The Control of Motor Units does not maximize Force Production

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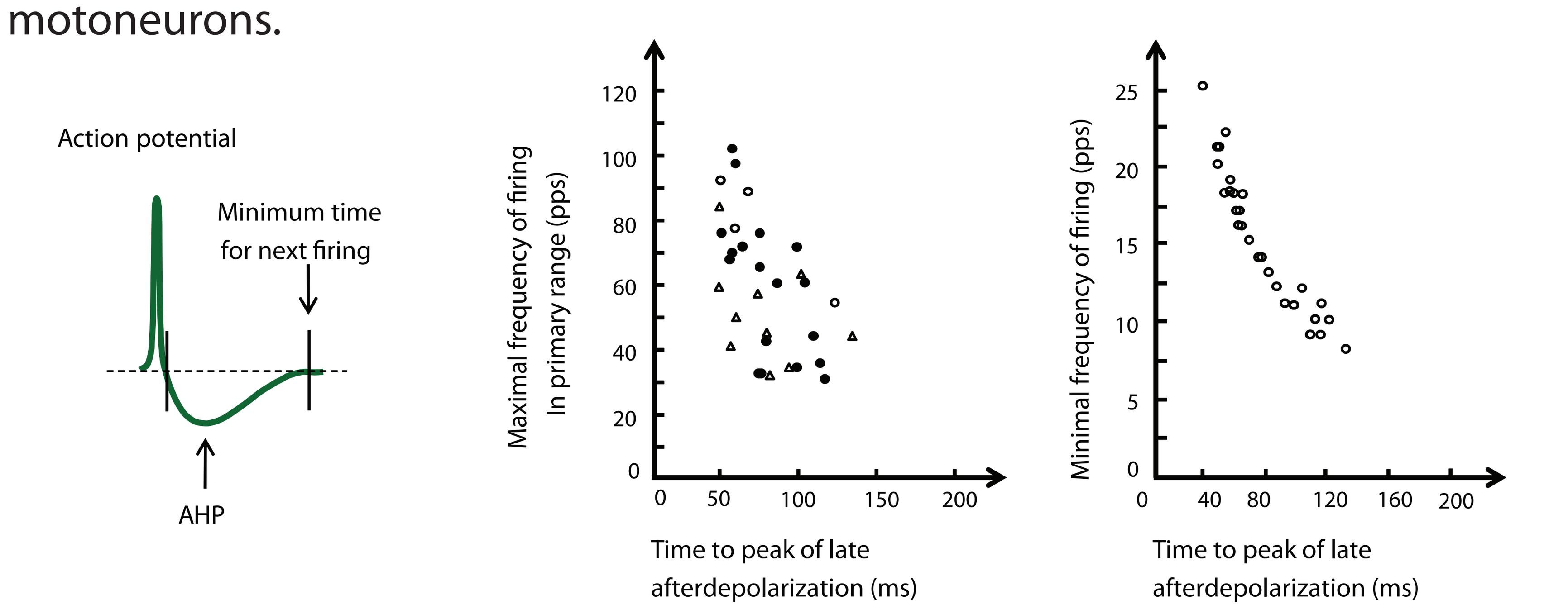
INTRODUCTION

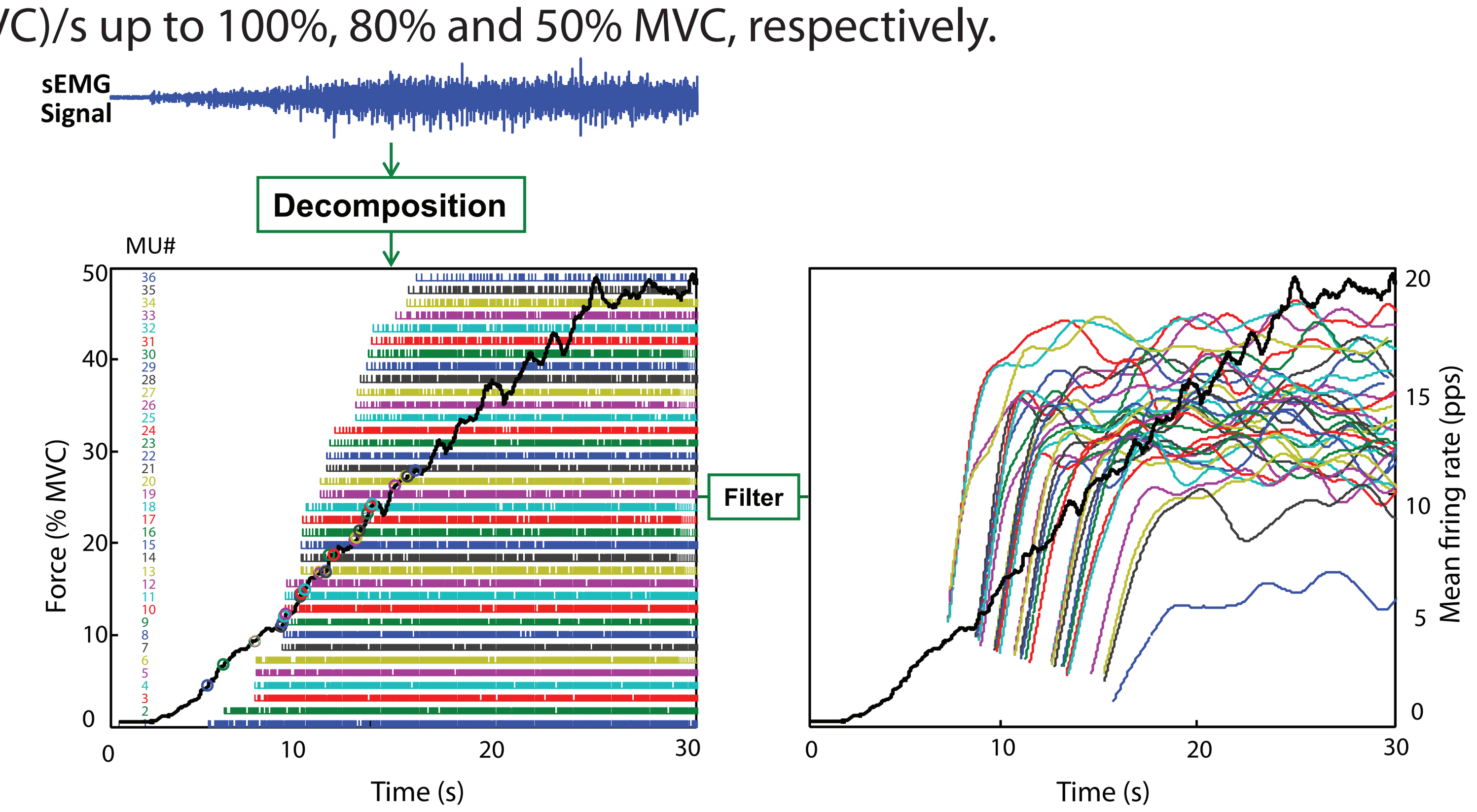
Early studies of the firing behavior of **electrically stimulated** animal motoneurons [Kernell 1965, Eccles et al. 1958] have generated the widely accepted hypothesis of a direct relationship between motoneuron firing rate and after-hyperpolarization (AHP).
It has been posited that the after-hyperpolarization determines motoneuron firing rate, leading to greater firing rates in phasic (higher-threshold, larger-diameter) motoneurons and lower firing rates in tonic (lower-threshold, smaller-diameter) motoneurons.



Figures adapted from Kernell D. (1965): The lower and higher firing rate limits of motoneurons are correlated with the motoneuron AHP.

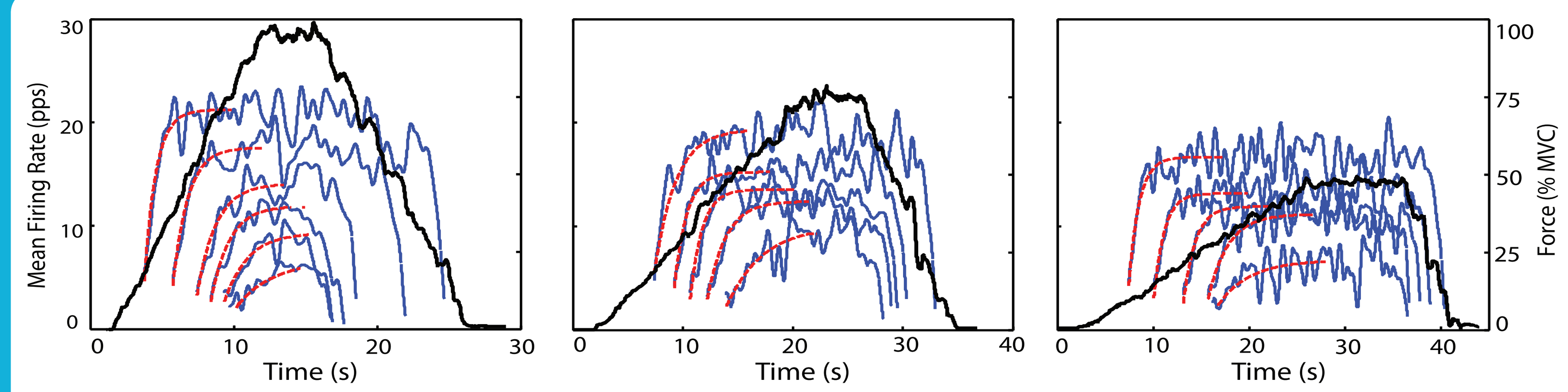
METHODS

We investigated motor unit (MU) firing behavior in 8 healthy human subjects (19-35 yr) performing **voluntary isometric contractions** with the First Dorsal Interosseous (FDI) muscle of the hand and the Vastus lateralis (VL) muscle of the quadriceps. Muscle force increased at a rate of 10%, 4% and 2% maximum voluntary contraction (MVC)/s up to 100%, 80% and 50% MVC, respectively.

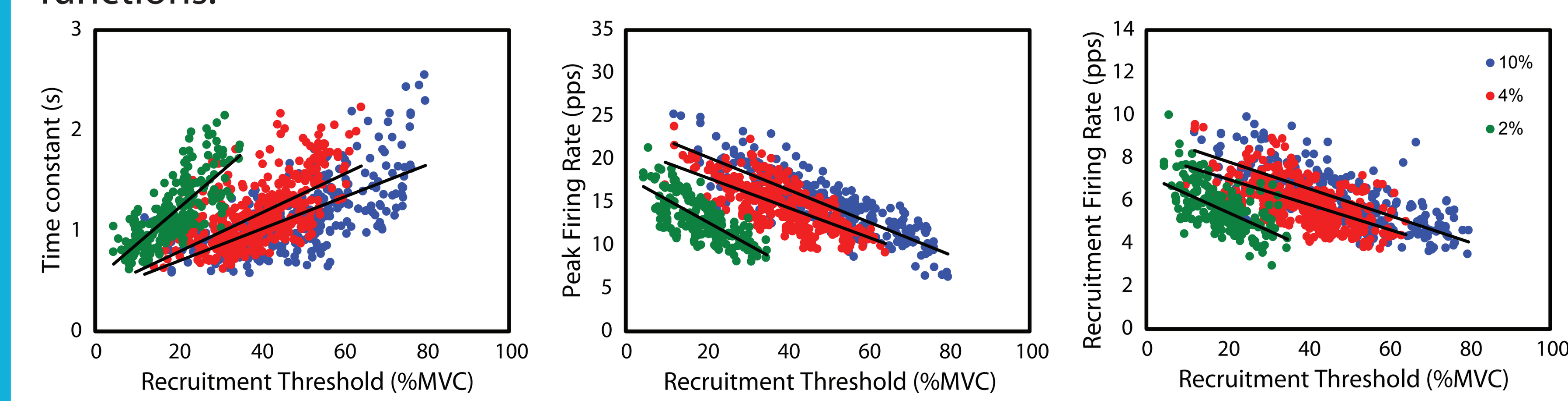


Analysis: Surface electromyographic (sEMG) signals were recorded during the force contractions and decomposed into the constituent MU action potential trains using the algorithm recently developed by De Luca et al. (2006) and Nawab et al. (2010). The mean firing rates of the MUs were calculated from the firing trains and the 1) firing rate at recruitment; 2) peak firing rate; 3) rate of firing rate increase were analyzed as a function of time and muscle force.

EXPERIMENTAL RESULTS



Firing Rate Trajectory (VL): The firing rates of MUs increase as negative exponential functions.



Trajectory Parameters (VL): The parameters of the firing rate trajectories, presented here for the VL muscle, may be expressed as a function of the recruitment threshold of the MUs: as a negative linear function for the firing rates at recruitment and peak firing rates, as a positive linear function for the time constant. The trajectory is only weakly influence by the force rate in the interval analyzed.

MODELING RESULTS

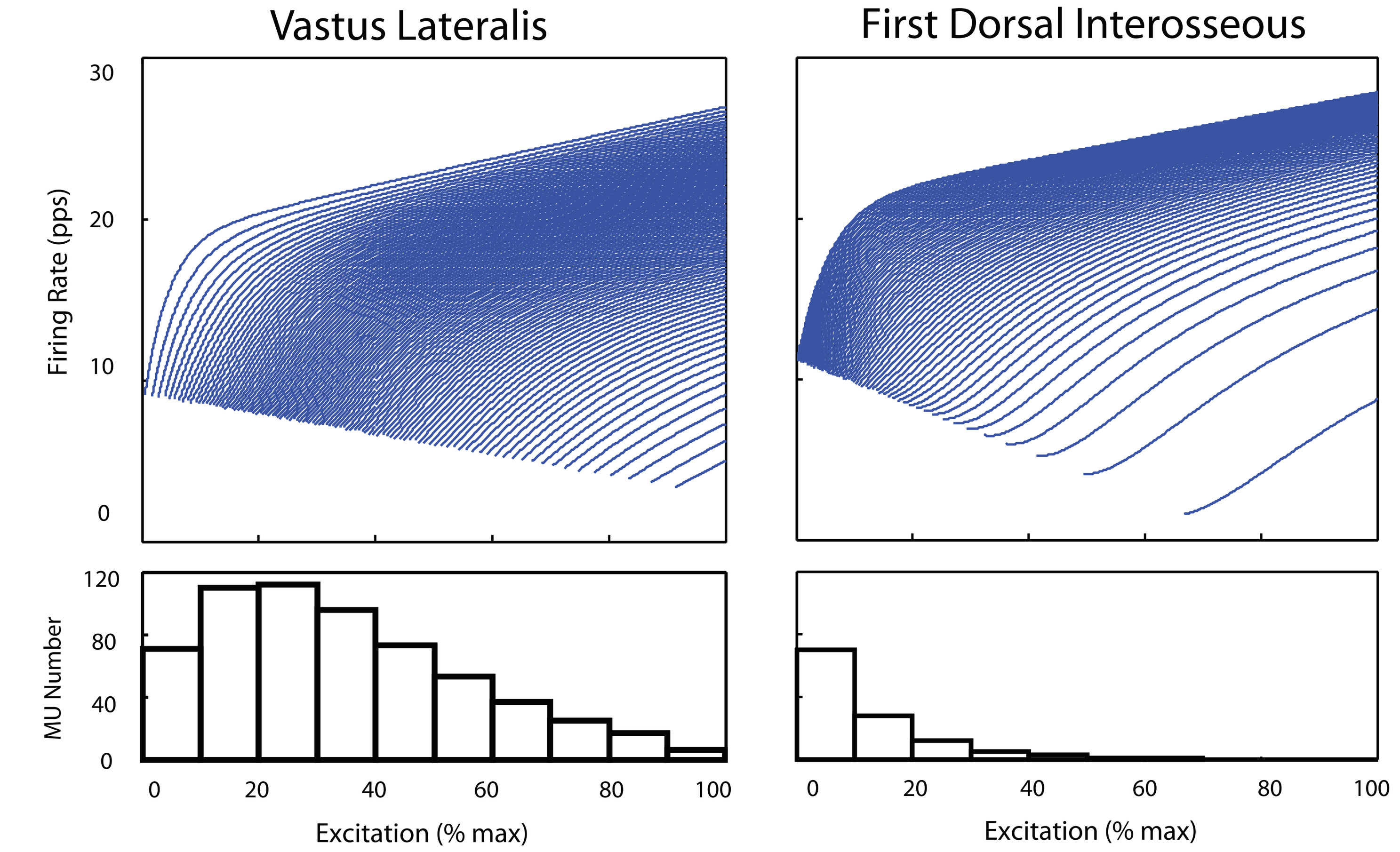
Firing Rate Spectrum: At any time and force, MU firing rate is inversely related to the recruitment threshold. This behavior was modeled in a set of equations.

For the VL muscle [De Luca & Hostage 2010, De Luca & Contessa 2012]:

$$\lambda_i(t,\varphi,\tau_i)=19+8\varphi-(21+116e^{-\varphi/0.2})\tau_i-e^{(\tau r_i-t)/1.6\tau_i+0.4}[9.9+8\varphi+(-14.7-116e^{-\varphi/0.2})\tau_i]$$, and

$$\%\text{active MUs} = 0.0058s\varphi(1\text{-}360e^{-5.9\varphi})+100(1-e^{-9.5\varphi})$$, with

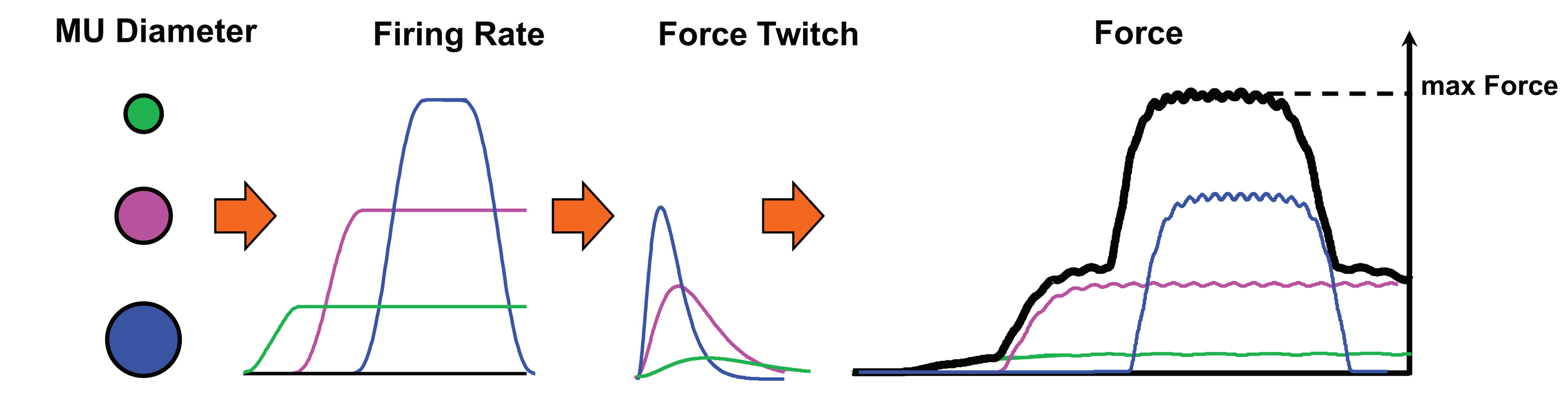
φ: normalized excitation to the motoneuron pool, $0<\varphi<1$
λ_i: firing rate of MU i at the excitation level φ
τ_i: recruitment threshold of MU i, with $0<\tau_i<0.95$ and $\tau_i+1>\tau_i$
s: number of spindles in the muscle (here s=440 [De Luca & Kline 2012])



CONCLUSIONS

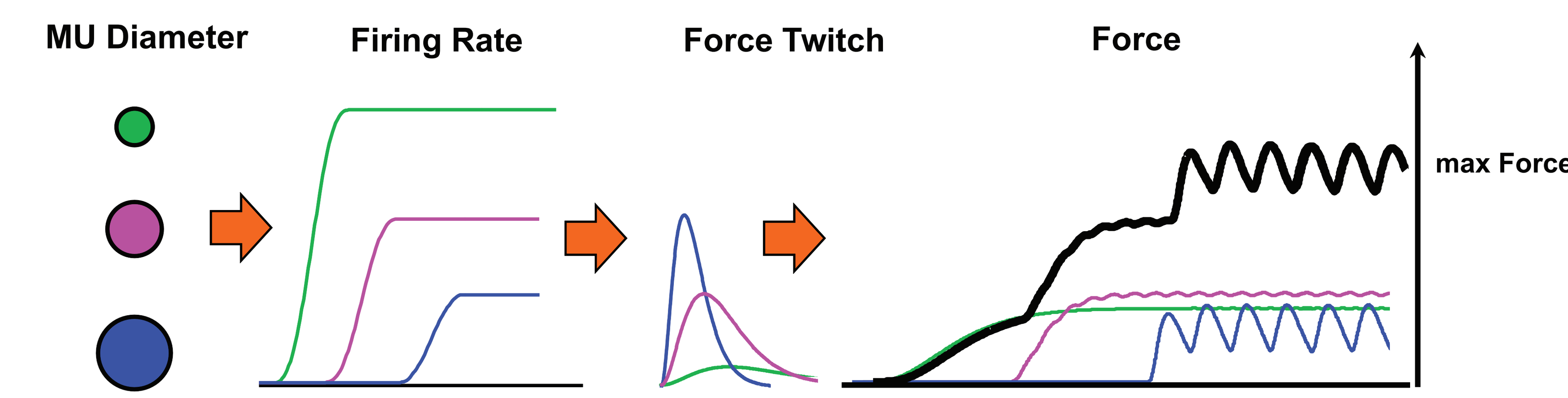
We believe that the disparate reports between our results obtained from human subjects performing voluntary contractions and the early studies performed on animal motoneurons stem from a different behavior of motoneurons when they are electrically vs. voluntarily activated.

Firing behavior of electrically stimulated motoneurons: Larger-diameter later-recruited motoneurons may have the capacity of firing at greater rates than smaller-diameter earlier-recruited MUs. This firing scheme maximizes muscle force and it provides smoother force (MU force twitches tetanize). However, the force cannot be sustained for long periods of time: the fast-firing later-recruited MUs fatigue fast.



Firing behavior of motoneurons during voluntary contractions: The higher-threshold, higher-amplitude and shorter-duration force-twitch MUs fire at lower rates and do not tetanize. This hierarchical control scheme:

- *does not enhance force, but a combination of force and time duration;*
- *provides effective force generation for the earlier-recruited MUs;*
- *reduces the fatigue of later-recruited MUs;*
- *when a high force is required, force smoothness is sacrificed for force sustainability.*



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