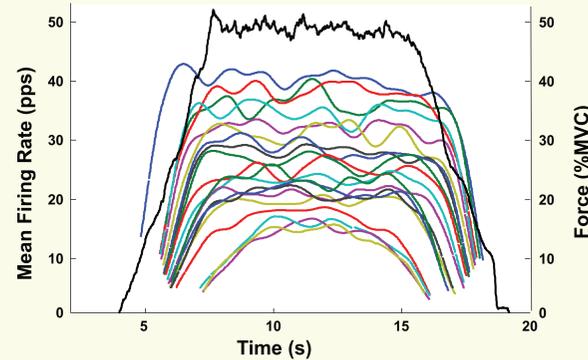


INTRODUCTION

Studies on the behavior of motor units (MUs) during voluntary contractions are commonly performed during linearly-varying or constant force contractions. In these force paradigms, MU recruitment and firing rates are organized in a strict hierarchical manner. MUs are activated in a hierarchical order, with the earlier-recruited MUs exhibiting greater firing rates than the later-recruited ones, a property known as Onion-Skin [1-2]. Also, all the MUs in the pool of a muscle receive a common excitation, known as Common Drive [3], and modulate their firing rate in unison.



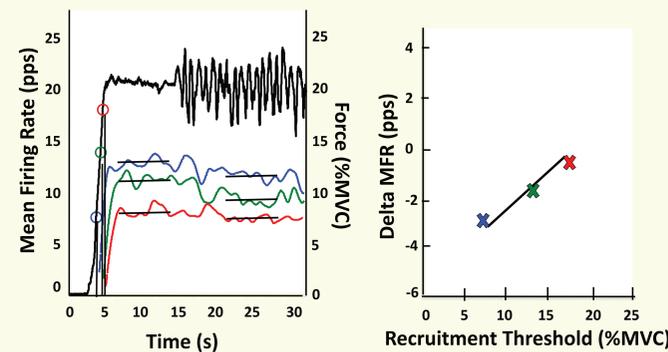
The purpose of this study is to investigate the firing behavior of motoneurons during **voluntary oscillatory contractions** in human subjects.

METHODS

We investigated MU firing behavior in 6 healthy subjects (21-26 yr) performing voluntary oscillatory contractions with the First Dorsal Interosseous (FDI) muscle of the hand.

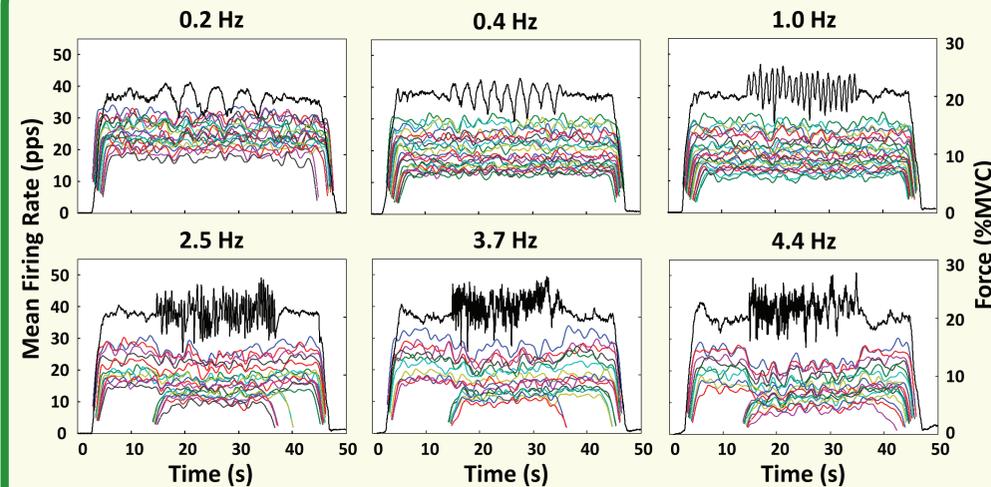
Muscle force was sustained at 20% of the subject's maximum voluntary contraction (MVC) force for 10 s, at which point a force oscillation was superimposed. The oscillation amplitude was 5% MVC peak-to-peak; the oscillation frequency increased from 0.2 to 0.4, 1, 2, 3, and 4 Hz in different trials.

Analysis: Surface electromyographic (sEMG) signals were recorded during the contractions and decomposed into the constituent MU action potential trains using the algorithm developed by De Luca et al. (2006) and Nawab et al. (2010).

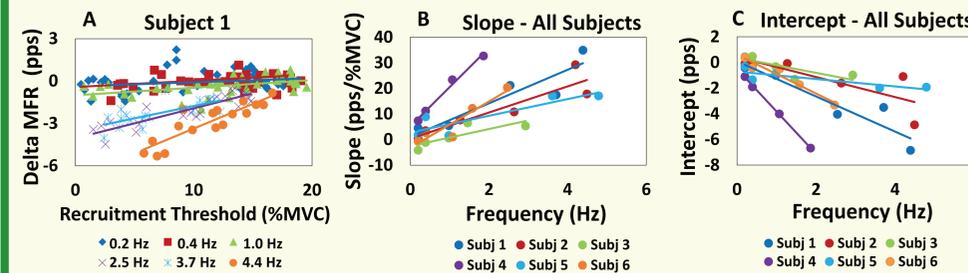


The MU mean firing rates (MFR) were calculated from the firing trains (right figure). The difference in MU MFR between the oscillatory force region and the constant force region (Delta MFR) was computed and plotted against the MU recruitment threshold. Regression analysis was used to investigate the relation between the difference in MFR and recruitment threshold for each oscillation frequency (left figure).

EMPIRICAL DATA



MU MFR with increasing oscillation frequency: Contractions at increasing oscillation frequency (reported at the top of each plot) for one subject are shown above. The black line indicates the muscle force performed by the subject. The colored lines represent the MFR of different MUs active during the contraction.



Analysis Results: **A)** Regression lines for the relation between Delta MFR and recruitment threshold for contractions at increasing oscillation frequency in one subject. Note that the slope of the relation increases whereas the intercept decreases with increasing frequency. **B & C)** Slope and intercept of the relation between Delta MFR and recruitment threshold as a function of increasing oscillation frequency for all subjects.

RESULTS

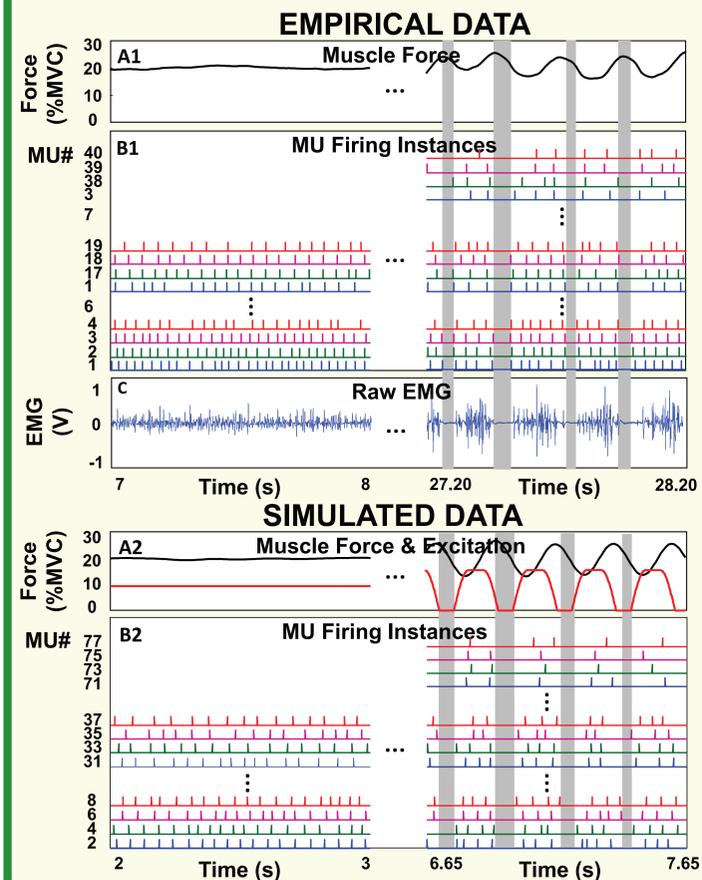
The following alterations in MU firing behavior with increasing oscillation frequency were noted:

- 1) The firing rates of lower-threshold MUs decreased when the force began to oscillate at frequencies >1Hz, and returned to their pre-oscillation level when the oscillation terminated.
- 2) The decrease was less pronounced for higher-threshold MUs.
- 3) The decrease was more pronounced at greater oscillation frequencies.
- 4) Additional higher-threshold MUs were recruited when the decrease in the firing rate in the lower-threshold ones was noted.

CONCLUSIONS

Our data show that the hierarchical regulation of MU firing activation can be manipulated with high-frequency (>1Hz) oscillatory contractions to provide an opportunistic access to increasing the activation of higher-threshold MUs while decreasing the activation requirements of lower-threshold ones.

This *transposition of firing activation* does not negate the Common Drive or Onion-Skin properties: an on-off pattern of input excitation to the motoneuron pool is sufficient to explain the observed transposed firing activation, as demonstrated in the figure below.



Empirical & Simulated Data: We simulated the MU firing behavior (**B2**) and the muscle force (**A2**) for a 1-s interval of constant and high-frequency (4.4 Hz) oscillatory contraction using the model of Contessa & De Luca (2013), which describes the Common-Drive and Onion-Skin properties of MU firing. Results showed that an on-off pattern of input excitation to all the MUs in the muscle was able to reproduce the empirical data (**A1 & B1**). The on-off excitation pattern was modeled to mimic the on-off behavior in the sEMG signal observed at frequencies >1Hz.

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