this agrees with the observation made by Newell and Carlton (1988, Experiment 1). Example 2 illustrates the prediction of PFUM if subjects are required to produce a constant force increment of 10 N starting from different preloads. In this example, $SD[F_o(t_p)]$ increases with preload level, and this was also observed by Newell and Carlton (1988, Experiment 2). The third and last example corresponds to their Experiment 3, with the ratio of preload to peak force being 1:2 for all four preloads. Again, the prediction is in qualitative agreement with the observation made by Newell and Carlton (1988, Experiment 3) in that $SD[F_o(t_p)]$ increases with preload level. In sum, then, these examples demonstrate that PFUM can account for the variability data of preload experiments.

Relation of $E[F_o(t)]$ and $SD[F_o(t)]$

It is a customary practice in experimental work on force production to relate mean and standard deviation of $F_o(t)$ to reveal the precision of performance. In general, standard deviation of force increases with the level of force produced. Most studies of this relation report a negatively accelerating function (e.g., Fullerton & Cattell, 1892; Jenkins, 1947; Newell & Carlton, 1985), although Schmidt et al. (1979) have described an increasing relation. In this section, the predictions PFUM for the relation between $SD[F_o(t)]$ and $E[F_o(t)]$ are investigated. This is carried out separately for the two modes of force-level control.

Figure 13. Predicted mean force $E[F_o(t)]$ as a function of time t and preload condition. (The time point $t = 0$ is marked by a large tick on the t axis. All curves are based on the parameters $m = 4$, $\rho = 0.05$ ms^{-1}, $a = 10$ cN, and $d = 50$ ms. However, the graphs differ with respect to b_T and b_P. Preload force 0 N: $b_T = 0$ and $b_P = 900$. Preload force 10 N: $b_T = 100$ and $b_P = 730$. Preload force 20 N: $b_T = 200$ and $b_P = 552$. Preload force 30 N: $b_T = 300$ and $b_P = 366$.)

We continue to assume that $L_1, \ldots, L_n$ are independent random variables.

Force-Level Control by b

Suppose that higher target force levels are produced by recruiting more FUs. In this case, the following result for the relation of $E[F_o(t)]$ and $SD[F_o(t)]$ is obtained:

Proposition 7. If force level is controlled only by the number b of FUs, then $SD[F_o(t)]$ increases as a square root function of $E[F_o(t)]$:

$$SD[F_o(t)] = \alpha \cdot \sqrt{E[F_o(t)]} \quad \alpha > 0, \quad (38)$$

where the constant α equals $\dfrac{SD[F_i(t)]}{\sqrt{E[F_i(t)]}}$.

Proof. Note that

$$E[F_o(t)] = b \cdot E[F_i(t)] \quad (39)$$

and

$$SD[F_o(t)]^2 = b \cdot SD[F_i(t)]^2 \quad (40)$$

must hold. Divide Equation 40 by Equation 39 and rearrange the resulting expression. The proof is complete.

Empirical Observations on the Relation of $E[F_o(t)]$ and $SD[F_o(t)]$. There are several studies that may be interpreted in terms of Proposition 7. In early experiments conducted by Fullerton and Cattell (1892), standing subjects produced a series of near-isometric pulls, ranging in peak force from 20 to 160 N. Fullerton and Cattell reported that the standard deviation of peak force was proportional to the square root of the corresponding mean force. Although this result appears to be consistent with PFUM, the authors did not report the time to peak force. Without an indication of its constancy, we do not have firm grounds for believing that subjects were only regulating b and not d. In the Newell and Carlton (1985) study, the standard deviation of peak force $F_o(t_p)$ for a fixed time to peak force was investigated. The isometric task required elbow flexion pulls with peak forces ranging between 2.5% and 90% of maximum effort peak force. They also observed that the standard deviation of peak force increased in a negatively accelerated fashion with mean peak force.

An alternative way of characterizing the precision of force control is in terms of the coefficient of variation:

$$c \equiv \frac{SD[F_o(t)]}{E[F_o(t)]}. \quad (41)$$

Several researchers have summarized their results by plotting c against various targets for peak force, the latter corresponding (normally) to $E[F_o(t)]$ (Fullerton & Cattell, 1892; Gordon & Ghez, 1987a, 1987b; Hening et al., 1988; Jenkins, 1947; Noble & Bahrick, 1956). These plots were motivated by applying Weber's law to the domain of force production. Weber's law states that the Weber fraction $\Delta s/s$ should be constant for all values of s, where s denotes the stimulus magnitude and Δs the difference limen (cf. Luce & Galanter, 1963). In the domain of force production, the coefficient of variation is considered analogous with Weber's fraction. The general finding is that c decreases markedly at the smallest values of $E[F_o(t)]$. However,

outside this region, Weber's law holds moderately well, although there is a continuing tendency for the fraction to decrease.

Both the function generated by c and the standard deviation function (i.e., $SD[F_o(t)]$ as a function of $E[F_o(t)]$) convey essentially the same information. This is best seen by dividing Equation 38 on both sides by $E[F_o(t)]$; thus, one obtains c as a function of $E[F_o(t)]$:

$$c = \frac{\alpha}{\sqrt{E[F_o(t)]}}. \quad (42)$$

Equation 42 predicts an initial marked decrease of c for small values of $E[F_o(t)]$ and a relative constancy of c beyond this initial decrease. This agrees qualitatively with corresponding empirical findings (Fullerton & Cattell, 1892; Gordon & Ghez, 1987a, 1987b; Hening et al., 1988; Jenkins, 1947; Noble & Bahrick, 1956).

Force-Level Control by d

Interestingly, quite different conclusions might be reached regarding the relation of $E[F_o(t)]$ and $SD[F_o(t)]$ if force is controlled by varying the duration of the force contribution by each FU. Specific assumptions about the force–time function $u(\cdot)$ and about the CDF of L are, however, necessary to assess this relation. As an example, suppose that $u(\cdot)$ is rectangular and $F(\cdot)$ is a special Erlangian distribution. Consider the values of $SD[F_o(t)]$ and $E[F_o(t)]$ at peak force depicted in Figures 8 and 12, respectively, which were computed on the basis of these assumptions for particular model parameters. Figure 14 shows a plot of $SD[F_o(t)]$ against $E[F_o(t)]$ for this case. Although at lower peak forces $SD[F_o(t)]$ increases with $E[F_o(t)]$, $SD[F_o(t)]$ decreases markedly for large values of $E[F_o(t)]$. In motor control, it is surprising to encounter a situation where variability does not continue to increase through the range of a physical dimension; but even more remarkably, PFUM suggests that variability may actually decrease under certain circumstances.

Yet data exist (Sherwood & Schmidt, 1980, Experiment 2) where this is the case. Sherwood and Schmidt reported an inverted-U-shaped function between force and standard deviation of produced force in an isometric elbow flexion task. The target forces ranged from 58 N close to a maximum level of 276 N. The standard deviation of force increased linearly up to approximately 65% of maximum force and declined thereafter. Unfortunately, Sherwood and Schmidt did not provide the time to peak force in their original work. However, Newell and Carlton (1985, p. 239) attributed this decrease in force variability to a concomitant lengthening in time to peak force, which would be consistent with the idea of PFUM, that higher force levels were controlled by d and thus reduced force variability with increasing force level. Of course, further research in this area is warranted.

One may appreciate that PFUM would be able to predict several shapes of the function relating $SD[F_o(t)]$ and $E[F_o(t)]$ if force level were controlled by different combinations of b and d. This might account for the discrepant estimates in the literature of this function as reviewed by Newell et al. (1984).
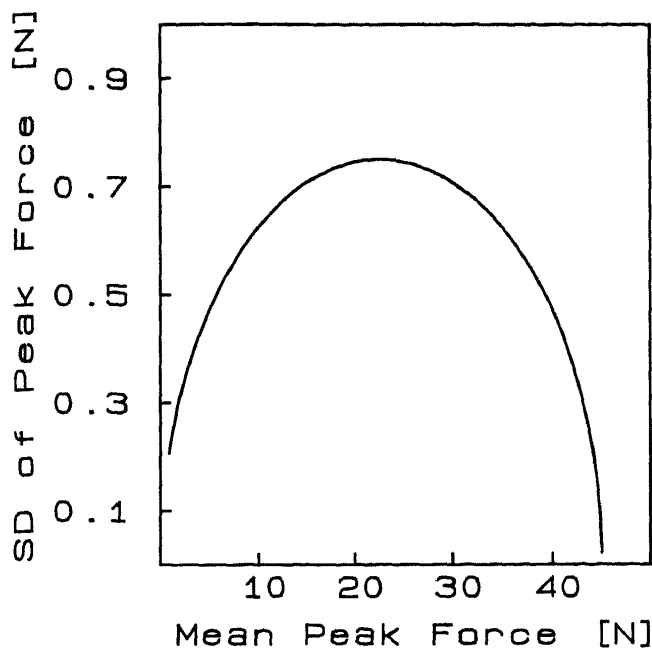
Figure 14. An example of an inverted-U-shaped standard deviation function predicted by the parallel force unit model. (The figure was obtained by plotting the standard deviation $SD[F_o(t_p)]$ shown in Figure 12 against the corresponding mean $E[F_o(t_p)]$ shown in Figure 8. The curves for $m = 4$ and $m = 5$ superimpose.)

On the Time to Attain a Predetermined Force Level

In the introduction, we suggested that the development of force in brief impulsive responses could have implications for measuring the times of those responses. Reference was made to Angel's (1973) study in which RT varied systematically with peak force. We suggested that this dependence could have arisen because the response was defined as the crossing of a predetermined force level, or threshold, which is constant across conditions. Different rates of force increase associated with different peak forces would then affect the time to attain the threshold. Angel assessed force levels using a force transducer, but note that this point also applies when a mechanical device, such as a microswitch, provides the threshold. This characterization of a relation between force and measured response time would appear to fall within the domain of PFUM. However, so far, PFUM has been formulated in terms of force changing as a function of time, $F_o(\cdot)$. To understand the implications of the model for measuring the time of a response, the roles of force and time need to be switched. Thus, in this section, we consider the motor delay $T(f)$ to achieve a predetermined force level f.[13]

Throughout most of the RT literature, the motor delay is assumed to be a constant delay, and therefore it does not contribute to the variance of the total RT. The main reason for this assumption is that it simplifies the building of mathematical models of RT (cf. Luce, 1986; Meijers & Eijkman, 1977; Ulrich & Giray, 1986); however, it also receives support from empirical studies of repetitive tapping (Wing, 1980; Wing & Kristofferson, 1973) and synchronous bimanual responding (Ulrich & Stapf, 1984; Wing, 1982) in which estimates of motor delay variability are relatively small. How can low estimates of motor delay variability be squared with the variable onset latencies of

the single FUs in PFUM? A theoretical rationale for the low values, which is in line with PFUM, was proposed by Meijers and Eijkman (1974). They treated the motor delay in terms of mth order statistics, that is, as the onset time $T_{m:b}$ for the mth unit of b units with randomly distributed onset latencies. They demonstrated that the variance of $T_{m:b}$ decreases rapidly as the number b increases. Hence, they argued that the temporal precision of the motor process will be high as long as many units are activated, even when the single-unit onset times exhibit a large time jitter. In this analysis, the use of the mth order statistic implies that the $m - 1$ units preceding the onset of the mth unit should remain active at least up to that point. Strictly speaking, this only applies when activation times, d, are sufficiently long. However, in the following section, we describe a simulation study, based on PFUM, which indicated that the observations of Meijers and Eijkman (1974) also hold for relatively brief pulses. In light of the simulation results, we then consider studies on the relation between the force and time of discrete responses.

Simulation of Threshold Force Attainment Time

In an earlier section we analyzed the mean force–time function $E[F_o(\cdot)]$ predicted by PFUM and showed how changes in the number b of recruited FUs and the duration d of the FU force–time function affected peak force $E[F_o(t_p)]$ and time to peak force t_p. Our present concern is with characterizing the observed force–time function in terms of its timing. We should like to know, for example, over repeated trials, what are the mean and standard deviation of times taken to reach a particular level of force. The evaluation of varying times to cross fixed force thresholds may be contrasted with our use in a preceding section of the constancy of times to attain varying force levels as support for the scalability property of PFUM.

In the simulation (see Table 3 for results) we used, as before, Erlangian distributed FU onset latencies $L_1, \ldots, L_n$ with parameters $p = 0.05$ ms, $m = 4$, and rectangular-shaped force–time functions $u(\cdot)$ with amplitude $a = 5$ cN. This combination of parameters produced the peak forces (F_p) and times to peak forces (T_p) shown in the first 2 columns. We assess the effect of varying b and d (while keeping all other parameters in the model constant) in terms of times defined relative to a low and a high fixed force threshold, f_1 and f_2, where $0 < f_1 < f_2$. The motor delays between the central command and the observed force first attaining levels f_1 and f_2 we denote $T(f_1)$ and $T(f_2)$. The associated interval $R = T(f_2) - T(f_1)$ we term the *rise time*.

The results of the simulation given in Table 3 are for force levels $f_1 = 20$ cN and $f_2 = 200$ cN, with 200 or 400 FUs combined factorially with FU force–time function durations of 40

[13] The time interval $T(f)$ between central command and overt response (keypress) has been variously termed *response delay* (Wing & Kristofferson, 1973), *motor time* (e.g., Meijers & Eijkman, 1974), *motor subsystem latency* (Meijers & Eijkman, 1977), and *motor delay* (e.g., Vorberg & Hambuch, 1978). Others subsumed $T(f)$ under more general terms, such as *irreducible minimum RT* (Woodworth & Schlosberg, 1954) or *residual latency* (Luce, 1986).

Table 3

Parallel Force Unit Model Simulation of the Effects of Number b of Force Units and Force Unit Duration d on Timing Measures

Measure	F_p	T_p	$T(f_1)$	$T(f_2)$	R
		$b = 200, d = 40$ ms			
Mean	447	84	20	46	26
SD	30	8	3	3	3
		$b = 400, d = 40$ ms			
Mean	879	83	16	35	19
SD	46	6	2	2	3
		$b = 200, d = 80$ ms			
Mean	748	109	20	46	26
SD	29	5	3	3	4
		$b = 400, d = 80$ ms			
Mean	1,482	109	16	35	19
SD	42	4	2	2	3

Note. The means and standard deviations of various timing measures (see text for explanation) are based on 750 trials each. The unit of peak force F_p in the first column is the centinewton; all other column entries are in milliseconds. The entries in the first and all other columns are rounded to the nearest centinewton and millisecond, respectively.

or 80 ms, which give various peak force values and associated times to peak force as shown in the first 2 columns.[14]

There are difficulties in estimating mean and variance functions in order to relate them to PFUM. The predicted relations are based on time t relative to an unobservable event, namely the moment at which the central command occurs. If we were to choose an arbitrary point, such as the peak force, in order to align the force–time function prior to averaging, we clearly would bias the estimates, for example, reducing $\text{Var}[F_o(t_p)]$. Gordon and Ghez (1987a, p. 245) suggested alignment on force onset. According to the simulations, the timing accuracy on crossing a prespecified force level is very high. As an alternative, we therefore suggest that such a time point could equally well be used as a reference for averaging observed force–time functions.

In the following section, we consider the relation of the simulation results on changing b and d to behavioral data on timing. However, first we draw attention to a general property of PFUM, evident in Table 3, in which the means of the motor delays $T(f_1)$ and $T(f_2)$ are seen to be considerably shorter than the mean FU latency (which was set at 80 ms). This underestimation by the motor delay of the FU onset latency reflects a simple principle referred to by Raab (1962), in the context of variability in afferent latencies, as *statistical facilitation*. With dispersion of onset delays over several channels, the time of onset of activity regardless of channel is, on average, less than the average onset time of any given channel. There is a facilitation of the onset time defined over the group relative to the time that would be obtained if only one unit were present.

Statistical facilitation affects not only mean latency but also timing precision. In the simulation, although the variability of latency L is quite large, $\text{SD}[L] = 40$ ms, the observed motor

delay standard deviations are very small. The tapping study of Wing and Kristofferson (1973) and the bimanual RT study of Ulrich and Stapf (1984) provide independent estimates of the standard deviations of motor delays that are of the order of only a few milliseconds. PFUM thus affords a viable account of such low estimates of the variance of motor delays.

Motor Delays Related to Force Output

In psychological research, the time of a response (most commonly of interest in RT experiments but also of importance in the study of timing) is often identified by the depression of a switch that closes an electrical circuit. This requires a brief force in excess of some threshold. Depending on the mechanics of the switch, the required force may be lower or higher, but, as in the simulation of the preceding section, it is likely to be constant across conditions. The results of the simulation clearly demonstrate that, under certain conditions, the time of a response (whether defined on a low threshold, f_1, or a high threshold, f_2) will be inversely related to peak force. This is the case if peak force is adjusted in terms of b, the number of recruited FUs, but not if changes in peak force are achieved by altering d, the duration of the FU force–time function.

At least two RT experiments provide evidence that there can be alterations in peak force without change in RT, consistent with force control based on adjustment of FU duration. In a finger-press task that required the production of brief force pulses with response duration unconstrained, Ivry (1986, Experiment 1) reported that changes in peak force (for targets of 4.5, 7.5, or 10.5 N) had no effect on either simple or choice RT. Because time to peak force and impulse duration increased with peak force, this would suggest that subjects varied FU duration in order to vary peak force. This strategy would tend to keep the rate of force rise constant over different peak forces. A complementary task, in which subjects had to vary the duration of brief isometric finger-press force pulses with force unconstrained, was studied by Carlton et al. (1987, Experiment 1). As mentioned earlier, they reported that time to peak force and peak force increased with duration. However, despite the changes in peak force, they also observed no effect on simple or choice RT. Again, with PFUM, we would assume that subjects adjusted FU duration without change in number of recruited FUs. Earlier work by Klemmer (1957) on RT also showed a constancy over different force levels. Although he did not report time to peak force, rate of force rise was constant over conditions, indicating that control of force was carried out by manipulation of FU duration.

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[14] The values in the first 2 columns support a claim made earlier (see the Remarks on the Concept of Peak Force section) in which we suggested that the difference between the "double" random variable $F_o(T_p)$ and $F_o(t_p)$ is negligible as long as b is large. From Equation 19 with $(b-d)$ combinations 200–40, 400–40, 200–80, and 400–80 [FUs–ms], one obtains the predicted values $t_p = 82, 82, 109,$ and 109 ms. These values agree well with the means of T_p in Table 3. Accordingly, by Equations 13 and 32, values of 424, 849, 733, and 1,466 cN for $E[F_o(t_p)]$, and 35, 49, 31, and 44 cN for $\text{SD}[F_o(t_p)]$, are obtained. These values clearly approximate the corresponding means and standard deviations of F_p listed in Table 3.

Several studies provide evidence of changes in FU recruitment in the adjustment of peak force. In the introduction, we referred to Angel's (1973) observations of variation in simple RT with response force (see Figure 1). His systematic manipulation of stimulus intensity resulted in decreases in RT that were associated with increased response force. Under PFUM, the shortening of RT with higher peak forces is attributed to increases in the number of recruited FUs. Reduction of RT with force in a task that required graded control of force is reported in Carlton et al. (1987, Experiment 2). Subjects were required to produce peak forces to targets in the range 2.5–8.5 N. Although the instructions left impulse duration unconstrained, it was found that subjects maintained a relatively constant time to peak force, and RT (both simple and choice) decreased with increasing force.

Changes in response timing with peak force have also been reported in a task that required subjects to produce sequences of accurately timed isometric force pulses (Keele, Ivry, & Pokorny, 1987). Subjects were required to stress different elements of a rhythmic temporal pattern by approximately doubling the force on that response from the normal level (which was about 4 N). Keele et al. observed that the accenting usually decreased the length of the interval (measured at 10 cN) terminated by that response. They attributed the effect to "more rapidly mobilized muscular forces" (Keele et al., 1987, p. 110) with stronger forces, a view consistent with PFUM.

We have considered data from tasks in which force might be adjusted either by change in FU duration (which would leave RT unaltered) or by changing the number of FUs (which would lead to an inverse relation between peak force and RT). However, it is clearly a simplification to suppose that subjects would always adopt one mode of control to the exclusion of another. Indeed, in a study by Haagh, Spijkers, van den Boogaart, and van Boxtel (1987), both a reduction in RT and an increase in time to peak force was evident as force increased from 5% up to 50% of maximum voluntary force. This suggests both an increase in b and an increase in d. Moreover, tasks have been described that, under PFUM, would necessarily require control on both dimensions. Siegel (1988) asked subjects to produce isometric force impulses on a hand dynamometer to a target of 98 N. He required them to control the rate (time to peak force) to levels 40% and 20% of the most rapid impulses. To reduce the rate of rise of force under PFUM requires a reduction in number of FUs. However, this would result in a reduction of peak force, and this must be compensated for by an increase in FU duration. (A concrete example of the operation of such a constraint may be found in Table 1.) Although the latter would leave RT unaffected, the drop in number of FUs predicts an increase in RT, and this is what Siegel observed. A similar result over a more complicated set of conditions was also reported by Carlton and Newell (1987).

PFUM might also be helpful in understanding a deficit in force production observed in Parkinson's disease patients and reported by Stelmach and Worringham (1988). Subjects with Parkinson's disease and age-matched control subjects were required to aim at different target force levels in a simple RT task. The authors reported longer RTs, longer times to peak force, lower rates of force development, and more irregular force–time functions in the Parkinsonian group than in the control

group. In the framework of PFUM, one might speculate that this performance difference reflects a difference in the basis of control, whereby Parkinsonian subjects use fewer larger amplitude FUs and adjust peak force by changing FU duration rather than altering the number of FUs recruited. It is interesting in this regard to recall that we earlier inferred this same mode of control in the case of a patient with Huntington's chorea, also a basal ganglia disorder, described by Hefter et al. (1987). The basis for that inference was the constancy of maximum rate of change of force for different peak forces. Furthermore, Bahill et al. (1978) have suggested that, in the case of peripheral nerve deficit (unilateral abducens nerve paralysis) affecting eye movements, patients tended to modify impulse width rather than amplitude. In each of these cases, the interpretation under PFUM would be that an impairment in the ability to increase the amplitude of brief force impulses by increasing b is compensated for by an increase in d. Thus, the model appears to have application to disordered as well as normal motor performance.

Discussion

In this article, we have developed a theory (PFUM) in which it is assumed that the voluntary production of a brief force impulse involves the concerted action of a large number of distinct FUs. Each FU is assumed to have some deterministic force–time function associated with the lumped effects of the contraction properties of muscle fibers and the mechanical characteristics of the skeletomuscular system. The level of force produced may be adjusted by varying the number of active FUs (recruitment) or by altering the duration of the FU force–time function. If the time of onset of each FU has an appreciable temporal uncertainty relative to its period of activity, the buildup of the observed overall force to its peak value will be extended, as will the decay period. The greater the onset variability, the longer the periods of buildup and decay and, unless the duration of the FU force–time function is increased, the lower the peak force attained.

The body of this article is concerned with deriving predictions for this theory, and the major points are summarized in Table 4.

As an analogy for PFUM, suppose several people are struggling to lift a very heavy object, such as a piano, over an obstruction, such as a step. Individually, none of them are strong enough to raise the piano. However, good teamwork, probably based on someone taking the lead with a "One, two, three, lift" command, results in overlap of the times of their individual efforts. By this means, the summation of their individual lifts may be sufficient to take the piano over the step. The point of the analogy is that, in tasks where an individual must generate a force impulse, coordination of activity over several potentially independent muscles is often required. Given, further, that each muscle is composed of a large number of separate muscle fibers, the situation is akin to the piano-moving analogy in having several independent units contributing to the total force. Just as the efficacy of the piano movers' lifting may be seen to be a function of the degree to which the individual members can act in concert, so in our theory we have been concerned with the nature of force summation over the separate force ele-

Table 4
Summary of Supported Predictions

Relation/property	Prediction	Data support
Scalability of mean force–time functions	If force level is controlled only by FU recruitment, then the rescaled mean force–time functions must superimpose.	Angel (1973), Freund & Büdingen (1978), Gordon & Ghez (1987a), Lee, Michaels, & Pai (1990)
	If force level is controlled only by FU duration, then both peak force and time to peak force increase. The scalability property is violated.	Carlton, Carlton, & Newell (1987, Experiment 1), Hefter, Homberg, Lange, & Freund (1987)
Relation of peak force and time to peak force	Mean maximum peak force increases in a negatively accelerated manner with time to peak force.	Carlton & Newell (1987), Newell & Carlton (1985)
Relation of M and SD of (peak) force (relation of coefficient of variation and mean force)	If force level is controlled only by recruitment, then SD increases in a negatively accelerated fashion with mean force. (Coefficient of variation decreases fast for small values of mean force but attains a relative constancy beyond this initial decrease.)	Fullerton & Cattell (1892), Gordon & Ghez (1987a, 1987b), Hening, Vicario, & Ghez (1988), Jenkins (1947), Newell & Carlton (1985), Noble & Bahrick (1956)
	If force is (also) controlled by FU duration, then SD can decrease with increasing mean force.	Newell & Carlton (1988, Experiment 4), Sherwood & Schmidt (1980)
Preload force and force variability	PFUM predicts relations between peak force, preload force level, and peak force variability.	Newell & Carlton (1988)
Force and mean response time	With constant t_p, RT decreases with force as the number of FUs increases (statistical facilitation).	Carlton et al. (1987, Experiment 2), Carlton & Newell (1987), Keele, Ivry, & Pokorny (1987), Siegel (1988), Stelmach & Worringham (1988)
	With force increase accompanied by lengthened t_p, RT is constant.	Carlton et al. (1987, Experiment 1), Ivry (1986, Experiment 1)

Note. FU = force unit; M = mean; SD = standard deviation; PFUM = parallel force unit model; RT = reaction time.

ments composed of fibers within muscles. However, in contrast to the analogy, in our modeling we did not assume the existence of a team leader giving explicit instructions to achieve coordination. Whatever consistency is observed in the development of brief force pulses, the extent to which there is invariance in the time to peak force over different force levels is an emergent characteristic. The behavior of the system is a consequence of the stochastic properties of the system's elements all acting independently rather than being the result of any structured, executive control processes.

Although the theory has a considerable number of implications for the nature of force–time relations in brief force impulses, it might appear that PFUM is no more than a formalization in mathematical terms of a rather simplistic view of the neurophysiology of multifibered muscle. To a certain extent, this is indeed the way we perceive our work. However, we would argue that the exercise of putting these ideas into a form that allows the generation of quantitative predictions is not trivial. When assumptions that are required to derive predictions are made explicit, gaps in empirical understanding become apparent. Deducing the properties of the theory in terms of formal propositions serves to sharpen the sophistication of interpretations of existing data; relations among various observed phenomena may become comprehensible. Limitations on previously accepted forms of data analysis and presentation may become evident, and new, more insightful measures based on procedures that are theoretically more sound may suggest themselves. And it may be hoped that the theory will help structure intuitions so that they may better guide future research.

However, any exercise in quantitative modeling necessarily leans heavily on its assumptions. These are critical not only in simplifying the theoretical development of predictions but also in maintaining a model's identifiability. As more parameters are included in a model, its fit to a body of data will improve, but the possibility of estimating unique, stable, and interpretable values for those parameters becomes more remote. For this reason, when developing PFUM, we made a decision to be selective in incorporating empirical results, for example, from the very extensive neurophysiological literature concerning the subtle patterning of motoneuronal activity. But now that we have developed the theory to the point where it is capable of providing at least a qualitative account of a substantial body of behavioral research, it is time to reexamine some of those assumptions. What are the consequences, if any, for PFUM if some of the assumptions are not valid? What are the implications for future research? In addressing these questions, we take points from three different levels of the analysis of movement: neurophysiological, biomechanical, and behavioral.

Neurophysiological Data Overlooked?

To discuss those aspects of muscle neurophysiology that might seem most directly in conflict with the assumptions of PFUM, it is necessary to consider studies in which the force–time functions associated with the activity of individual MUs throughout a muscle are sampled during steady contractions using *spike-triggered averaging* (STA). In this method, which was first used by Buchtal and Schmalbruch (1970), a fine-wire electrode is inserted into the muscle, and a recording is made of

the electrical spike activity of a single fiber while the force produced by the pull of the muscle across its joint is monitored by a sensitive transducer. The tension developed in a steady contraction is then averaged with respect to each successive depolarization spike of the fiber, which will coincide in time with all the other muscle fibers that, together with the driving motoneuron, constitute the MU. The averaging causes slight fluctuations in the tension record that are time locked to the MU to stand out from random fluctuations in tension due to the unsynchronized activity of other, unrelated MUs. From a behavioral perspective, the STA is a useful characterization of muscle function because it reflects not only the MU characteristics but also the effects of biomechanical factors intervening between muscle fiber and the external point at which force can be measured. In terms of PFUM, it may be considered to correspond to the FU force–time function.

By sampling across MUs throughout a muscle, it has been shown with the STA approach that single-unit twitch amplitudes are geometrically distributed—larger amplitude MUs being relatively less common (Milner-Brown, Stein, & Yemm, 1973). Such variation in twitch amplitude may be attributed to differences both in the number of fibers connected to a given motoneuron and in the cross-sectional area of the individual fibers. In contractions of slowly increasing force, there is orderly recruitment of MUs by size according to the level of force. Motoneurons that result in relatively small twitch tensions during the contraction of their muscle fibers are recruited prior to MUs that produce larger twitch tensions (Henneman, 1957). This finding, often referred to as the *size principle*, has been shown to apply to many muscles under quite different conditions (Henneman & Mendell, 1981), although the rank ordering is not always perfectly preserved (Thomas, Ross, & Stein, 1986).

PFUM could, in principle, be generalized to allow for subsets of FUs with force–time functions that differ on characteristics such as amplitude. However, as the theory stands, the size principle raises certain issues. First, consider the consequence of different amplitude contributions (and, quite possibly, different durations) from different FUs. Clearly, this would constitute a violation of Assumption $\mathcal{A}_5$, that all FUs have the same force–time function. And, not only does the size principle indicate that not all FUs are identical, but also, at least in slow contractions, there is nonrandom recruitment from the set of available FUs. To the extent that recruitment in brief contractions might also be ordered by size, this would render invalid the assumption that the latencies of individual FUs can be characterized by a single random variable, L. One consequence is that even if peak force were being controlled by the number of FUs, there would no longer be scaling of the force–time function with increase in peak force. Instead, the duration of the overall force–time function would increase with the addition of the larger FUs coming in after longer delays (and for longer periods) at higher force levels. It thus becomes important to ask whether the orderly recruitment of MUs according to the size principle applies to rapid, ballistic contractions or whether it is limited to slowly developed contractions?

Rapid isometric contractions have been studied in terms of MU recruitment order. In such contractions, the electrical activity in the agonist muscle recorded in the surface EMG largely precedes the force pulse. A method for examining an order of

MU recruitment under these circumstances was suggested by Desmedt and Godaux (1977). Subjects were instructed to produce brief pulses of varying peak force, and MU characteristics were then related to this peak force. It was found that more large MUs were recruited at a given force than would have been expected from data obtained in trials where the force is increased slowly. Given the short duration of the overall EMG burst, it is clear that the active MUs must be recruited in close temporal proximity. If, as is suggested by Thomas et al.'s (1987) data on isotonic contractions, there is appreciable variability in the times of onset of MU activity, there will be a high probability of fluctuations in the onset order of different MUs associated with brief, isometric force impulses. Clearly, it would be desirable to have additional neurophysiological data on recruitment order and temporal dispersion in brief ballistic contractions.

However, there are relevant behavioral data that suggest uniformity of FUs. The study of Freund and Büdingen (1978) described earlier included an additional task. This required subjects to produce brief force increases of 10 N from different baseline forces. Despite variation in baseline forces over the range 0–40 N, neither the time to peak force nor the rate of rise of force varied. Constancy of rate was also earlier described by Klemmer (1957) for baseline forces in the range 0–7 N. These preload studies suggest that the characteristics of the recruited set of FUs do not depend on baseline force, and this is consistent with Assumption $\mathcal{A}_5$.

A second important set of neurophysiological data that casts doubt on the validity of Assumption $\mathcal{A}_4$ stems from a study of isometric wrist flexion torque production by Sanes and Jennings (1984). These authors provided data on force pulses produced by wrist flexion that indicate the presence of antagonist activity in isometric tasks. Their recorded force impulses show a similar time course to those recorded by Freund and Büdingen (1978). However, although the baseline flexion torque (preload level) is zero, a small but distinct undershoot was found on the tail end of the impulse. Inspection of the accompanying EMG traces revealed clear antagonist activity. This finding suggests that the offset of the force impulse may be actively driven, rather than arising purely through the cessation of agonist activity. Meinck, Benecke, Meyer, Höhne, and Conrad (1984) also observed activation of the antagonist in the production of brief force pulses involving isometric finger flexion. This antagonist activity could be suppressed by subjects if they were instructed to passively relax after matching the target force as fast as possible. However, subjects found this condition more difficult, and practice was required if subjects were to avoid active reduction of the force. Active curtailment by the antagonist of isometric force impulses has also been documented for elbow flexion, particularly for impulses of shorter duration (Corcos et al., in press; Ghez & Gordon, 1987). This finding was subsequently confirmed for elbow flexor isometric force pulses by Ghez and Gordon (1987), who concluded that briefer pulses (with rise times to peak less than 120 ms) may be actively curtailed by a burst of activity in the antagonist muscle.

In light of such observations, it would therefore appear that within PFUM, the overall force $F_o(t)$ should be treated as a summation of both positive and negative contributions. Such a view might be developed in a number of ways. The force–time

function of each FU might be assumed to be first positive and then negative. That is, negative (or antagonist) activity might be taken to be tightly linked in time to the preceding positive (or agonist) activity in a manner similar to that proposed by Darling and Cooke (1987) for isotonic muscle activation in arm positioning tasks. Or, one might suppose that there are independent classes of positive and negative FUs. Depending on the particular assumptions made about the phase of positive and negative force contributions relative to the temporal dispersion of their onsets, quite different mean force–time functions might obtain. And, unlike the special cases of PFUM that we discussed earlier, the variance of $F_0(t)$ would not necessarily be related to the level of force. Thus, in general, it would appear that future work in this area will need careful consideration of model identifiability of whether two distinct models can be discriminated on the basis of behavioral measures of observed force–time functions.

Biomechanical Factors Not Taken Into Account?

Although we have allowed neurophysiology to shape the assumptions of PFUM, our concern in this article has been primarily with overt behavior, with force measured at the effector level rather than with muscle tension per se. It is thus important to appreciate that there are various biomechanical factors that may qualify the use of data on MU activity to infer FU properties. An excellent review of a number of approaches to modeling the relation between (deterministic) neural activation of muscle and resultant joint motion was provided by Winters and Stark (1987). They favored a class of models based on Hill's (1938) conception of muscle as a contractile element arranged in series with a viscoelastic element and connected in parallel to a joint with inertial and elastic properties. To describe the relation between neural activation and muscle torque, up to eight parameters are required. For the general case, in which there is change in muscle length, the relation is nonlinear due to factors such as a dependence of tendon stiffness on muscle length (Proske & Morgan, 1987). However, when the task is isometric, involving no change in muscle length, the data are described reasonably well with models having only one or two parameters. These parameters depend only on the joint and whether torque is being directed into flexion or extension.

In our analysis of PFUM, mechanical effects are lumped together with muscle fiber contractile properties in the definition of the FU force–time function. If the latter changes with muscle length (or joint angle), the assumptions of PFUM will be violated. Thus, it would seem more appropriate to investigate PFUM in tasks where muscle contraction is isometric or nearly isometric. Nonetheless, there may be interest in applying observations on the form and consistency of brief force pulses to overt movement trajectories. Thus, for example, Abrams, Meyer, and Kornblum (1989) suggested that in eye movements and limb movements, kinematic aspects such as the increase in variability of movement end points with movement velocity may have a common basis arising in neuromotor noise. They proposed that the generation of a movement involves the selection of a prototypical force–time function that may be scaled in time or amplitude. It is tempting to suggest that PFUM could provide an account of these dimensions of control, of the partic-

ular form of resulting force–time function, and of the consequent noise characteristics. However, if the focus is to be shifted to tasks performed under isotonic conditions where muscle length is changing appreciably, allowance must be made for nonlinearities such as those reviewed by Winters and Stark (1987). Although explicit modeling of each source of such effects would be one strategy to developing PFUM, an alternative is to relax the assumption of a deterministic single-unit force–time function $u(\cdot)$. PFUM could be generalized to force–time functions, which change randomly from trial to trial. We have assayed several computer simulations in which $u(\cdot)$ varies from trial to trial. Although at a preliminary stage, this work probably will help specify under what range of conditions results would be expected to resemble the predictions based on a deterministic function $u(\cdot)$.

Role of Feedback Overlooked?

In describing step changes in force, Cordo (1987) identified initial ballistic and subsequent adjustment phases to voluntary aimed isometric contractions. His analyses indicated a feedback basis for the corrections, much as argued for the role of feedback in hand-positioning movements (Keele, 1981; Keele & Posner, 1968). In this article, we have treated brief force impulses rather than the step changes studied by Cordo. But adjustment to the initial specification (e.g., in our terms, of recruitment level, FU duration, or both), if not necessarily on the basis of concurrent feedback, has been suggested by Ghez and his collaborators in their research on the production of brief impulses. In the production of targeted force impulses, most of the variance (between 70% and 96%) is accounted for by the peak value of the second derivative of force (Gordon & Ghez, 1987a). Because this peak value occurs relatively early (50 ms after the onset of force change), it is reasonable to identify it as a product of open-loop control that may be accounted for by PFUM. However, the remaining variance, which is not accounted for, invites interpretation. This is provided by Gordon and Ghez (1987b) in terms of a process that internally monitors the unfolding neural commands.

The monitoring process proposed by Gordon and Ghez (1987b) falls outside the assumptions embodied in PFUM. It could be argued that, because the process only accounts for a relatively small proportion of the variance, it should be of little concern in quantitative, psychological modeling. However, there is no reason why, eventually, PFUM might not be adapted to include feedback adjustment. Conversely, we would like to see accounts of feedback processing that take explicit account of the nature and consequences of irreducible noise. But, for the present, on the grounds of keeping the number of parameters down in the interests of mathematical tractability and model identifiability, we favor the strategy of studying force development in tasks that design away the complications introduced by subjects using concurrent feedback control.

In the performance of motor skills, it is generally recognized that subjects may use feedback at several levels (e.g., Schmidt, 1975). At lower levels, modifications to motor activity based on the feedback may take place without conscious intervention and with a relatively brief time course so that the feedback loop is contained within a trial. Such concurrent feedback process-

ing may be contrasted with the use of knowledge of results in which modifications to action may extend over several trials, may be subject to conscious strategic control, and may be based on symbolic representation of the outcome of prior motor activity (Salmoni, Schmidt, & Walter, 1984).

Two contrasting options for the control of peak force (recruitment, b, or duration, d) have been identified within PFUM, but no variation in these parameters has been considered. Yet subjects may use their knowledge of results to make small, corrective adjustments to the controlled parameter in the course of a block of trials even though the experimental conditions are held constant. Thus, in a more realistic version of PFUM, b might be treated as a random variable, say B, allowing recruitment to vary from trial to trial. In this case, $F_o(t)$ would represent a random number of random variables:

$$F_o(t) = \sum_{i=1}^{B} F_i(t). \tag{43}$$

Probability theory provides several tools to handle this generalization (cf. Ross, 1980, p. 85). Thus, for example, to show that the theoretical results for mean $F_o(t)$ hold under variation in b, one need only replace the constant b by $E[B]$ in the relevant expressions in Equation 44. However, the mathematical treatment of $Var[F_o(t)]$ is more cumbersome. Nonetheless, computations that we have done with b treated as a random variable indicate variance properties that are similar to the predictions set out earlier in this article.

In a preceding section, we explored the implications of PFUM for measures of response time in terms of systematic changes in peak force over different experimental conditions associated with either b or d as the controlled parameter. Although we already noted that Angel (1973) reported systematic changes in mean RT with mean force, it is also relevant that he found no statistically significant relation between response magnitude and RT over a series of trials where stimulus intensity was held constant. The simulation in Table 3 showed that, on average, systematic change in number of FUs results in an increase in peak force and a shortening of RT. In the absence of a negative correlation between peak force and RT, it is tempting to infer that any variation in peak force in the case of Angel's data was not due to random variation in b. However, a check for covariation between RT and T_p (in case of variation in d) would seem advisable before concluding that the observed variation falls within the amount predicted simply by temporal dispersion of onsets as treated in an earlier section. Moreover, in a repetitive responding task, Keele et al. (1987) found small but statistically reliable negative correlations between the peak force of brief isometric responses and the interval (defined on crossing a low threshold) terminated by that response.

Absence of correlation between the time of response and peak force (or time of peak force) would appear consistent with absence of appreciable variation in b or d. However, suppose b and d were true constants. Under PFUM, while the observed force-time function might fluctuate from trial to trial in shape due to temporal dispersion of onsets, one would predict that there should be constancy of the area under the curve. There would, in other words, be a negative correlation between peak force and duration of the force pulse over trials within a condi-

tion. We know of no published data that bear on isometric contractions, although Newell, Carlton, and Carlton (1982) reported significant negative correlations between peak force and force duration under isotonic arm movement conditions. However, in our discussion, we have identified a number of factors that could contribute to variation in b or d and thereby lead to variability in the area under the observed force-time function. The latter source of variability would tend to reduce the negative correlation produced by the temporal dispersion of onsets. It is thus clear that future research into the production of brief force pulses must include analyses of trial-to-trial random variation of this area in relation to the underlying dimensions of control afforded by b and d.

Conclusion

In conclusion, we have shown that with simple mathematical principles it is possible to derive quantitative predictions for the time course of force-time functions and their precision. These predictions have been shown to be in qualitative agreement with a wide range of extant data on the production of brief isometric force impulses. We anticipate that future research will follow a more quantitative approach that would allow fitting of data and estimation of parameters within the model. Nevertheless, even the qualitative approach taken in this review has started to build a bridge across the gap between neurophysiological and behavioral perspectives on that most elemental component of movement, the production of force.

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Appendix A

Glossary

The following is a list of the main symbols and abbreviations used in the order of appearance in the text. Note that symbols in boldface represent random variables. An italic letter followed by ($\cdot$) denotes a function, for example, $f(\cdot)$, whereas an italic letter without ($\cdot$) denotes a constant or a parameter.

Abbreviations

RT	Reaction time
STA	Spike-triggered averaging
MU	Motor unit
EMG	Electromyogram
FU	Force unit
PDF	Probability density function
CDF	Cumulative density function

Random Variables

$\mathbf{F}_0(t)$	Observed force level at time t
$\mathbf{F}_i(t)$	Force contribution of the ith FU at time t
$\mathbf{L}_i$	Latency of the ith FU
$\mathbf{T}(f)$	Motor delay (time to attain force f)
$\mathbf{T}_p$	Time to peak force in a single trial
$\mathbf{F}_p$	Single-trial peak force

Operators, Functions, and Constants

n	Maximum number of FUs
b	Number of FUs recruited on a given trial
t	Time
$u(\cdot)$	Force–time function of a FU
A	Impulse of a FU: Area under function $u(\cdot)$
$z(\cdot)$	The normalized function of $u(\cdot)$
$h(\cdot)$	The convolution of $z(\cdot)$ and $f(\cdot)$
d	FU duration
a	Constant force level of a FU
m	Shape parameter of the Erlangian distribution
ρ	Scale parameter of the Erlangian distribution
$E[\cdot]$	Expectation
$\text{Var}[\cdot]$	Variance
$\text{SD}[\cdot]$	Standard deviation
$f(\cdot)$	PDF of L
$F(\cdot)$	CDF of L
t_p	Time of peak force of mean-force time function
t_m	Time of maximum force variance of variance-force time function
f_1, f_2	Predetermined force levels with $f_2 > f_1$

Appendix B

Proof of Equations 36 and 37

The force contribution $F_i(t)$ of a tonic FU at time t is defined by

$$F_i(t) = \begin{cases} 0 \text{ for } t \geq L + d \\ a \text{ for } t < L + d. \end{cases} \qquad (A1)$$

Hence, the mean of $F_i(t)$ is

$$E[F_i(t)] = 0 \cdot \Pr\{L + d \leq t\} + a \cdot \Pr\{L + d > t\}$$

$$= a \cdot [1 - \Pr\{L + d \leq t\}]$$

$$= a \cdot [1 - F(t - d)]. \qquad (A2)$$

The variance of $F_i(t)$ is computed in an analogous manner:

$$\text{Var}[F_i(t)] = E[F_i(t)^2] - E[F_i(t)]^2$$

$$= a^2 \cdot [1 - F(t - d)] - a^2 \cdot [1 - F(t - d)]^2$$

$$= a^2 \cdot [1 - F(t - d)] \cdot F(t - d). \qquad (A3)$$

Let $F_T(t)$ be the total force produced by all b_T tonic FUs; then

$$E[F_T(t)] = b_T \cdot a \cdot [1 - F(t - d)] \qquad (A4)$$

and

$$\text{Var}[F_T(t)] = b_T \cdot a^2 \cdot [1 - F(t - d)] \cdot F(t - d). \qquad (A5)$$

The total force produced by all b_P phasic FUs is denoted by $F_P(t)$. Note that the mean and the variance of $F_P(t)$ must be identical to Equations 13 and 32, respectively. Because $F_o(t) = F_T(t) + F_P(t)$, we add Equations A4 and 13 to compute $E[F_o(t)]$. Likewise, we add Equations A5 and 32 to compute $\text{Var}[F_o(t)]$. After simplifying, the desired results are obtained. The proof is complete.