Motor unit firing statistics and the Fuglevand model

To the Editor: In the May 2005 issue of the Journal of Neurophysiology, Moritz and coworkers report new findings on human motor unit properties during voluntary isometric contractions. A unique contribution of this paper is the extensive range of voluntary forces (4–85% MVC [maximal voluntary contraction]) used to explore the correlations between recruitment and discharge rates. Those familiar with isolating single units from needle/fine-wire EMG recordings will appreciate the difficulty of getting stable discrimination of units at these high contraction levels. The experimental data were then used to update some parameters in the Fuglevand motor unit model (Fuglevand et al. 1993), resulting in better predictive value of the model when compared with the experimentally measured relationship between mean force and its variability (see Fig. 6E, Moritz et al. 2005).

The definitive data set for the hypotheses addressed in the paper would require simultaneous recording of multiple motor units from a single subject across the full range of forces, and repeating this in a number of individuals. Because such heroism remains mythical, Moritz and colleagues take the next best approach: data from 38 units recorded from 18 subjects were normalized to % MVC. It is unfortunate that in Table 1 there is no indication whether any of the units were recorded from the same subject in a single experiment because this may well have added some anecdotal support to the conclusions.

Arguably, the most important changes to the model arising from the experimental data include: 1) setting minimal rhythmic firing rate proportional to recruitment threshold; 2) setting maximal firing rate proportional to recruitment threshold; and 3) making the coefficient of variation (CV) of the interspike intervals (ISIs) a function of recruitment threshold. The first modification is a refreshing innovation for the Fuglevand model that has a broad basis of support in previous animal and human literature (e.g., Erim et al. 1996; Gossen et al. 2003; Kernell et al. 1999).

With respect to the second modification, I believe a word of caution is warranted before modelers implement this change. As the authors state, their estimates of peak discharge rate are complicated by the ability to reliably discriminate single units over the full contraction range (Fig. 4 legend, Mortiz et al. 2005). A methodological bias could result in underestimation of the peak discharge rate in motor units with low recruitment thresholds arising in part from the rapidly deteriorating signal-to-noise ratio of intramuscular EMG with increased voluntary force. In addition to this potential methodological bias, the 12 units that the authors select for a clear plateau in discharge rate (Fig. 4, inset, Mortiz et al. 2005), are perhaps significantly correlated with recruitment threshold only as a result of the one data point near 60% MVC on the x-axis. Thus it may be prudent to await additional evidence of the linear relationship between peak discharge rate and recruitment threshold before the ubiquitous “onion-skin” phenomenon (De Luca and Erim 1994) is eliminated from the Fuglevand model.

The last modification is also of some interest because it addresses the issue of the relationship between variability and mean firing rate. It is often incorrectly asserted that firing rate variability decreases with an increase in mean firing rate and the naive reader may find justification for this assertion in the abstract and discussion sections. Histograms of ISIs for many neurons recorded in vivo show a skewed probability distribution that is often fit to a Poisson or gamma function. This is also true for motoneurons firing near their minimal rhythmic firing rate. As the excitatory drive to a motoneuron is increased, the mean ISI decreases and the ISI histogram loses its skew. The ISI histogram is now better fit by a normal or Gaussian distribution (Clamann 1969; Fuglevand et al. 1993). With further increases in excitatory drive, the mean ISI decreases and the width of the histogram, quantified by the SD, also decreases. Typically a plot of SD versus mean ISI is used to illustrate this relationship (Person and Kudina 1972) and has been fit with a straight line indicating a constant coefficient of variation of about 20% (see Fuglevand et al. 1993). Perhaps intuitively it would seem that the low SD at small values of mean ISI, i.e., at faster firing rates, indicates that firing rate variability has decreased. However, by inverting the interval data to obtain the firing rate it can be verified analytically that this will result in the SD of firing rate increasing as the square root of the mean (see Stein et al. 2005). I suggest that when comparing statistical measures the best practice is to compare like with like—ISI variability-to-mean ISI or rate variability-to-mean rate—because it is helpful to have axes in the same units and it facilitates comparison to the literature on stochastic point processes.

The data from the three units in Fig. 3 (Moritz et al. 2005) are replotted here to illustrate that the data conform to the expected qualitative distribution for the statistical behavior of human motor units during isometric contractions. The explicit

![Interspike Intervals](image)

FIG. 1. Data from the 3 units in Fig. 3 of Moritz et al. (2005) were measured and replotted. A linear regression was calculated for unit 6 and a curved line was calculated using Eq. 1 and the resampled data. Traditionally the above relationship has been fit with a straight line, indicating a constant CV for the interspike interval. The authors demonstrate that it may be time to revise the constant CV assumption in favor of a CV that varies with the mean (curved line). Perhaps not intuitive from the figure is the fact that if the axes were plotted as the SD and mean discharge rate, the regression line would also show a positive correlation. That is, firing rate variability, measured by the SD, increases as a function of mean rate, not the opposite as is often stated (Stein et al. 2005).
suggestion by Moritz and colleagues is that this relationship is better explained by an exponential fit (Eq. 1, Mortiz et al. 2005) rather than the typical linear regression. I would have preferred having Eq. 1 expressed with \( CV_{\text{ISI}} \) as a function of recruitment threshold expressed as excitatory input (RTE in Fuglevand et al. 1993) rather than force output. The latter formulation seems akin to putting the cart before the horse. Aside from this, by adding this subtle tweak the model output more closely approximates the experimental data (Fig. 6E, Mortiz et al. 2005).

If the nonlinear relationship between the SD versus mean ISI continues to be upheld experimentally, I speculate that the resulting increase in motor output variability at low forces may have broad impact for optimal control theories of sensorimotor systems (Scott 2004; Todorov 2005).

**REFERENCES**


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**REPLY**

To the Editor: The study by Moritz et al. (2005) demonstrated significant improvements in the performance of the Fuglevand model at matching the force fluctuations that occur during steady contractions by implementing a decreasing coefficient of variation (CV) for motor unit discharge with increases in muscle force. The exponential decline for discharge rate variability was derived from recordings of individual motor units discharging across a wide range of forces.

As suggested by Jones, it is appropriate to display variability on axes with the same units, and the figure in Panel A shows the relation between SD and mean interspike interval (ISI). As evident from the scatter in this plot, however, it is difficult to fit a single equation that describes this relation. Instead, by plotting the SD of ISI relative to the force above recruitment threshold (Panel B), the exponential relation becomes obvious. Consequently, the Fuglevand model was revised to include variability in motor unit discharge relative to force above recruitment threshold.

Interpretation of the relation between SD and mean ISI is complicated by the saturation in motor unit discharge rates. As motor units approach peak levels of activation, there is a progressively smaller increase, or even a plateau, in discharge rate. This results in little change in ISI for each motor unit at short intervals and obscures the plateau that is reached in discharge variability. This plateau in variability is evident as the clustering of data points between 5 and 10 ms in Panel A and the associated ‘tail region’ is obvious for motor units #25 and #38 that were re-plotted by Jones, as well as most motor units in the Moritz et al. study. Consequently, the linear fit to the relation between the SD and mean ISI does not capture information about discharge variability at forces when motor unit discharge rates are near maximal.

Jones has also suggested that variability in motor unit discharge might have been better expressed in terms of the excitatory input delivered to the motor neuron pool. The advantage of the approach used by Moritz et al., however, is that finger force was directly measured experimentally, and the relation between exci-

**FIG. 1.** Two forms of displaying discharge rate variability of single motor units. A: The SD relative to the mean interspike interval (ISI) for the 38 motor units followed over a range of forces in Moritz et al. (2005). B: The same data are plotted as a function of index finger force above the recruitment threshold of each motor unit.
tation and force is not conserved in the model when motor unit 
number, recruitment range, or twitch force range are varied.

Regardless of how the data are presented, it should be noted 
that a linear relation between the SD and mean ISI does not 
necessarily indicate a constant coefficient of variation (CV = 
SD/mean). The relation between the SD and mean has to be 
linear and proportional for the coefficient of variation to be 
constant. For motor unit #6 re-plotted by Jones, the coefficient 
of variation for ISI was 2.5 times greater at long ISIs compared 
with short ISIs, despite a nearly linear relation. Furthermore, 
the Moritz et al. data do not display the purported relation in 
which the SD of discharge rate increased as the square root of 
the mean discharge rate (Stein et al. 2005).

The demonstration that discharge rate variability decreased 
rapidly as force rose above recruitment for each motor unit was 
the major factor resulting in a close match between simulated and 
experimentally measured force variability across the entire work-
ing range of the muscle. Of far less consequence to this aspect of 
the model’s performance were the observations that minimal and 
peak discharge rate increased with recruitment threshold. Reliable 
recording of maximal discharge rate is difficult, and both the 
discrete isometric contractions used by Moritz et al. and the 
continuous ramp contractions used in other studies suffer from 
limitations. During ramp contractions to 40% or 80% MVC, for 
example, the force at the peak of the ramp may not be sufficiently 
high to elicit maximal discharge rates from high-threshold motor 
units, which could lead to the conclusion that high-threshold 
motor units have lower maximal discharge rates (De Luca et al. 
1982). As emphasized by Moritz et al., the relation between 
maximal discharge rate and recruitment threshold remains an 
unresolved issue and probably depends on the task in which these 
measurements are made. Nonetheless, the recordings of single 
motor unit activity by Moritz et al. provided clear evidence of 
alterations in the relative variability of discharge rate within 
individual motor units.

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