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Further evidence against a force-velocity trade-off in muscle driven dynamic lever systems

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Abstract

Levers impose a force-velocity trade-off. In static conditions, a larger moment arm increases a muscle's force capacity, and a smaller moment arm amplifies output velocity. However, muscle force is influenced by contractile velocity and fiber length, while contractile velocity is influenced by the inertial properties of the lever system. We hypothesize that these dynamic effects constrain the functional output of a muscle-lever system. We predict that there is an optimal moment arm to maximize output velocity for any given muscle-lever configuration. Here we test this hypothesis by computationally building and systematically modifying a simple lever system. We generated 3600 modifications of this model with muscles with varying optimal fiber lengths, moment arms and starting normalized muscle lengths. For each model we simulated the motion that results from 100% activation and extracted the maximum output lever velocity. In contrast to a tradeoff between force and velocity in a lever system, we found that there was, instead, an optimal moment arm which maximized both velocity and total impulse. Increasing output velocity always required increasing output force. From this we conclude that in a dynamic lever system where muscle activation is held constant, there is no tradeoff between force and velocity.

Key words: Mechanical advantage, force-velocity tradeoff, dynamic lever system

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Introduction

Biomechanists often use the geometry of a lever system to infer the speed of the movement it could produce (1–3). In quasi-static conditions, the influence of lever geometry is straightforward. The large mechanical advantage of a crowbar, for instance (large input lever and small output lever), amplifies the force and reduces the velocity of the tip relative to the point of force application. As you decrease mechanical advantage, by applying force closer to the fulcrum, the force amplification (output/input force) decreases while velocity amplification (output/input velocity) increases. Many have inferred from this that there is a force-velocity tradeoff in a lever system (4), with greater mechanical advantage (input/output lever arm) producing larger output forces and smaller input/output lever ratios producing faster output velocities.

Yet, as McHenry pointed out (5,6), the velocity of a lever system is not wholly determined by geometry; inertia must be considered . He demonstrated that, for spring driven motions, maximum output speed was limited by the available energy and not lever geometry. While maximum output force increased with mechanical advantage, output velocity did not (7). Arnold rebutted with a dynamic analysis that demonstrated that output speed does linearly change with mechanical advantage when the input power of the actuator is held constant (4). These two approaches differ not in the accuracy of their mathematical reasoning, but in their underlying assumptions. Arnold held power input into the system constant while McHenry held energy constant and allowed power to emerge from system dynamics. As comparative biomechanists, we are particularly interested in applications of these principles to biological systems. Given that very few biological systems are able to hold input power constant across motion (8–10), we find McHenry's analysis a convincing counterexample to the dogma of a universal force-velocity tradeoff in lever systems. However, his example system, the Locust leg is driven by a spring (11–13) . Springs drive only a small subset of

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biological motions, thus his example may not provide a robust foundation to replace the framework he challenges.

A broader range of biological motions are driven by muscle contraction. Since the muscle's power and energy are influenced by force-length-velocity effects, in muscle driven motions neither input power nor energy are constant across lever geometries. Thus, in order to expand McHenry's analysis, here we explore how changing mechanical advantage influences output speed when a motion is driven by a fully-activated Hill-type muscle.

Force-velocity effects confound the relationship between geometry and output speed in lever systems driven by muscle contraction. Larger mechanical advantage amplifies the force of the muscle but at the cost of an increased contractile speed (14). Increasing muscle velocity, in turn, reduces the input force. Consequently, lever arms can act both to amplify (by increasing mechanical advantage) and reduce (by increasing contractile velocity) muscle forces. Thus, we hypothesize that in a muscle-driven lever system there is an optimal mechanical advantage above which dynamic factors limit output velocity. Further, since force-velocity effects are proportional to muscle fiber length and are a function of the resistive forces acting on the system, we also hypothesize that the optimal mechanical advantage will vary with muscle optimal fiber length and the inertia of the system.

Methods

To test our hypotheses we built a computational model of a simple lever system using OpenSim V. 4.0(15), scripting in MATLAB (MathWorks; Natick, MA). Our model was composed of an output lever (length 0.12 m, width and height 0.04 m) that pivoted around a pin joint, a stand to connect the pin-joint to the world and a muscle that originated on the stand, wrapped around a wrap cylinder

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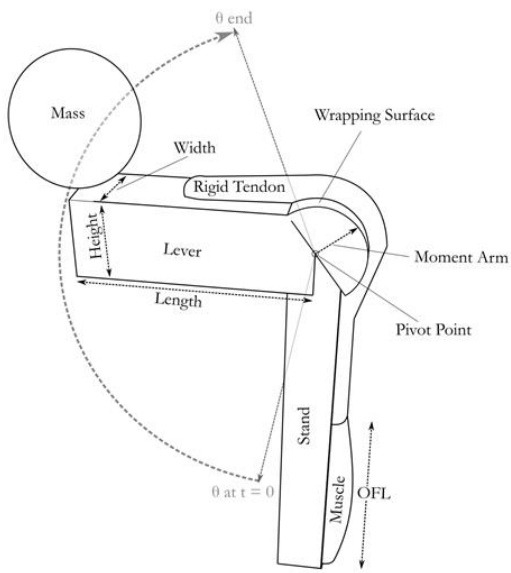
and attached to the lever (figure 1). These values were chosen to approximate the tarsometatarsus of the guinea fowl since detailed experimental data was available(16). The diameter of the wrapping surface defined the input lever or moment arm of the muscle acting at this joint and allowed the muscle to change length and rotate the lever without altering the line of action. The muscle implemented was a Millard2012EquilibriumMuscle muscle model using default length-tension and force-velocity (17) values with a non-compliant tendon and a fixed pennation angle of zero. The lever had the inertial properties of a rectangular rod defined by its volume with a density of water (997 kg m^{-3}). Gravity was not included in the model. To simulate the system driving a mass, we welded a mass on the end of the lever in the shape of a sphere with the density of water. We constrained the lever's range of motion to 150 degrees with a joint limiting force stiffness of 20, damping of 5 and transition range of 2.5 degrees.



We generated 3600 modifications of this model with different muscle optimal fiber lengths (OFL:(0.01:0.01:0.1 m), moment arms (0.0005:0.0005:0.02 m), starting normalized muscle lengths (0.8,1.1,1.4) and driven masses (0.01 ,0.5, 2 kg). Since muscle-tendon unit length changed with moment arm, we adjusted the tendon slack length for each model such that the equilibrium normalized fiber length for the passive muscle was within 0.01 units of a fixed starting fiber length. We held the volume of the muscle constant across changes in optimal fiber length. Since the

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maximum isometric force of a muscle is a function of its cross-sectional area, iso-volumetric muscles imply that the force capacity, F_{max}, is inversely related to optimal fiber length, OFL, such that

$$F_{max}OFL = \frac{M\,T_s}{\rho},$$

where M is muscle mass, T_s is the specific tension of the muscle and ρ is muscle density. The muscle was modeled on the sum of the lateral and medial gastrocnemius muscles of the guinea fowl(16), with a muscle mass of 17g, a specific tension of 3e5 N/m^2 and a muscle density of 1060 kg/m^3. For each modified model, we simulated motion resulting from 100% activation of the muscle model across the full range of motion of the joint in 0.0005 second time steps.

At each time step we extracted the joint angle, angular velocity and acceleration of the lever as well as the muscle active-fiber force, fiber length, and fiber velocity. We trimmed this data to the time range over which the velocity of the mass was increasing. To distinguish the torque required to accelerate the lever from that available to accelerate the mass, we calculated them separately. The force acting to accelerate the mass was calculated from the torque accelerating the mass, τ_m, and the distance from the center of the mass to the pivot, d.

$$F_m = \frac{\tau_m}{d}$$

The torque acting to accelerate the mass was calculated from the acceleration of the mass and its moment of inertia rotating around the pivot, calculated with the parallel axis theorem;

$$\tau_m = \frac{2}{5}mr^2 + md^2$$

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where d is the distance from the center of mass to the pivot point,h r is the diameter of the added mass, and *m* is the mass of the added mass. The torque acting to accelerate the lever was similarly calculated.

Additionally, impulse of the muscle and impulse applied to the mass were calculated as the integral of the active fiber force of the muscle and the force applied to the mass, respectively.

Results

Hypothesis 1: In muscle driven lever systems, there is an optimal moment arm above which dynamic factors dominate the influence of increased mechanical advantage. In line with our hypothesis, we found that for every muscle tested, maximum output velocity is low for levers with small moment arms, increases to a maximum, then declines as moment arm increases further. Three factors influence output velocity. Larger moment arms increase both the multiplier between muscle force and output force and the distance over which the muscle contracts to do work. Each of these in isolation would increase output velocity with increasing moment arm. Yet, countering these factors,

Table 1. Lever output velocity varies driven mass and muscle properties, starting normalized fiber length (staring n.OFL), muscle optimal fiber length (OFL), the ratio of moment arm to muscle optimal fiber length, MA/OFL, the maximum output velocity of the driven mass, Max Vel, the maximum muscle contraction velocity, Max Musc Vel, the normalized muscle contraction distance, nDist, the impulse acting on the driven mass, Output Impulse, and the total muscle work. The moment arm that maximizes output velocity also maximizes output impulse and does not occur at a maximum or minimum value. This optimal moment arm for maximizing output velocity changes with starting muscle length and driven mass.

Driven Mass	Starting n.FL		OFL (m)	Ma / OFL	Max Vel Rad/s	Max Musc Vel m/sec	nDist	output Impulse / muscle Impulse	Output Impulse Ns	Total muscle work Nm
2	1.1	min MA	0.05	0.01	7.2	0.07	0.03	0.004	6.9e4	2.2e4
		opt MA	0.05	0.16	18.3	2.9	0.42	0.078	1.7e5	5.6e4
		max MA	0.05	0.4	12.9	5.2	0.66	0.164	1.2e5	2.5e4
2	1.4	opt MA	0.05	0.19	18.9	3.6	0.50	0.068	1.8e5	5.7e4
	0.8	opt MA	0.05	0.1	14.5	1.5	0.26	0.05	1.4e5	4.4e4
0.5	0.8	opt MA	0.05	0.8	27.7	2.2	0.21	0.128	4.9e4	1.7e4
0.01	0.8	opt MA	0.05	0.05	64.2	3.2	0.13	0.318	1.7e3	0.4e4

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muscle force drops precipitously with increasing moment arm due to increasing contraction velocity. These competing effects create an optimal moment arm ratio for maximum output velocities.

Hypothesis 2: Optimal moment arm is a function of muscle OFL and the driven mass.

As we change the OFL, but still drive a 2kg mass, the inverted-U relationship between moment arm

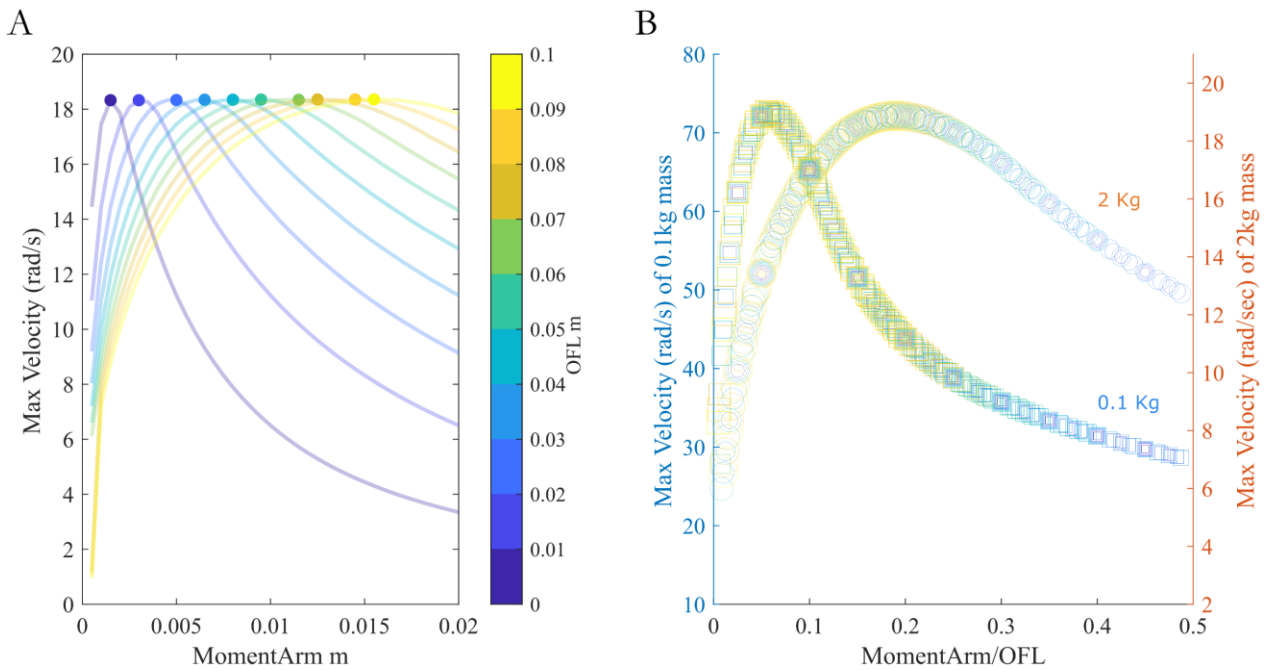

Figure 2: (A) Maximum velocity as a function of moment arm for a system driving a 2 kg mass across a range of muscle OFLs. Filled circle designates optimal moment arm for generating maximum output velocity. There is an optimal moment arm and it varies by optimal fiber length. (B) Maximum velocity as a function of OFL normalized moment arm for systems driving both 2kg (circles) and 0.1 kg masses (squares). The data from panel A collapses such that there is an optimal moment arm/OFl ratio that generates maximum output velocity. That optimum ratio changes with driven mass. In both plots, optimal fiber length is represented by color.

and output velocity does not change, but the moment arm that generates the maximum velocity does (Figure 2A). The optimal moment arm increases with OFL linearly, as suggested (14). If we plot output velocity vs normalized moment arm [moment arm/OFL], the data collapse along one curve, as shown in Figure 2B. Thus, for any muscle with a given OFL and starting length, there is a moment arm that will optimize the velocity of a driven mass.

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The optimal normalized moment arm changes with both muscle start length and driven mass as well as muscle starting length (Table 1). The optimum moment arm/OFL is larger with greater resistive forces (Table 1).

Discussion

Bone morphology is thus not sufficient to infer the performance of a lever system. We have shown here that for a muscle driven system, the moment arm and output speed are not linearly related. For every muscle tested there was an inverted-U relationship between moment arm and output velocity. Moreover, our results suggest that the constant power assumptions made by Arnold et al do not best reflect the capabilities of vertebrate muscle. Therefore, contrary to predictions from static or quasi-static analyses, there is a range of morphologies where smaller mechanical advantage decreases output velocity (Fig 2a). It is important to note that this is consistent with the ratio of input to output velocity changing linearly with mechanical advantage at any instant. We simply suggest that this ratio does not predict the maximum velocity of the whole motion. Therefore, in agreement with McHenry's analysis (18), inertia and motor/muscle properties must be considered to properly predict the output velocity of a muscle-driven lever system.

How, then, do leverage, muscle properties and inertia interact to produce an optimum? We would expect from a static analysis that the smallest moment arms would produce the largest output velocities. Instead we found the opposite. To resolve this, it is important to consider how lever arms affect torque. In contrast to a static or quasi-static analysis, in a dynamic system, an increase in velocity must be driven by an increase in torque. Holding all else constant, a decrease in moment arm decreases the torque available to drive the motion. Thus, in a dynamic system driven by an ideal actuator (one that could produce constant force), output velocity would decrease alongside output force with decreasing moment arm. Output velocity, then, drops off at small moment arms because

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torques are limited by small moment arms. Why, then, does output velocity also drop at larger moment arms despite increasing mechanical advantage? In our models, this drop off is due to muscle-force velocity effects. At larger moment arms, the muscle contraction velocity increases (Table 1), decreasing force capacity. Thus, we can explain the shape of the output velocity-moment arm plot as the interaction of two opposing factors: mechanical advantage and force-velocity effects. At small moment arms, large muscle force capacity is offset by a small mechanical advantage, minimizing torque (14,19).At large moment arms, large mechanical advantage is offset by small muscle force capacity. The optimum occurs in-between.

The size of the optimal moment arm is not universal, however, and is influenced by several factors. For instance, we show that (for a given driven mass) output velocity is invariant across systems with the same ratio of moment arm to muscle optimal fiber length; the moment arm that generates the greatest output velocity increases with muscle optimal fiber length. This implies that a difference in moment arm between two individuals could be compensated for by an equivalent change in muscle properties. Furthermore, the optimal moment arm also changes with starting fiber length (Table 1) and driven mass. Force is maximized at larger moment arms for slow motions and at smaller moment arms for fast motions (Table 1) due to higher muscle contractile velocities in systems with low resistive forces. Therefore, even for a single individual, changing the joint posture (i.e. starting muscle length) or the inertia of the system (i.e. throwing a different sized ball) can alter the moment arm that will maximize output velocity. Further, we found that changes in the inertia of the system can have a greater influence on output velocity than changes in moment arm (Table 1, Fig 2B). This suggests that adaptations in cursorial animals to minimize limb inertial properties may have had a larger influence on velocity than changes in mechanical advantage.

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In summary, we suggest that there is no force-velocity tradeoff in muscle-driven lever systems when looking across a whole motion since increasing output velocity always requires increasing output force. We find that moment arm that maximizes both output force and velocity decreases with resistive forces and muscle optimal fiber length. The analysis of lever systems which include the dynamic muscle and inertia effects yield an improved quantitative framework to form and function. Our results suggest that the focus on adaptations for speed should shift from lever mechanics alone to include the interaction between lever mechanics, muscle morphology and system inertia.

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Data Availability

The code used in the project and the generated data are available at DataDryad https://datadryad.org/stash/share/AqKLIaK7A1NgxKoLYGD7SX7Nab92qANnrhrInx-9RRc.

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