# Effects of muscle mass on performance and implications for scale

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## **Summary**

Skeletal muscle exhibits an inverse relationship between force and velocity (FV relationship). This relationship is widely attributed to the contractile proteins actin and myosin. However, velocity is depressed in sub-maximally recruited muscle in a way inexplicable by actin-myosin interactions and is speculatively attributed to physical constraints such as the mass of the muscle. If muscle inertia is an important determinant of shortening velocity, we would predict the effect of recruitment would be greater in larger muscles. We characterized the effect of recruitment on the FV relationship of the plantaris muscle of two frog species (41-fold difference in muscle mass). There was a significant effect of recruitment on the FV relationship (p < .005), and this effect was significantly greater in the larger species (p < .005). This suggests that muscle inertia is an important determinant of shortening velocity and has implications for the scaling of locomotor performance and musculoskeletal modeling.

### Introduction

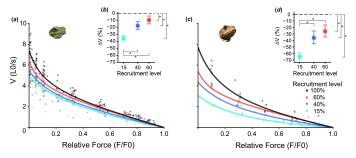
The FV relationship characterizes muscle contraction and is a key determinant of locomotor performance. Actin-myosin kinetics drive muscle contraction, and it is thought this alone shapes the FV relationship [1]. However, observed effects of muscle recruitment on FV properties are inexplicable under this paradigm and are instead attributed to physical properties of muscle, such as mass [2]. As a corollary, recent models suggest mass reducing shortening speed in large muscles due to area:volume scaling [3, 4]. With increasing size, volume increases faster than area, so muscle mass increases at a faster rate than the force available to accelerate the mass, potentially reducing the velocity that a muscle can achieve during a contraction. Here, we ask whether inertia can shape the FV relationship. We predict reductions in FV with recruitment in both species, but this effect will be greater in the larger vs. smaller species if inertia is a factor in contractile dynamics.

#### Methods

Large (Rhinella marina; N=6, muscle mass = 0.7233 + 0.1877 g) and small (Hyla cineria; N=14, , muscle mass = 0.0177 + 0.0068 g) frogs were euthanized and the plantaris muscles and innervating sciatic nerves were dissected out. The isotonic FV curve and maximum shortening velocity ( $V_{max}$ ) of these muscles were then determined at a range of recruitment levels in vitro. Muscle recruitment level was varied by varying the stimulus voltage such that isometric force was 60, 40 and 10% of peak isometric force at 100% recruitment. We used linear mixed effects models to test for an effect of recruitment and the interaction between species and recruitment on  $V_{max}$ .

#### **Results and Discussion**

In both species, submaximal recruitment  $V_{\rm max}$  was significantly slower than maximal (Figure 1). There was a significant interaction of species/mass and recruitment (p < .005), such that recruitment-mediated depression was greater in the larger species. This effect was remarkably consistent across recruitment levels. The magnitude and consistency of the observed size-recruitment effects is in line with our hypothesis, suggesting physical constraints, such as inertia, are important determinants of muscle shortening velocity.



**Figure 1**: Composite FV curves for each recruitment condition in the diminutive frog (a) and largest toad (c), with fixed-effect coefficient estimates and 95% CI's for the effect of recruitment on shortening velocity (inset, b, d). Estimates are the % difference from shortening velocity at 100% recruitment.

## **Conclusions**

Our results suggest that physical constraints, such as mass, mediate the FV relationship. Our findings have implications for the scaling of locomotor performance, such as maximal running speed allometry. Our findings could also inform modelling work. Musculoskeletal models rely on scaling up properties measured in smaller muscle, with no consideration for the effects of mass on contraction dynamics.

#### Acknowledgments

Work supported by HSFP grant, GAANN fellowship, and UCR graduate Vaughan Shoemaker fellowship.

## References

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