Advantages of the Onion-Skin scheme of motor unit firing during voluntary contractions

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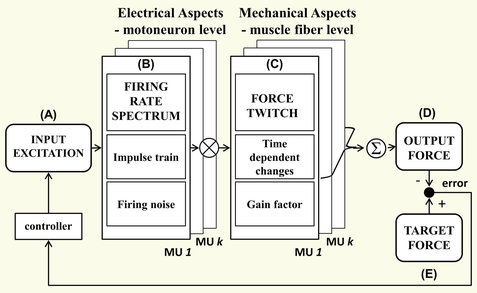
INTRODUCTION

Over the past five decades, the notion that higher-threshold shorter-after-hyperpolarization (AHP) motoneurons have greater firing rates than lower-threshold longer-AHP ones has been commonly accepted. This notion, here named the **AHP scheme**, derived from observations in electrically stimulated cat motoneurons and supports the assumption that motor unit (MU) firing rates match their mechanical properties to "optimize" force generation [1,2]. That is, lower-threshold MUs have wider and smaller force twitches that require lower firing rates to tetanize.
In contrast, we have shown that earlier-recruited MUs maitain higher firing rates than later recruited ones during voluntary isometric contractions, resulting in an inverse orderly hierarchy of firing rate curves named the **Onion-Skin scheme** [3-5].

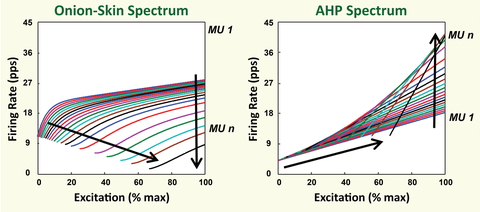
The purpose of this study is to use a novel model of muscle force generation [6] to compare the force characteristics produced by the two schemes during constant-force contractions in the first dorsal interosseous (FDI) and vastus lateralis (VL) muscles.

METHODS

The model used for the simulation of the MU firing rate and force behavior is a modified version of that developed by Contessa and De Luca (2013) for the FDI and VL.



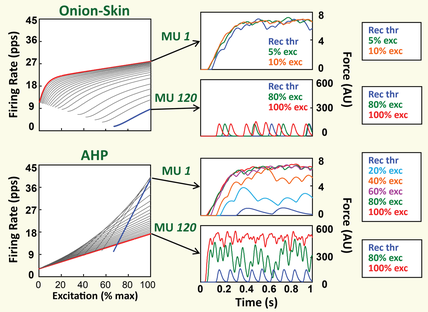
Force Model Schematic: (A) The input excitation drives the firing behavior of all MUs in the muscle. **(B)** The firing rate spectrum describes the firing behavior of MUs as a function of input excitation. **(C)** The force twitch spectrum describes the MU mechanical properties. **(D)** Muscle force output is the summation of the force contrIbutions of all MUs. **(E)** A force feedback allows simulation of force sustained at given targets.



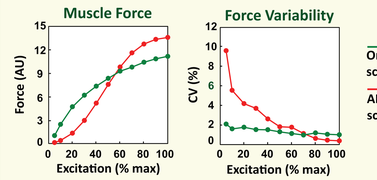
Firing Rate Spectra: Onion-Skin) The spectrum was derived from empirical data from voluntary isometric linearly-varying/constant contractions in humans [6]. **AHP)** The spectrum was modeled based on the hypothesis that MU firing rates provide "optimal" force twitch fusion for all MUs [1,2].

MU firing rates and force were simulated at constant levels of input excitation ranging from 5 to 10% and increasing to 100% maximal excitation in steps of 10% for both schemes. At each input excitation level, we calculated: a) the number of active MUs; b) their firing rate; c) their force output; and d) the force output of the whole muscle.

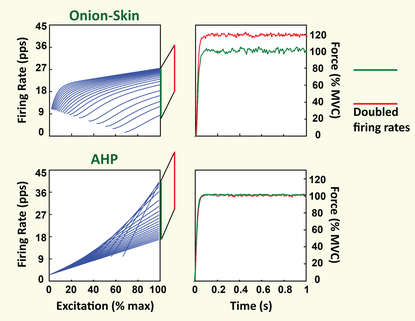
SIMULATION RESULTS (FDI)



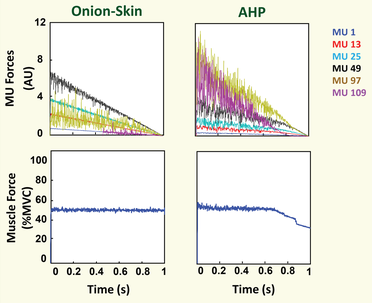
Low- vs. High-threshold MU Forces: Onion-Skin) The force generated by the earliest recruited MU is fully fused within 5% input excitation from its recruitment. The force generated by the last recruited MU does not fully fused even at maximal excitation.
AHP) All MUs fuse around maximal input excitation.



Force Generation Capacity & Force Variability: The Onion-Skin scheme produces more absolute and smoother force than the AHP scheme up to 60% input excitation. When approaching maximal excitation, the AHP scheme can produce greater and smoother force.



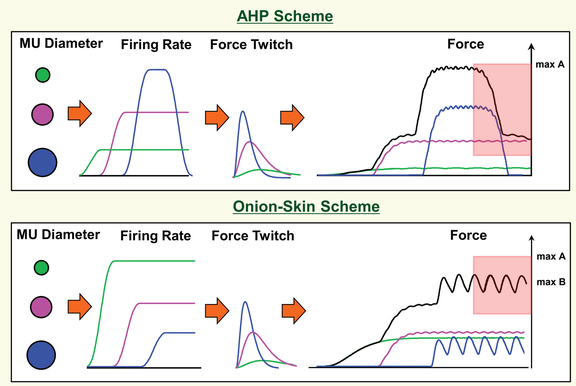
Maximal Force Generation Capacity: Onion-Skin) If MU firing rates are artificially doubled from their values at maximal excitation, the whole muscle force output increases from the value at maximal excitation by ~ 20% MVC.
AHP) MUs are fully fused at 100% excitation. Hence, muscle force output cannot increase even if MU firing rates are increased from their vaue at maximal input excitation.



Muscle Endurance Time: During a simulated contraction sustained at 50% maximum voluntary contraction, the forces of the individual MUs, and consequently the force of the whole muscle, decline faster for the higher-threshold faster-firing MUs in the AHP scheme than in the Onion-Skin scheme. The endurance limit is reached earlier in the AHP scheme than in the Onion-Skin scheme.

CONCLUSIONS

Our results for both the FDI and the VL show that the Onion-Skin scheme has distinct advantages:
1) Lower-threshold MUs produce more force at lower excitation levels. Thus, a relatevely fewer number of lower-threshold MUs, in most part oxidative and able to sustain force for extended time, are required for lower force production.
2) It produces smoother force, especially at the lower force levels that are used for normal daily activities.
3) Higher-threshold MUs never fully fuse, maintaining the potential for a force "reserve capacity" that might be available in extraordinary circumstances.
4) It provides more sustainable contractions .



AHP Scheme vs. Onion-Skin Scheme: As summarized in the figure above, the Onion-Skin scheme is not designed to maximize muscle force, as proposed for the AHP scheme. Instead, it generates force more quickly and more smoothly when force is initiated, and it provides lower maximal force with the capacity to sustain it over longer time. Smoother force production enables accurate performance of daily tasks. Higher-threshold MUs maintain a reserve capacity that could be accessible in extraordinary circumstances.
These features support the flight-or-fight reflexive response in the presence of danger and are more conducive to evolutionary survival.

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