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When Skeletons Are Geared for Speed: The Morphology, Biomechanics, and Energetics of Rapid Animal Motion

Matthew J. McHenry¹

Department of Ecology & Evolution, University of California, Irvine, CA 92697-2525, USA

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¹E-mail: mmchenry@uci.edu

Synopsis A skeleton amplifies the minute contractions of muscles to animate the body of an animal. The degree that a muscular contraction displaces an appendage is determined by the gearing provided by the joints of a skeleton. Species that move rapidly commonly possess joints with relatively high gears that produce a large output displacement. However, the speed of an appendage can depend on dynamics that obscure how this motion is influenced by the skeleton. The aim of this review is to resolve mechanical principles that govern the relationship between the gearing and speed of skeletal joints. Forward dynamic models of three rapid force-transmission systems were examined with simulations that varied the gearing of a joint. The leg of a locust, the raptorial appendage of a mantis shrimp, and the jaw of a toad are all driven by the conversion of stored elastic energy into kinetic energy. A locust achieves this conversion with high efficiency when it kicks and thereby applies nearly all stored energy into fast movement. This conversion is unaffected by differences in the leverage of the knee joint, as demonstrated by a maximum kicking speed that was found to be independent of gearing. In contrast, the mantis shrimp creates drag as it strikes toward a prey and thereby loses energy. As a consequence, high gears displace the raptorial appendage relatively far and yield slower motion than do low gears. The muscle that opens a toad’s jaw also dissipates energy during ballistic capture of prey. This loss of energy is reduced when jaw opening occurs from the slower muscle contraction produced by a high gear within the jaw. Therefore, the speed of these lever systems is dictated by how gearing affects the efficiency of the conversion of potential energy into kinetic energy. In this way, the energetics of force transmission mediate the relationship between the gearing of a skeletal joint and the maximum speed of its motion.

Introduction

The joints of a rigid skeleton serve as gears that create motion by amplifying muscular contraction. The relationship between gearing and force production is well understood from a long history of research (Hildebrand and Goslow 2001). However, it is less clear how the geometry of a skeleton affects the capacity of an animal to move quickly. Therefore, the aim of this article is to resolve general principles that govern the relationship between the gearing and speed of a skeleton.

The geometry of a skeleton has traditionally been thought to dictate its capacity to move at high speed. In a simple lever, gearing is defined by the displacement advantage (DA), which is the distance between

a point of force application and the fulcrum of a lever (l_{out}) divided by the distance between the fulcrum and insertion of a muscle (l_{in}). The DA of a lever system indicates the degree that a muscular contraction is amplified to displace a skeletal element. If one assumes that the muscle shortens at a fixed velocity (v_{in}), then the output velocity (v_{out}) is equal to the product of the input and DA (i.e., $v_{out} = DA v_{in}$). Like the large-diameter gears on the crank of a bicycle that are used at high speed, a high-DA system may be considered to have a relatively high gear because it creates a large output displacement per unit input displacement. Under the assumption of a fixed velocity of input, lever systems with a higher DA are endowed with a

capacity to move more rapidly than are systems with a lower DA. In other words, high gears produce fast motion. A classic example that appears to support this model is offered by the leg bones of mammals, in which the limb joints of a horse have a higher DA than do those of a slow-moving armadillo (Smith and Savage 1956). A more rigorously comparative example is offered by the feeding apparatus of fishes; species that feed on evasive prey have higher gears than do species that feed on slow-moving hard prey (Westneat 1995; Wainwright et al. 2004). If high gears may be assumed to move relatively quickly, then an investigator may infer speed from morphometrics. Examples of this inference include gearing in the rigid skeletons of dinosaurs (Barrett and Reyfeld 2006; Sakamoto 2010), fishes (Muller 1987; Westneat 1995), and in a variety of hydrostatic skeletons (Kier and Smith 1985).

An alternative perspective on the relationship between gearing and speed comes from a consideration of musculoskeletal dynamics. For example, experimental manipulation of gearing in the leg muscles of a frog (*Xenopus laevis*) has shown that muscles may shorten more slowly in systems with a higher DA (Richards 2011). Muscles that actuate a lever with a relatively high gear have less leverage and consequently encounter a load that causes the muscle to contract more slowly. Therefore, the gains in speed of a high gear may be offset by a slower rate of shortening by the actuator. This possibility violates the assumed fixed input velocity in the traditional geometric model of the speed of lever (Smith and Savage 1956). To account for how a force-transmission system may affect the speed of both actuators and loads, models of forward dynamics can simulate the motion of both from a consideration of mechanics (Zajac 1993; Daniel 1995; Lappin 2006). The present study adopts this approach by considering models of three different fast-moving musculoskeletal systems: a locust's leg, a mantis shrimp's raptorial appendage, and a toad's jaw.

The mechanics and energetics of lever systems

The three lever systems considered presently share some fundamental similarities. Each system accelerates a structure by applying a torque (τ) at a joint. Therefore, Newton's second law of motion for rotation provides a governing equation for each of these systems:

$$I\ddot{\gamma} = \tau, \quad (1)$$

where I is the moment of inertia of the rotating body and $\ddot{\gamma}$ is its angular acceleration. The moment of

inertia reflects the mass distribution of the system, which is a fixed quantity in the present models. The torque varies with γ (in all models) and its first derivative (in the mantis shrimp and toad). Therefore, Equation (1) represents a second-order differential equation that may be integrated over time to simulate movement in the angular position. I have solved this equation numerically for each model with an explicit eighth-order Runge-Kutta method (the 'ode45' function in Matlab, based on Dormand and Prince 1980) with a zero initial velocity. A linear velocity for each simulation was calculated as the product of angular velocity and the distance between the point of rotation and the center of mass ($v_{\text{out}} = \dot{\gamma}l_{\text{out}}$). This distance was calculated from the mass and moment of inertia, as follows:

$$l_{\text{out}} = \sqrt{\frac{I}{m}}. \quad (2)$$

All three systems are powered by stored elastic energy. Therefore, each may be model as creating motion where elastic energy is converted to kinetic energy. This conversion is executed with high efficiency in the kick of a locust's leg, which permits a model that assumes conservation of energy (Bennet-Clark 1975). In contrast, energy is lost to the creation of hydrodynamic forces in the mantis shrimp or by viscous dissipation in a muscle in the toad's jaw. Therefore, models of force-transmission systems cannot generally assume conservation and energetic losses. Energy loss therefore has the potential to influence the relationship between the gearing and the speed of an appendage. For this reason, the conversion of elastic energy (E_E) to kinetic energy (E_K) may be tracked as functions of the instantaneous spring length and the rate of angular rotation:

$$E_E = \frac{1}{2}kL^2, \quad (3)$$

$$E_K = \frac{1}{2}I\dot{\gamma}^2. \quad (4)$$

Furthermore, the transmission efficiency (η) for each simulation may be calculated from the maximum values for kinetic and elastic energy:

$$\eta = \frac{E_{K, \text{max}}}{E_{E, \text{max}}}. \quad (5)$$

In this study, the effect of gearing on the speed and energetics of motion were determined in each model by running a series of simulations. Simulations differed only in the gearing of the force-transmission system and therefore were supplied with an equivalent amount of elastic energy.

Therefore, the analysis of each model considered the effect of gearing with a fixed input of energy.

Gearing does not affect maximum speed in a locust's leg

The metathoracic leg of the locust (*Schistocerca gregaria*) is a classic model system for understanding musculoskeletal mechanics that produce explosively rapid motion (Fig. 1A and B). The leg may be extended within milliseconds in the course of a jump or a defensive kick toward another animal. Its motion is driven entirely by elastic structures in the joint between the femur and tibia that are deformed by muscular contraction prior to the start of motion (Brown 1967). The relative simplicity of this structure makes the mechanics of a kick a particularly tractable subject for modeling (Bennet-Clark 1975).

A model for the mechanics of a locust's kick focuses on the torque generated at the joint between the femur and tibia (Fig. 1B). The elastic structures in this joint may be modeled as a spring with a

stiffness (k) that generates force in proportion to the distance that it is stretched beyond its resting length (L). The component of this force that is normal to the in-lever force creates the torque that increases the angular position of the tibia (γ), as shown in the following equation (McHenry 2011):

$$\tau = l_{in} k L \sin \gamma. \quad (6)$$

The governing equation for a kick (Equation 1) was solved with this relationship for torque using initial conditions ($\dot{\gamma}_0 = 6^\circ$, $\dot{\gamma} = 0^\circ \text{ s}^{-1}$, $L_0 = 1.5 \text{ mm}$) and parameter values ($l_{in} = 0.76$, $I = 6.3 \text{ g mm}^2$, $m = 21 \text{ mg}$, $l_{out} = 17.3 \text{ mm}$, $k = 0.3 \text{ N mm}^{-1}$) from previous investigations (Bennet-Clark 1975; Burrows and Morris 2001). The motion predicted in these simulations has been verified to approximate measured kinematics of kicking (Burrows and Morris 2001; McHenry 2011).

Simulations that differed in gearing provide the basis for examining its effect on speed. For example, the in-lever length was increased by 50% ($l_{in} = 1.52$, $DA = 11.4$) to create a model with a low gear relative

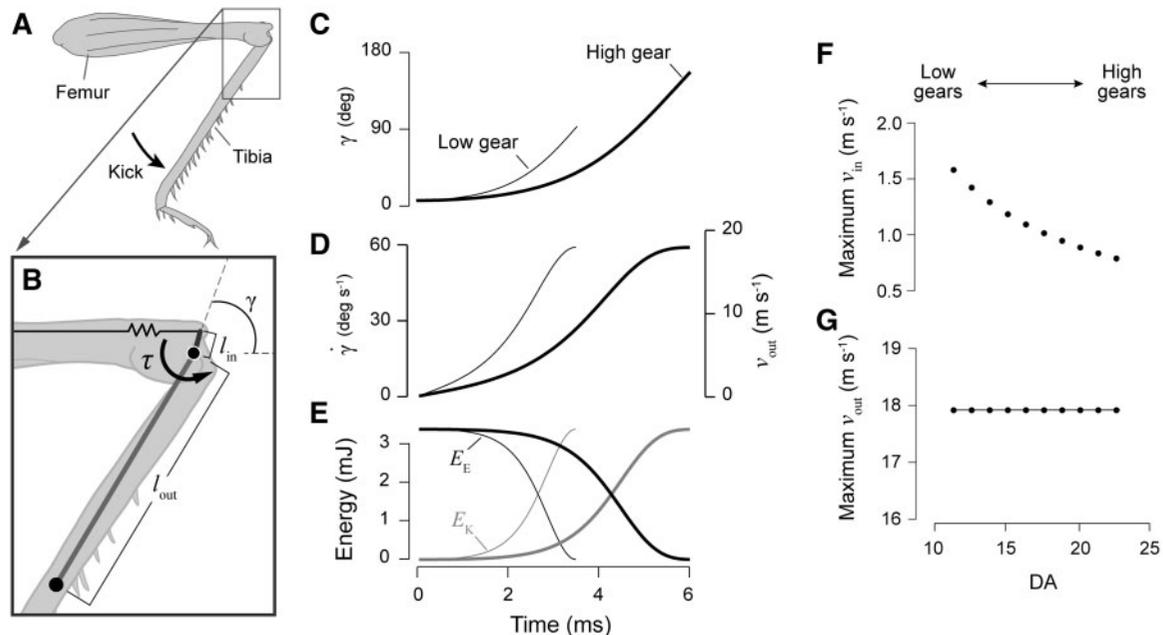


Fig. 1 The speed of a locust's kick. (A) A schematic illustration of the metathoracic leg of a locust shows the relative position of the femur and tibia and direction of a kick (arrow). (B) An blow-up of the joint between these segments shows the angular position of the tibia relative to the femur (γ), the torque generated by the leg spring (τ), the position of the leg spring, and the length of the in-lever (l_{in}) and out-lever (l_{out}). (C–E) Two simulations of different in-lever lengths demonstrate differences in the kinematics and energetics that emerge from different gearing. The simulation for the system with the low gear ($l_{in} = 1.52 \text{ mm}$, $DA = 11.4$, thin lines) ceases before the high gear ($l_{in} = 0.76 \text{ mm}$, $DA = 22.7$, thick lines) because the leg spring arrives at its resting length more quickly. As a consequence, (C) the low gear rotates less, but (D) achieves an equal maximum rate of rotation and velocity. (E) For both systems, elastic energy (black lines) is completely transferred into kinetic energy (gray lines) because the model (Equations 1 and 6) assumes conservation of energy. (F–G) A series of simulations demonstrates how changes in gearing affect the maximum input and output velocities of kicking due to a difference in l_{in} ($0.76 \text{ mm} < l_{in} < 1.52 \text{ mm}$) that alters the gearing of the model ($11.4 < DA < 22.8$). (G) The maximum output velocity was calculated analytically (black line, Equation 10) from the energetics of the system.

to the high gear of the measured in-lever length ($l_{in}=0.76$, $DA=22.7$). This low-gear system completed its kick in less time than did the high-gear system (Fig. 1C), as the leg spring reached its resting length more rapidly. This is because the greater in-lever length of the low gear enhanced the generation of torque by the leg spring (Equation 5) to create a relatively high acceleration. Despite its greater acceleration, the low gear attained a maximum speed equivalent to that of the high gear (Fig. 1D).

A series of simulations provide a more comprehensive view of the effects of gearing. The in-lever length was varied among simulations at a regular interval for 10 values across a wide range ($0.76\text{ mm} < l_{in} < 1.52\text{ mm}$) to produce a series of lever systems that differed in their DA ($11.4 < DA < 22.8$). These simulations predicted that an increase in DA caused a monotonic decrease in the rate of shortening by the spring (Fig. 1F), but a constant output velocity. Therefore, the systems with higher gears achieved maximum speeds that were no greater than those of lower gears. This result was a direct consequence of the conservation of energy that was assumed for the locust leg. All of the stored elastic energy at the start of a kick was converted into kinetic energy. Simulations yielded the same kinetic energy, and therefore speed, because they were provided with equal elastic energy. However, conservation of energy is often not an appropriate assumption and systems that are not highly efficient have the potential for a different relationship between the gearing and speed of a skeletal joint.

High gears slow the mantis shrimp's raptorial appendage

The explosive predatory strike of a mantis shrimp (*Gonodactylus smithii*) is one of the fastest motions among animals. The raptorial appendage is capable of accelerating at more than 10,000 times the acceleration of gravity in a few milliseconds (Patek et al. 2004; Patek and Caldwell 2005). This feat is especially impressive given that these marine animals must overcome the resistance generated by the surrounding water. Because of this generation of fluid forces, the raptorial appendage loses energy over the course of a strike. Therefore, the mantis shrimp offers a useful case study for examining the relationship between gearing and speed for a skeletal system that does not conserve energy.

Like the kick of a locust, the mantis shrimp's strike is powered by stored elastic energy. This storage occurs within the exoskeleton of the raptorial

appendage within a stiff “V”-shaped element (the meral-V, Fig. 2) at the distal end of a segment (the merus). The meral-V functions as a torsion spring that is centered at its juncture with the merus. A strike commences when this spring is released and the stored energy abducts the meral-V, which engages a four-bar linkage system that drives skeletal elements to collide with the prey. A four-bar linkage is a type of force-transmission system composed of skeletal elements that function as four rigid struts that are linked end-to-end in a circuit by pin joints (Paul 1979). The abduction of the meral-V during a strike increases the input angle (θ) to this system, which rotates the “striking body” toward the prey (Fig. 2) (Patek et al. 2007). The gearing between input angle and the output angle of the striking body (γ) varies with the lengths of the links. Analogous to the DA of a lever, the gearing of a linkage system is measured as the kinematic transmission (KT), which is the ratio of change in output angle per unit change in input angle:

$$KT = \frac{d\gamma}{d\theta}. \quad (7)$$

The KT of the raptorial appendage increases substantially over the course of a strike, but a particular linkage geometry may be characterized by its minimum value (KT_{min}) (McHenry et al. 2012). Therefore, a four-bar linkage system with a relatively large value for KT_{min} represents a system with a relatively high gear.

Similar to the locust's kick, the predatory strike of a mantis shrimp may be predicted from a model of its mechanics. Because the striking body is submerged under water, its moment of inertia is determined by its distribution of solid mass and the added mass of the surrounding water. These factors may be combined through experimental measurement and hydrodynamic modeling to yield a total moment of inertia for the striking body ($I=7.8324 \times 10^9\text{ kg m}^2$ for $m=0.23\text{ g}$) (McHenry et al. 2012). The net torque that acts on the striking body is generated by the meral-V spring and the drag generated by its motion. These opposing torques may be articulated as a difference in the following equation (McHenry et al. 2012):

$$\tau = \frac{k_t(\theta - \theta_r)}{KT} - \frac{1}{2}\rho Dh^5 \left(\frac{d\gamma}{dt}\right)^2, \quad (8)$$

where k_t is the torsion spring stiffness, θ_r is the resting position of the spring, ρ is the density of water, h is the length of the striking body, and D is the drag

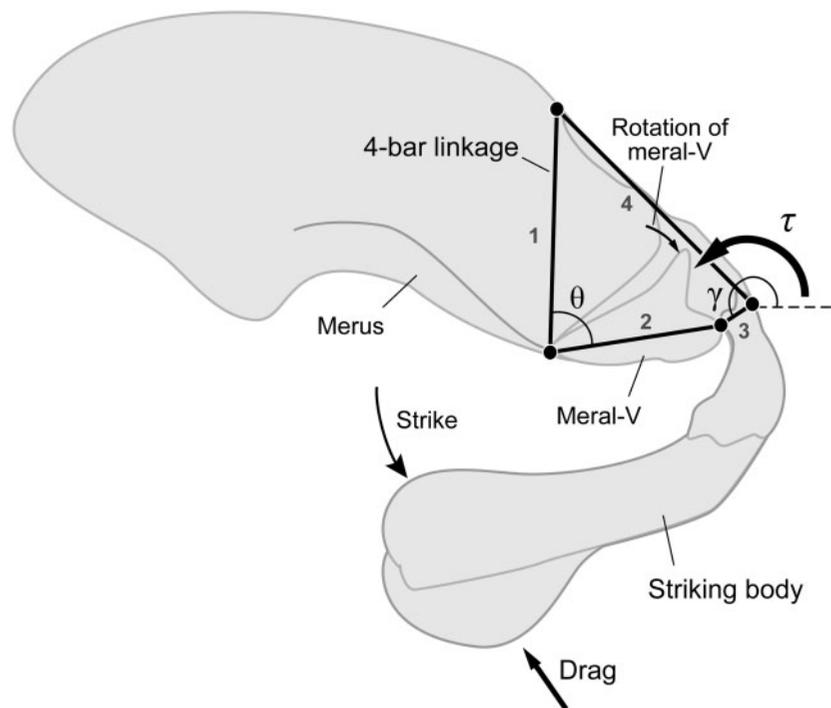


Fig. 2 A model of the mechanics of the predatory strike of a mantis shrimp. The strike is powered by a torsion spring that generates torque (τ) at the intersection of the merus and meral-V. Upon release, the meral-V rotates away from the merus (small arrow). This motion engages a four-bar linkage system (black lines numbered 1–4, Patek et al. 2007) that is comprised of rigid elements of the exoskeleton. Within this system, rotation of the meral-V serves as an input angle (θ) that increases over the strike and serves to increase the output angle (γ). Changes in this angle are reflected in the motion of distal skeletal elements that are fused to link 3, which function as a uniform rigid mass (the striking body) that collides with prey. This motion is resisted by the drag generated by the surrounding water. These mechanics were modeled in simulations (Equations 1 and 8).

torque product, which is a coefficient that varies with the shape of the striking body. Measurements of all of these parameters ($k_t = 0.01 \text{ N m}^{-1}$, $\theta_r = 92.3^\circ$, $\rho = 998 \text{ kg m}^{-3}$, $D = 0.076$, $h = 10.9 \text{ mm}$), in addition to the initial conditions ($\theta_o = 80.0^\circ$, $\dot{\theta}_o = 0^\circ$), provide the necessary inputs for a simulation. The function describing the variation in KT with θ may be determined numerically from measurements of the length of linkages ($l_1 = 6.5 \text{ mm}$, $l_2 = 4.2 \text{ mm}$, $l_3 = 1.6 \text{ mm}$ and $l_4 = 7.6 \text{ mm}$). Simulations of this model by numerical integration of Equation (1) have previously been shown to accurately predict measurements of the impulse of a predatory strike (McHenry et al. 2012).

The mantis shrimp model was used to examine the effects of gearing on strike speed. As a consequence of its geometry, the KT of this linkage system increases substantially with a relatively small decrease in the length of the link coupled to the striking body (link 3 in Fig. 2). Consequently, a system with a high gear was created with a shorter length of this link (e.g. $l_3 = 0.55 \text{ mm}$, $\text{KT}_{\min} = 6.19$) than for a system with a relatively low gear (e.g. $l_3 = 0.95 \text{ mm}$, $\text{KT}_{\min} = 3.40$, Fig. 2A).

Simulations of these two versions of the model were conducted with all other parameter values set equal. Despite this similarity in parameters, the high-gear system achieved a slower maximum speed with lower acceleration than the low gear system.

The difference in speed for simulations that used low and high gears may be understood by considering the energetics of the simulated strikes. Both began with an equivalent amount of stored elastic energy, which decreased over the strike as the meral spring approached its resting position (Fig. 3C). The high gear caused the striking body to traverse a relatively greater distance over the strike (Fig. 3Ai and Bi), losing energy to drag all along the way (Fig. 3Ci and D). As a consequence, the high gear paradoxically yielded a slower maximum speed because a greater amount of the elastic energy was lost to drag over its relatively long excursion.

The effects of gearing are reflected among simulations that span a wide range of KT_{\min} values. KT_{\min} was increased ($1.90 < \text{KT}_{\min} < 7.48$) by decreasing the length of link 3 ($0.47 < l_3 < 1.57$) to produce versions of the model with higher gears. These simulations

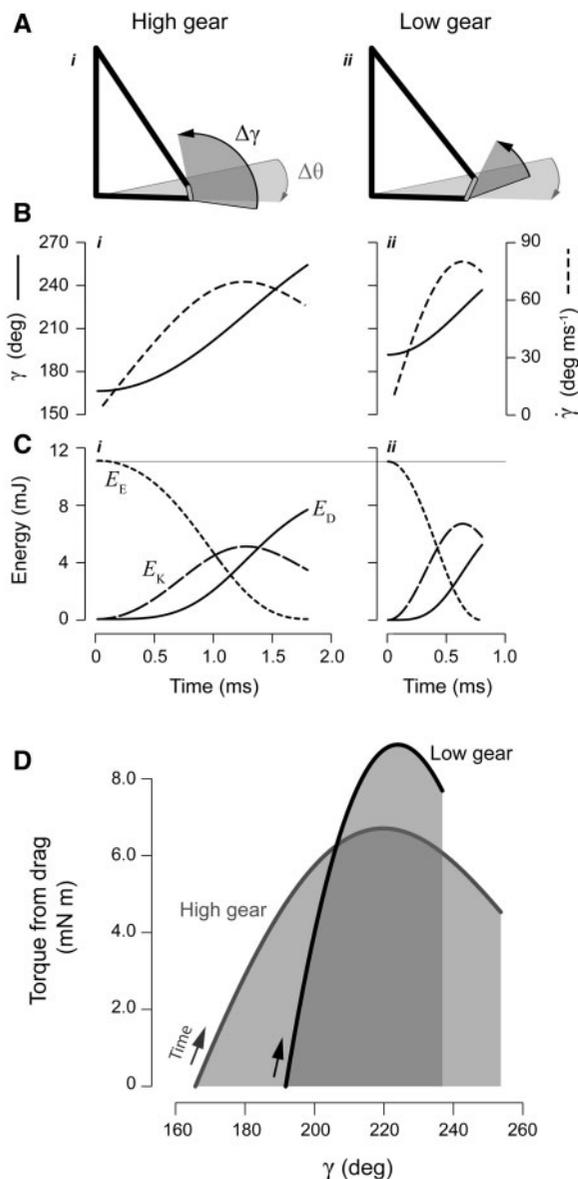


Fig. 3 A comparison of strike mechanics in mantis-shrimp simulations that differ in gearing. **(A)** A difference in the length of link 3 (Fig. 2) created models with a relatively (i) high gear ($l_3 = 0.55$ mm, $KT_{\min} = 6.19$), compared to the system with a (ii) low gear ($l_3 = 0.95$ mm, $KT_{\min} = 3.40$). **(B)** The output angle (γ , solid line) and rate of change in that angle ($\dot{\gamma}$, dashed line) are shown for the (i) high gear and (ii) low gear models. **(C)** The energetics of the same strikes are shown in how elastic energy (E_E , dotted line) declines as kinetic energy (E_K , dashed line) rises and energy is lost by generating drag (E_D , solid line). **(D)** The torque created by drag is plotted as a function of output angle, where the area under the curve for the low gear (dark gray) and high gear (light gray) models is equal to the energy lost over the strike for each simulation.

found that maximum speed decreased monotonically with KT_{\min} (Fig. 4). This decline in speed was mirrored in a loss of transmission efficiency, as the striking body progressively lost a greater amount of

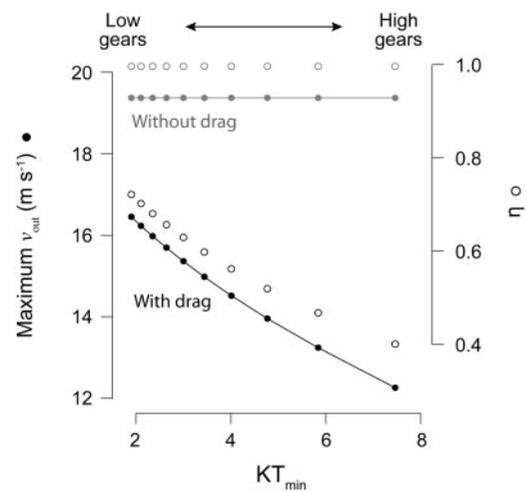


Fig. 4 The effect of gearing and drag on strike speed in the mantis shrimp. Ten simulations of the mantis shrimp model were performed that included (black) and excluded (gray) drag. A range of values for KT ($1.90 < KT_{\min} < 7.48$) were created among simulations by varying the length of link 3 (Fig. 2, $0.47 < l_3 < 1.57$). The maximum output velocity (filled circles) and transmission efficiency (open circles) are plotted for each simulation. The maximum speed was predicted (lines) from the energetics of the system (Equation 10).

energy to drag with greater KT_{\min} (Fig. 4). In contrast, running the same simulations without the drag force (i.e., $\eta = 1$) yielded a constant maximum speed, as seen in the energetically conservative kick of the locust (Fig. 1G). Therefore, the efficiency of a strike mediates the relationship between gearing and speed in the mantis shrimp.

High gears speed up ballistic capture of prey by toads

The jaw of the toad (*Bufo alvarius*) is a force-transmission system that offers an interesting contrast to the strike by mantis shrimp. Toads use ballistic projection of the tongue to capture prey in a terrestrial environment and therefore do not lose significant energy from drag. Instead, energy is lost by viscous dissipation within the muscle that powers opening of the jaw. Therefore, efficiency has the potential to play a mediating role in the speed of this lever system, but in a different manner because energetic losses occur within the actuator.

The toad's jaw shares some similarities with the locust's leg. It functions as a simple lever that is actuated by the depressor mandibulae, which opens the mouth rapidly during projection of the tongue. Using a catch mechanism, this muscle is active prior to opening of the mouth and thereby stores elastic energy within the muscle that rapidly accelerates the jaw (Nishikawa and Gans 1992; Nishikawa 1997; Lappin et al. 2006). Lappin et al. (2006) modeled

these mechanics and verified its predictions by experiments on kinematics and muscle physiology. This model was presently formulated in a similar manner as the above-described models, but with an actuator that included both elastic and damping components (Lappin et al. 2006). Specifically, the muscle was modeled as a Kelvin–Voigt material, which behaves like a spring in parallel with a dashpot (Fig. 5A). The torque created by a pair of these muscles was defined by the following equation:

$$\tau = 2l_{in} \cos \gamma (-kL - \mu \dot{l}_{in}) \quad (9)$$

where μ is the damping coefficient for the muscle. In this case, γ was defined with respect to the position of the jaw when the muscle is at its resting length, with negative values (but a positive first derivative) during simulations. Numerical solutions to Equation (1) using this definition of torque were conducted using initial conditions ($\dot{\gamma} = 0^\circ \text{ s}^{-1}$, and $\gamma_0 = -73.4^\circ$ for $L_0 = 3.2 \text{ mm}$) and parameter values ($I = 1.16 \times 10^{-6} \text{ kgm}^2$, $m = 1.29 \text{ g}$, $l_{out} = 30 \text{ mm}$, $\mu = 4.6 \text{ N s m}^{-1}$) calculated from previous measurements (Lappin et al. 2006). The gearing of the system was altered to evaluate its influence on the mechanical performance of the motion.

The transmission efficiency of the toad's jaw affects its maximum speed of opening. For example, the initial muscle length was equal in simulations using a relatively high gear ($l_{in} = 3.3 \text{ mm}$, $DA = 9.01$) and a low gear ($l_{in} = 5.0 \text{ mm}$, $DA = 6.00$). However, this difference in gearing yielded simulations that differed in the energy dissipated by the muscle. This lost energy was calculated by integrating the force created by the muscle's viscosity (equal to $2\mu \dot{l}_{in} \gamma$) over its change in length (Fig. 5B). The high-gear simulation predicted a slower muscle contraction, which resulted in less viscous loss (2.50 mJ) compared to that of the low gear (2.89 mJ). As seen in the locust model (Fig. 1), the greater leverage of a low-gear system causes the actuator to encounter less resistance and consequently to shorten more rapidly. However, this more rapid contraction is less efficient. Although the high gear contracts more slowly, its smaller energetic loss and superior DA create an output velocity that exceeds the low gear due to its higher efficiency. This effect was considered over a series of simulations that spanned the same range of DA values (Fig. 5C and D). These simulations predicted a monotonic decline in the input velocity, but a more dramatic increase in output velocity. This trend reflects how transmission efficiency (Equation 5) varies as a function of DA. In contrast to the mantis shrimp (Fig. 4), transmission efficiency in the toad's jaw creates a positive relationship between

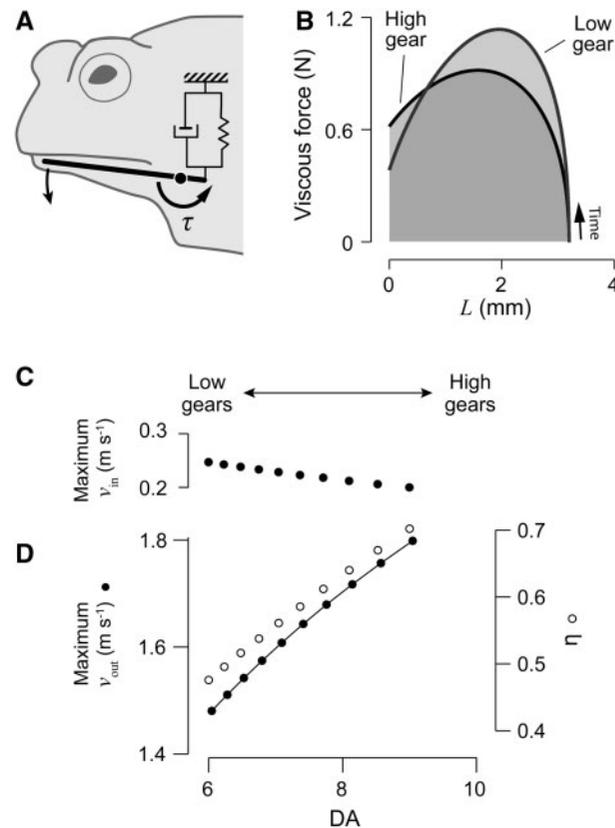


Fig. 5 The toad jaw during ballistic capture of prey. (A) The jaw rapidly opens using elastic energy stored within a muscle that can be modeled as a Kelvin–Voigt material. (B) The energy dissipated by this muscle during contraction can be calculated as the integral of the viscous force over changes in muscle length (L) in simulations of jaw opening. This calculation was made for simulations that used a relatively high gear ($l_{in} = 3.33 \text{ mm}$, $DA = 9.01$, black curve) and a low gear ($l_{in} = 5.00 \text{ mm}$, $DA = 6.00$, gray curve). (C–D) DA was varied over a series of simulations by altering the in-lever length to the jaw–lever system. For each simulation, the maximum speed of the in-lever (C) and out-lever (D) were calculated (filled circles). The transmission efficiency was calculated from each of these simulations (open circles), which provided the basis for calculating the maximum output speed analytically (black curve, Equation 10).

the speed of gearing and the maximum output speed because the energetic losses are on the input end of the force-transmission system.

Efficiency mediates the relationship between gearing and speed

The three systems considered presently offer contrasting relationships between the gearing and speed of a skeletal system. This relationship can be articulated mathematically from a consideration of energetics. The kinetic energy generated by these systems is equivalent to the product of the energy provided by the actuator (E_A) and its transmission efficiency

(Equation 5). One finds the following equation for the maximum speed by setting this product equal to the kinetic energy:

$$v_{\max} = \sqrt{\frac{2E_A\eta}{m}}. \quad (10)$$

This relationship indicates that speed will vary with the geometry of a force-transmission system if its gearing affects either the actuator energy or the transmission efficiency.

The locust-leg model illustrates a case in which speed is independent of gearing. This model was assumed to possess ideal transmission efficiency ($\eta = 1$) and all simulations were provided with equal stored elastic energy (i.e., $E_A = E_E$, Equation 3). An analytical calculation of maximum speed (Equation 10) matches the numerical prediction (Fig. 1G) and demonstrates no variation with differences in gearing. Therefore, gearing does not affect maximum speed in the locust's leg because this change in geometry has no effect on either transmission efficiency or on actuator energy.

Gearing affects speed in the mantis shrimp and toad models because of its influence on transmission efficiency. When drag was removed from the mantis shrimp model, differences in KT showed no effect on maximum speed (Fig. 4), which replicated the energetics of the locust model. However, the inclusion of drag caused transmission efficiency to decrease monotonically with KT_{\min} and maximum speed consequently exhibited the same negative trend (Fig. 4). This speed may be predicted analytically (Equation 10) from the values of efficiency calculated from the simulations. The same is true of the toad model, in which efficiency exhibited a positive relationship with the DA, and consequently the speed, of the system (Fig. 5D).

Energetics may be applied to understand the function of a broad array of force-transmission systems. For example, the apparatus fish use in feeding offers one of the best-studied force-transmission systems among a diversity of animals. Studies of this system have demonstrated compelling correlations between the evasiveness of prey and the KT for the linkage system that transmit force for protrusion of the jaw, even after correcting for the shared ancestry of related species (Westneat 1995). The rigorous comparative statistics in these analyses support the traditional two-species comparisons that suggest that higher gears appear in the skeletons of animals that move quickly (Smith and Savage 1956). The present results challenge the notion that skeletal geometry alone dictates the speed of a system. However, this

work does offer a number of hypotheses for understanding differences in gearing between related species.

There are a number of possible explanations for the positive correlation between the gearing of the feeding apparatus and the evasiveness of prey in fishes. First, it is possible that species possessing a skeleton with a higher KT are no faster than their low-KT relatives. If the efficiency and actuator energy used for capturing prey do not vary with KT (as in a locust's kick, Fig. 1), then speed would be predicted to be independent of gearing. It is perhaps more likely that high-KT gearing enhances energetic loss through the generation of fluid forces (as in the mantis shrimp, Fig. 3). This situation would predict a negative relationship between speed and KT, if the muscles yield similar work among these species. It is possible that a greater KT is beneficial for feeding without creating a more rapid feeding strike. High-KT species are predicted to exhibit relatively more protrusion of the jaw, which alone benefits the hydrodynamics of prey capture (Holzman et al. 2008).

Alternatively, KT may be positively correlated with strike speed among fishes under at least two different conditions. As illustrated by the ballistic feeding of the toad (Fig. 5), higher gears yield faster motion if energetic losses occur primarily on the input end of the force-transmission system. Furthermore, if the muscles used for feeding are larger in species with higher KT, then those species would actuate the system with greater actuator energy and thereby strike with both greater speed and greater protrusion of the jaw. Distinguishing among these hypotheses would be greatly aided by measurements of strike speed and of the mass of the muscles used in feeding.

In summary, the relationship between the gearing and speed of a force-transmission system may be understood from a consideration of energetics. Each of the three very different systems modeled in the present study exhibited fundamentally distinct effects of gearing on speed due to their energetic properties. This framework offers a perspective on the study of musculoskeletal mechanics that may contrast a consideration that is based solely on morphology.

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