# Force fluctuations in a simulated motoneuron pool

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*Abstract*— **Force fluctuations, even for maintained isometric force, have many origins and are attributed to noise, errors and variabilities associated with different elements of the sensory-motor system. Part of the random-like fluctuations of the force is due to the motor pathway per se and much work has been focused in quantifying the fluctuations and in determining their dependence on variables such as number of motor units, discharge rate variability of each motor unit, etc. A recently developed simulator of the neuromuscular control system was utilized here to verify stochastic features of the simulated force signal generated by the soleus muscle for different mean force levels. The mean force level increased in a sigmoidal fashion as the intensity of the descending drive increased. The standard deviation of force as a function of mean force level resulted in an approximate parabola, while the coefficient of variation of force decreased monotonically with mean force level. Force power spectrum was strongly concentrated in the 0-5 Hz frequency range. Individual motor unit force signals showed a tendency for decreased force variability as overall muscle force level increased, helping to explain the relation found between muscle force variability and mean muscle force. Comparisons are made with results from the literature of simulations of other muscles and the differences and similarities are discussed.**

*Keywords*— **force variability, motor units, neuronal models, neuromuscular system.**

## I. INTRODUCTION

Normal subjects exhibit fluctuations in force along time (called here force variability for short) when pushing or pulling against a fixed object [1,2]. Excessive force variability, e.g., due to disease, hampers the performance of movements and may lead to difficulties in keeping the appropriate posture to avoid falls. For the few muscles that have been tested, the literature shows that the standard deviation of a force developed against a fixed object exerted with a constant volitional effort increases with the mean value of the force [3]. On the other hand, the force coefficient of variation has usually been found to decrease with the intensity of the exerted force [1,3]. Mathematical modeling and simulation have been important tools in the study of the mechanisms behind the experimental results reported in the literature concerning force variability [3-6]. The objective of the present paper was to investigate how features such as the standard deviation and coefficient of variation of force vary as a function of force in a recently developed comprehensive neuromuscular model of leg muscles and their neural control [7]. Previous investigations in the literature on force variability employed a popular phenomenological model [8]. In this model, the spike trains of each motoneuron have their statistical features appropriately defined to mimic those found in nature. In the new model [7] each motoneuron is modeled as a two-compartment dynamical system with parameters based on biophysical data. The motoneuron pools are driven by several dozens of axons, each carrying a Poisson point process.

## II. MATERIALS AND METHODS

### A. The simulator

The soleus muscle was controlled in the simulator by 900 motoneurons, 800 being of type S, 50 of type FR and 50 of type FF. The individual motoneurons were represented by two-compartment models with fast and slow dynamics in the soma and a passive dendritic compartment [7]. The Hodgkin-Huxley-like dynamics were approximated by the pulse activation method [9] for computational efficiency. The synaptic inputs activated dendritic conductances according to a two-state kinetic model [10], which provided computational efficiency and good biological reality. The descending drive was enacted by 100 axons, each carrying an independent Poisson process spike train. Each of these axons activated a randomly selected fraction of 20% of the motoneuron pool. A motor unit twitch was implemented as the impulse response of a critically damped second order system.  The peak amplitude ranges of the twitches employed in the simulations were the default values given in the simulator: from 10.5 to 12.5 gf for the S type motor units, 12.5 to 30.0 gf for the FR type motor units and 30.0 to 50.0 for the FF type motor units.

### B. Procedures

All possibilities of random parameter variations were disabled prior to starting the simulations so that a similar network could be used for every simulation run. The mean interspike interval values of each Poisson process of the corticomotoneuronal pathway were varied from 1 ms to 10ms, which means that the mean rate of each descending axon was varied from 100 Hz to 1000 Hz. This range approximately covered the generation of contraction forces varying from 0 up to about 80% the maximum muscle force ($f_{max}$). The value of $f_{max}$ was measured from a simulation where the nerve to the muscle was stimulated by a 100 Hz train of pulses. In the simulations reported here, no Renshaw cells were included, so the motoneuron pool responded only to the drive from the corticomotoneuronal pathway. In spite of the stochastic nature of the system, only a single

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simulation run was used to obtain the force signal corresponding to a given parameter set due to the long times involved in any simulation.

## III. RESULTS

Following the activation of the descending Poisson trains the force increased towards a plateau value, around which it oscillated randomly. Fig. 1 shows several force signals in response to different levels of fixed intensity descending drive. The bottom signal was generated in response to a 133 Hz mean rate of Poisson per axon while the uppermost was due to a 1000 Hz Poisson drive per axon.

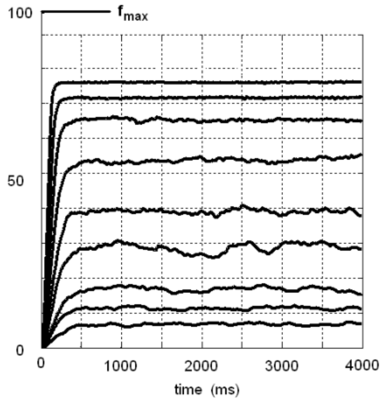

Fig. 1 Muscle force as a function of time for different activation levels, increasing from bottom to top. The ordinate is a percentage of $f_{max}$.

The two highest levels of force corresponded to the recruitment of the first 800 and 850 motoneurons, respectively. This means that only for the 1000 Hz Poisson descending drive trains did the FR motoneurons get recruited. For all the other mean rates of the Poisson drive trains only the type S motoneurons were recruited. The increase in force level in response to the increase in descending drive intensity followed a sigmoidal-like relation, as shown in Fig. 2.

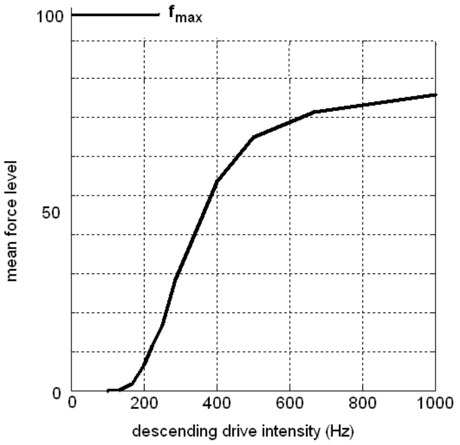

Fig. 2 Mean muscle force level as a function of the intensity of the descending drive (the mean rate of each of its Poisson spike trains).

There was an increase in force variability up to medium levels of force followed by a decrease when the mean force levels were larger. This can be seen qualitatively in Fig. 1, and quantitatively in Fig. 3.

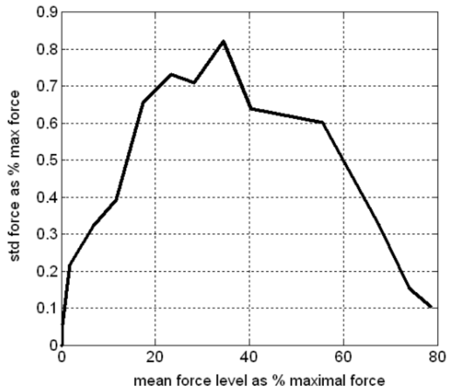

Fig. 3 Standard deviation of force as a function of the mean force, both indicated as a percentage of the maximum force.

On the other hand, the relation between the coefficient of variation (CV=standard deviation/mean) and the mean force followed a hyperbolic type of relation (Fig. 4).

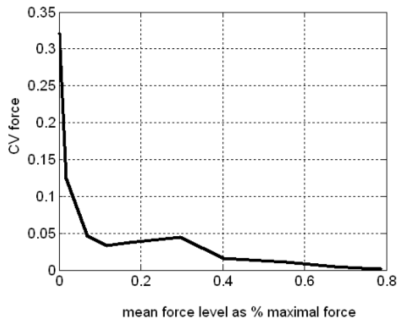

Fig. 4 Coefficient of variation of force as a function of the mean force, the latter indicated as a percentage of the maximum force.

Next, an analysis was made of the CVs of the forces generated individually by the motor units 1, 267, 533 and 800 from the pool. These were chosen equispaced in terms of their mean recruitment thresholds. Two points were chosen arbitrarily on the ascending limb of the curve of Fig. 3 and two on the descending limb. The corresponding descending drive intensities were found to be 200 Hz, 250 Hz, 400 Hz and 500 Hz, respectively. The resulting values of motor unit force CV in percentage may be seen on Table 1. These results suggest that a given motor unit tended to decrease its force variability in the model as the drive intensity increased, or (from Fig. 2) as the muscle mean force level increased. On the other hand, at a fixed drive intensity, the higher threshold MNs tended to command forces with higher CVs.

Table 1 Coefficient of variation (in %) of force generated by individual motor units 1, 267, 533 and 800 for descending drive frequencies shown on the first line (Poisson rate per descending axon). In three cases the motoneuron did not fire, so the CV is not defined.

| | 200 Hz | 250 Hz | 400 Hz | 500 Hz |
|---|---|---|---|---|
| MN 1 | 98.80 | 4.73 | 2.50 | 1.45 |
| MN 267 | 10.77 | 11.55 | 7.18 | 1.28 |
| MN 533 | -------- | 32.4 | 12.6 | 2.21 |
| MN 800 | -------- | ------- | 11.41 | 2.26 |

Finally, for a mean force level about 60% MVC (point in the descending limb in Figure 3) the power spectrum of the force signal (taken in the 1-4s interval) resulted as shown in Figure 5. Power was concentrated at low frequencies, 73% of the total power being in the range from 0 to 4 Hz.

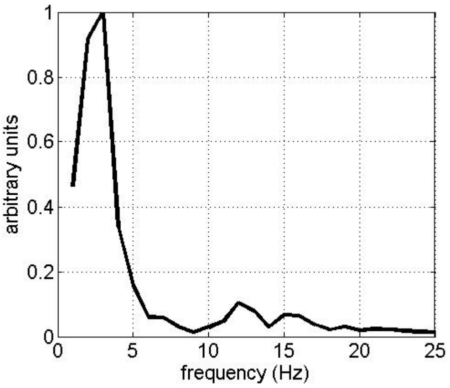

Fig. 5 Force power spectrum estimated by Welch's method for a force level about 60% MVC.

## IV. DISCUSSION

Initially, the results will be compared with those described in the literature using the phenomenological model of [8]. The force curves in Fig. 1 resemble those described in [1,5] except for the smaller variability found here for the higher force signals (see below). The sigmoidal-like relationship between force and descending drive intensity shown in Fig. 2 is similar to that described in [1]. Simulations with specific model parameter values reported a monotonic increasing function relating force standard deviation to mean force [1,3] while others reported a peaking or saturation-like effect at higher force levels [5,6]. The result in Fig. 3 is not in accordance with these previous results from the literature. However, Keenan et al [4] ran an extensive Monte Carlo simulation using wide parameter ranges for the phenomenological model and found a large number of curves reminding that in Fig. 3, i.e., showing an initial increase in force standard deviation followed by a decrease. These same authors reported that only for narrow parameter ranges could they find reasonably good agreement between experimental and simulated data on the basis of functions that related variables such as those in Fig. 3 as well as others. The CV as a function of mean force curve of Fig. 4, resembling a hyperbolic curve, was similar to previous reports [3,1]. Finally, the force power spectrum shown in Fig. 5 was similar to those shown in [5] for experimental data (50% MVC) from a small hand muscle and for a specific computer simulation that included a 1Hz frequency modulation of the descending drive. Here, our power spectrum was obtained without any modulation of the descending drive. In [6] the authors obtained a spectrum with a power concentration as shown in Fig. 5 when the motor units were simulated with a "high" level of synchronism.

It is important to point out that, except for [4], the other papers adjusted the model parameters to yield appropriate fittings to experimental curves relating standard deviation and coefficient of variation of force as a function of mean force. The muscles involved were usually small hand muscles. In the simulations reported here, practically the default values of the simulator were employed, as found in www.remoto.leb.usp.br and in [7].

The results based on the simulations are useful from at least two perspectives: *i* allowing the analysis of the influences of the elements, parameters or variables of the system on the force variability, *ii* giving predictions of how the given muscle should behave if the modeling hypotheses are appropriate. With respect to the latter, an additional important consequence is that if experimental data are not reproduced well by the simulations, new hypotheses are generated, which point to new experiments, to improvements in the modeling and perhaps to conceptual changes.

The results reported here have not dealt with the problem of evaluating the effects of different model features or parameter values on force variability. There were some efforts in the literature to study the influence of different parameters of the neuromuscular system on force variability [1,3-6] based on the phenomenological neuromuscular model of [8]. Number of motoneurons in the pool, the relation between twitch peak of the largest motor unit and that of the smallest motor unit, the level of discharge irregularity of the motoneurons and the degree of synchronism between the motoneurons were all shown to have significant effects on force variability. A similar effort seems worthwhile using the new model proposed in [7] but is outside the scope of the present paper. However, from some of the data presented here, one can grasp why the standard deviation versus mean force curve showed a falling limb (Fig. 3). In Table 1 one sees that for increased muscle force level (i.e., higher descending drive) the force variability of each motor unit decreases. One reason is that the motoneurons tend to fire more regularly (not shown). In addition, at higher descending drives, the motor units tend to show a fused force signal near to its maximum (saturated) level (not shown), which also yields a lowered force variability. The difficulties of a mathematical approach to predict the muscle force variability in terms of the various elements of the neuromuscular system stem from the fact that the system is of high dimensionality, nonlinear and stochastic.

On the issue (*ii*) of the usefulness of simulation results in predicting an experimental outcome, the results presented here stand as a conjecture. This is so, because, to the author's knowledge, there is no experimental data available on the force variability behavior of the human soleus muscle. However, if the experimental results should indicate an increasing relation between the standard deviation of force and the mean force level (as has been found in other muscles with a less homogeneous fiber-type composition), then the present neuromuscular model would have to be changed either in terms of its parameter values (e.g., larger ranges of twitch peaks along the motoneuron pool as in [1]) or in its structure. Hence, the results shown in the present paper are a point of departure for future research that will try to integrate experimental and simulation data to further our understanding of motor control of the lower limbs in humans.

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