Title: Neural control of rhythmic limb motion is shaped by size and speed

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Abstract

Over many size and time scales, behaviors such as locomotion or feeding require mechanical movements. Size and time in turn determine a behavior’s dominant mechanical properties: mass, stiffness or viscous damping. The constraints for limbed behaviors can thus be quantified by two variables: limb size and limb speed, defining a ‘mechanics space’ that shows the relative magnitude of each mechanical property for animals ranging from fruit fly to elephant. The mechanics space has three distinct regions: 1) an inertia-dominated region; 2) a gravity or elastic-force-dominated region; and 3) a viscous-force-dominated region. In the mass-dominated region, associated with large limbs moving rapidly, muscle work is translated into primarily kinetic energy. Thus, stable motion requires compensatory control and active damping. In the elastic-force-dominated region, associated with small limbs moving slowly, muscle energy is translated into primarily gravitational or elastic potential energy. Thus, compensatory control and active damping are unnecessary. Lastly, in the viscous region, associated with small limbs moving quickly, joint viscosity acts to damp actuation, resulting in exclusively stable movements. Control and stability of a limb thus depends almost entirely on the size and speed of limb movement, and this has fundamental implications for neural control.
Introduction and Methods

Brains are embodied (1). All of an animal’s behaviors that determine its evolutionary success, e.g. locomotion, feeding, and mating, are fundamentally mechanical acts (2). Consequently, the mechanics of the body provides both opportunities for and constraints on the nervous system. Thus, while it is natural to consider how evolutionary pressure shapes neural structures that control these behaviors, such pressure can only be fully understood within the context of an animal’s mechanics (1). To understand this, it is often critical to determine how size and morphology affects muscle work available relative to energy required for a given motion, an approach that well characterizes the limits of maximal locomotory behavior (3–9). However, there is a second closely related question that is not addressed by considering energetic limitations and requirements: how do size and morphology affect how energy is allocated within a given behavior; i.e., how does scale affect allocation of muscle work into the corresponding appendage’s kinetic, potential, and viscous energy, and how does this allocation affect the control of a given motion. Using biological and dynamical scaling relationships, we will succinctly summarize the dynamics of biological appendages across a wide range of sizes and speeds, which will divide appendage motions into five broad regions. The division will reveal how the neural control of motion must differ among these regions and how control may be similar for diverse animals and behaviors that fall within a single region. Portions of some regions are inaccessible due to the limitations of biological tissue and structure, representing evolutionary constraints on what motions an animal can perform.

Mechanics strongly affect rhythmic motions such as protracting and retracting a leg during legged locomotion or rhythmically moving mouthparts during feeding. Biological nervous systems generate rhythms through an array of strategies such as pacemakers, pattern generating networks, multi-level feedback loops, or circuitry that generates inter muscle-group coordination (10). The resulting motion results as the motor outputs of these neural control mechanisms are transmitted through the appendage’s biomechanics – with environmental perturbations of the appendage affecting the forces on the appendage and its resultant motion (1, 11, 12). Therefore, a biomechanical analysis of an appendage’s movements can clarify how the structure and function of the nervous system and limb control depends on morphology.

Although morphology can vary widely among animals, two key parameters constrain movement: the size of the appendage being moved, and the period of time over which the appendage is moved (13, 14). These parameters constrain motion because the available energy, mass, elastic stiffness, and viscous damping of appendages and their joints all scale differently with respect to size and time (15–17). For example, since mass increases more rapidly with size (18) than joint stiffness or damping (16), the mass of a large animal (e.g., an elephant) has a far greater impact on its biomechanics than the mass of a small animal (e.g., a fruit fly). Similarly, across the same size range, a fast motion is disproportionately more affected by viscosity than a slow motion, because viscous force depends on movement speed. Consequently, even though limb movements of differently scaled behaviors often look similar, differences in size and speed will radically alter the parameters that govern the motion, and thus affect strategies available to the nervous system as it
controls motor output (6, 13). We will present and justify scaling laws for an appendage’s mass, stiffness, and damping across the whole range of existing animal appendages, and demonstrate that these scaling laws define a rich landscape for actuating a similar motion in radically different ways depending on an animal’s size and the speed of its motion. In addition, limits on muscle (4, 19, 20) and bone stress (21) rule out certain kinds of motions entirely.

Two questions will guide our analysis of the extreme heterogeneity of cyclic animal movements: First, when a muscle performs work on an appendage, does that work primarily increase the kinetic energy of the appendage (6, 22), the potential energy of the appendage (23–25), or is the work primarily dissipated through viscous effects (26)? Second, when unanticipated energy is added to the appendage due to an environmental perturbation, can the appendage shed this energy over a short period of time (e.g. as seen in insect legs, (27–30)), or does the appendage absorb the energy, altering its ongoing motion and disrupting the intended behavior? To address these two questions, we will simulate the movement of a generalized isometrically scaled ‘limb’, and quantify how energy in this modelled limb is distributed between kinetic (inertial), potential (elastic and gravitational), and viscous (damping) energy.

The model represents simplified geometry and dynamics of an arbitrary limb segment, e.g. the tibia of a human leg rotating about the knee or the tibia of an insect leg rotating about its femur-tibia joint (Figure 1A). The limb segment is assumed to be moved by an antagonistic pair of actuators, e.g. flexors and extensors, each with inherent elastic stiffness \( k_{el} \) and viscous damping \( c \) (Figure 1B). These actuators deliver the active force \( F \) to the limb segment only as they shorten. In animals, these actuators are muscle; however, some human-made actuators also fit this description (e.g. antagonistic braided pneumatic actuators) (31). The actuators connect to the limb with moment arm \( r \). The limb segment itself is assumed to have mass \( m \), length \( L \), and a corresponding moment of inertia \( J \). The limb is assumed to operate in a gravitational field with acceleration \( g \). The horizontal displacement of the center of mass is measured by \( x \), and the rotation of the limb segment is measured by \( \theta \).

Figure 1C states the model’s equations of motion. The dynamics are first written in a familiar form in terms of the linear displacement of the actuator \( x \). The actuator force, \( F \), is equal to the sum of the passive dynamics: mass times acceleration, \( m \ddot{x} \); damping times velocity, \( c \dot{x} \); and elastic stiffness times displacement, \( k_{el}x \), with all terms resulting in the following equation of motion:

\[
\sum F_{applied} = F_{inertial} + F_{viscous} + F_{elastic} = m \cdot \ddot{x} + c \cdot \dot{x} + k_{el} \cdot x.
\]

To better model rotation around rotary joints, the equation is converted into rotary form by summing the moments of the forces about the joint (see Supplementary materials). Each parameter in the rotary equation of motion is analogous to a term in the linear equation of motion (listed in Figure 1D). All terms are the same between the equations except for the rotary stiffness due to gravity, \( k_{r,grav} \). This represents the limb’s tendency to hang in parallel with the direction of gravity and oscillate when perturbed like a pendulum. Since the moment applied by gravity is proportional to the limb rotation \( \theta \) (for small theta) in the same way as the moment applied by elastic elements, these two terms can be grouped together.
Because energy is a critical currency underlying animal behavior, the rotary equation of motion is converted into a work-energy equation by integrating the equation of motion with respect to $\theta$ (see Supplementary materials). Again, each term in the work-energy equation is analogous to a term in the equation of motion. Actuator work is converted into the limb’s kinetic energy (Fig. 2A, yellow region), dissipated due to viscosity (Fig. 2A, orange region), or stored as the limb’s potential energy (Fig. 2A, red region). This color coding will be consistently used for Figures 2, 3, and 4.

Parameter values do not depend on scale in a uniform manner. Consequently, at different size and time ranges, the relative importance of each term changes. These relative terms then define the movement, from the size range for appendages that are 100 $\mu$m (the length of the limbs of the very smallest insects, such as *Megaphragma mymaripenne*), to 2 m long (the limb length of large elephants), and from cycle times for a movement from 1 ms to 100s, the time ranges over which cyclic limb behaviors are observed. Figure 1D lists how the physical parameters in the model scale with length. Each linear parameter has a rotary analogue, which is computed by the principle of virtual work (see Supplementary material). Note that the relative scaling of inertia, damping, and elastic stiffness is unaffected by the transformation to rotary analogues (i.e., inertia scales with length by two orders of magnitude more than the other parameters). However, the stiffness due to gravity does not scale in the same way as elastic stiffness, meaning that the larger an animal is, the greater the impact of gravitation-based, pendulum-like stiffness. Further details for derivation of the scaling laws is provided in the Supplementary Material.
Results

1) Energy partition as a function of scale.

Depending on the length scale $L$ and time scale $t$, work from the muscle is partitioned differentially among kinetic, potential, or viscous energy. This is true for two reasons. First, mass scales more strongly with length than does viscous damping and muscle stiffness, such that large appendages possess disproportionally more mass than small ones, and kinetic energy scales linearly with mass. Second, kinetic energy of the system and the rate at which it dissipates energy through viscosity both depend on the velocity of movement, meaning that slow motions are fundamentally different from fast motions in how energy is distributed between kinetic, potential, and viscous energy (Figure 2A). To better understand where actuator energy goes, we plot the actuator force versus the appendage displacement to generate a ‘work loop’ in each region (32) (Figure 2B–F). These work loops allow us to track how energy is partitioned within one cycle of motion.

First consider the region called ‘kinetic’ (top left of Figure 2A). Figure 2B shows that for fast motions of large appendages, the majority of muscle work is transformed into kinetic energy (yellow), with a small amount lost through viscous effects (orange). At this scale of movement, Newton’s First Law of Motion dominates: ‘an object in motion tends to stay in motion’. This is because very little of the energy provided by the muscles is stored within elastic components or dissipated via viscous effects, enabling the appendage’s motion to continue unimpeded. This size and cycle range (limbs larger than about 100 cm at cycle times of less than approximately 1 second – see Figure 2A) spans most locomotion movements of larger vertebrates. Since the appendage’s energy is mostly kinetic, it is often necessary to decelerate the appendage with some kind of braking, such as activation of an antagonistic actuator. In animal locomotion, this braking is often seen as an activation of antagonistic muscles to slow a swinging limb (6).

As appendage movement becomes slower, more muscle work is stored as potential energy, until an equal proportion of muscle work is converted into kinetic and potential energy at the line between the region labelled ‘kinetic’ and a region we call ‘quasi-static’, Figure 2A. Along this line, the appendage is oscillating at its resonant frequency. This line represents the most efficient form of motion, where energy is mostly conserved and exchanged between potential and kinetic energy, requiring the minimum amount of energy to be delivered by the muscles for a given $L$ (33). Movements for appendages that are smaller or slower than this line exist in this second region, the quasi-static region, where muscle work is primarily stored as potential energy (area marked ‘quasi-static’, Figure 2A). Despite the name ‘quasi-static’, such motion need not be slow in an absolute sense; it must only be slow enough that most muscle work is stored as potential energy, rather than being converted to kinetic energy or dissipated through viscous losses.

The work loops show that in the quasi-static region (Figure 2C and D), muscle energy is primarily converted into elastic potential energy (red), with kinetic energy and viscous damping being much smaller. Because these ‘dynamic’ forms of energy can be neglected, the dynamics of such a system are comparable to those of a static structure; in fact, the term ‘quasi-static’ comes from civil engineering literature, where such ‘quasi-static’ mechanics are a good approximation of how buildings and other structures respond to external forces (34).
For quasi-static movements, the kinetic energy of the appendage is always small relative to its potential energy. This is one reason why actuation of the appendage does not result in the ‘pendulum-like’ movements observed in a human leg during walking (13). Instead, the appendage moves across a series of positions where the muscles are in near-equilibrium with energy-storing components (i.e., elastic antagonistic muscle tendon units or massive limbs raised against gravity). To hold an appendage in a static position, the muscles must perform a constant level of work (in this specific case, generate a constant force at a constant contraction). Consequently, velocity can only be generated by changing the muscle work over time, either by driving the appendage with positive muscle power, or by decreasing muscle power and using stored potential energy to drive the appendage (27). In addition, the muscles do not need to ‘brake’ motions because the limb possesses effectively no kinetic energy, unlike motions in the kinetic region (6). If the primary form of potential energy storage is elastic, as in small animals such as insects, their posture may be maintained entirely passively, no matter their orientation relative to gravity (13).

As motions become faster, dynamic energy (e.g. kinetic and viscous) increases; however, as appendages become smaller, mass and thus kinetic energy decreases. As a result, most actuator energy is dissipated by viscous effects within the limb (Figure 2A, orange region; Figure 2E, orange). In this region, muscle work translates to limb velocity, qualitatively similar to in the kinetic region, yet the lack of inertia in the system will prevent the system from oscillating, unlike the kinetic region. As limbs become larger (length scale between 1 cm to 10 cm), motions again become kinetic, although substantial damping is still present (Figure 2A, yellow region; Figure 2F).

2) Response to perturbations as a function of scale.

In addition to the three actuation regions described so far, there are also two perturbation regions that categorize the system’s ability to remove unwanted energy added to the movement. If this energy is not removed, the animal may not successfully complete its intended motion. For large size ranges (above roughly 10 cm, dotted black line in Figure 3), the damping parameter $c$ is so small that most energy input into the appendage is conserved, and indefinitely exchanges between kinetic and potential energy. Such a system is called “underdamped”, because so little damping is present. In this case, lasting alterations to the ongoing motion may occur if excess kinetic energy is not removed from the appendage, e.g. via energetically costly eccentric muscle contractions (Figure 3B). However, a quasi-static system’s natural frequency is higher than that of its motion. Thus, while the limb oscillates after a perturbation as in the kinetic region, the amplitude of the perturbation-induced oscillation decays more quickly relative to the period of motion (Figure 3C).

For small size ranges (below roughly 10 cm, dotted line in Figure 3), the damping parameter is large enough that the appendage will dissipate excess energy. For a given length-scale, energy is removed at a particular rate. For slower motions (e.g. Figure 3D), energy is dissipated quickly relative to the cycle period $T$ of the ongoing motion, meaning that perturbations may not have a noticeable effect on motor output. However, for faster motions, energy is dissipated slowly relative to the cycle period, meaning that much like in the kinetic underdamped region, a perturbation may cause lasting alterations to the ongoing motion (Figures 3E and F).
The scaling analysis of mechanics allows us to plot a wide range of animal oscillatory behaviors to determine the mechanical consequences of control of these behaviors. Figure 4 plots the durations of several periodic animal behaviors against the length-scales of the animal or appendage that executes that behavior. While our collection of behaviors is not exhaustive, several intriguing patterns can be observed.

A remarkably diverse collection of appendage movements can be classified as quasi-static (Figure 4, red). Very slow limb movements in large vertebrates exist in this region (such as the slowest elephant locomotion (5)), as do postural movements in vertebrates (35). Slower movements of animals with larger appendages and faster movements for animals with smaller appendages, such as rodent limbs and slower moving insect legs (36–39) all fall within the quasi-static region. While human fingers can be actuated through multiple regions, most everyday motions of the hand exist in the quasi-static region (40).

A large class of diverse behaviors are found in the quasi-static overdamped region (Figure 4, red and below dotted line), including some leg movements of insects and small vertebrates (13), slow human hand motions (40), and the rhythmic protraction and retraction of the Aplysia feeding apparatus (41). All of these motions share common principles of actuation: muscle work is primarily stored as elastic potential energy, and extra energy added by perturbations is removed “for free” by viscosity present in the body.

Faster behaviors exist in the viscous region (Figure 4). Mice, cockroaches, mites, beetles, and fruit flies can all step at frequencies that would place the behavior within the viscous overdamped region, while pursuing prey (42), escaping predators (39, 43), or when heated to extreme temperatures (44). For all these behaviors, muscle work is resisted by internal joint viscosity. Additional rapid motions are omitted either because our assumptions regarding joint mechanism damping cannot be applied (e.g. insect flight) or because they are not periodic in nature (e.g. insect jumping).

How is it that so few behaviors are present in the upper left-hand corner of Figure 4? Estimates of bone stress (21) and muscle stress (19) (gray lines in Figure 4) suggest that such motions are impossible for biological systems. For motions in the kinetic region, the energy of motion is so great that the muscles and bones would be ripped apart when changing the direction of motion. These limits also show that the forces required for rapid motions in the viscous region would tear muscle. While these boundaries are approximate, they illustrate how our framework complements previous studies of the absolute limits on motion (3–9).

Across many orders of magnitude of time and length scale, our model predicts the motor output required to execute animal behaviors. By asking how muscle work is converted into appendage energy and how unwanted appendage energy is dissipated, we can sort all animal behaviors into three actuation regions, i.e., kinetic, viscous, and quasi-static, and two perturbation regions, i.e., overdamped and underdamped. Understanding the motor patterns required to actuate and control behavior informs and constrains the control performed by the nervous system, both between species that operate at different scales, and within a single species that spans different length scales (e.g., due to growth over an animal’s lifetime) and time scales (e.g. walking slowly versus running quickly).

Discussion
By analyzing the different proportional relationships of mass, viscous damping, elasticity, and gravity across a range of size and time ranges, we found three mechanical ‘regions’ of behavior: one in which inertia is dominant (the kinetic region), a second in which elasticity or gravity is dominant (the quasi-static region), and a third in which damping within the joint is dominant (the viscous region). Consequently, any control scheme for a limb must consider the region in which the limb will be moved in order to successfully control the limb. This consideration is agnostic as to what species the animal is and how that animal is actuating the movement – these regions are based only on the mechanics of the joint and the size of the limb.

The mechanical regions we have described have important consequences for the control of motion. For example, when large animals (such as humans or horses) move their legs during the swing phase of locomotion, neural input to the agonist muscles is high at the beginning of the motion, silent during the middle of the swing, and antagonistic muscles are activated at the end, reflecting the ability of the system to use inertia to continue the motion. In smaller animals, however, the amount of time in which the nervous system is ‘silent’ (i.e., the time that the limb proceeds passively) decreases, until, at the size of stick insects, the agonist muscles are active during the entire swing phase – reflecting the need of the nervous system to compensate for larger and larger elastic forces but smaller and smaller inertial forces (6, 13). It is this region difference (from kinetic to quasi-static) that explains the difference in the neural inputs during the swing phase of these locomotory movements.

Fundamental to this difference between horse and stick insect motor control is our assumption that the stiffness of the elastic forces with \( L \), not \( L^2 \). Elastic forces are often assumed to scale with \( L^2 \) (13, 28), perhaps because a muscle’s maximum force is proportional to \( L^2 \) (19). Perhaps unexpectedly, this observation actually supports our assumption; if muscle force is, roughly speaking, equal to its stiffness \( k \) times its length \( L \), then the only way for the muscle force to scale with \( L^2 \) would be for \( k \) to scale with \( L \). Indeed, recent biomechanical models have recognized and incorporated the same assumption that \( k \) scales with \( L \) (15, 16). Recognizing that \( k \) scales with \( L \) directly leads to the conclusion that for small animals, potential energy is primarily stored in elastic elements, but for large animals, potential energy is primarily stored via gravitationally-based, pendulum-like mechanics (see Supplementary materials, Figure S4).

Recognizing that potential energy is stored differently across scales suggests that some historical measures of dynamical scaling should be revisited and modified in the future. For example, the Froude Number, the ratio between centripetal force and gravity (33, 43, 45) is often used to characterize locomotion across scales, yet it does not consider elastic forces within the limb. This is appropriate for analysing the locomotion of fast-moving, large animals that locomote in the kinetic region, such as horses, because the inertial forces dominate the behavior and the pendular dynamics of the leg do in fact scale with \( L^2 \). However, for small animals that locomote within the quasi-static or viscous regions, the Froude number quantifies forces that are not dominant during the behavior (Figure S5). Consequently, the Froude number’s utility for locomotion in small animals may have to be re-evaluated.

The scaling analysis we have presented accounts for how size and speed affect allocation of actuator energy, i.e., it is an analysis of where generated energy ‘goes’. However, the actuators’ inherent properties may also limit how much energy they can produce. Although
previous studies have modelled scale-dependent limitations of muscles, tendons, and springs (3, 15), we do not consider the impact of actuator scaling in this study.

By not explicitly including the features and limitations of biological actuators in this study, our results can be applied to robots as well. Robots are often used as neuromechanical models of animals (10, 12, 16). However, a robot’s usefulness as a model depends on whether its mechanics match those of the animal it models (6). We interpret such ‘matching’ as a robot whose limbs have the same balance between kinetic, viscous, and potential energy as the animal during locomotion. Because the metals, polymers, and other materials used to construct robots have different mass and viscoelastic properties than biological tissues, a robot and animal with the same length scale may have very different mechanics. Instead, we propose that engineers balance these forms of energy, in two ways: First, the engineer must alter the robot’s mechanics with physical or virtual elasticity or viscosity to be proportional to those of the model animal. Second, the engineer must design the speed of the robot’s behavior such that it operates in the same dynamic region as the animal. For example, a robotic stick insect with legs one meter long may be an appropriate model, provided its joints have been given viscoelastic elements proportional to its leg mass, and it moves so slowly that its motions are quasi-static. Building robots whose motions occupy the same dynamic region as their model animal may lead to even more fruitful efforts in biologically inspired robotics.

In this study, we show that the limb morphology of animals has direct and important consequences for the control of that limb. These consequences greatly affect how energy is partitioned in the limb and the limb’s ability to resist perturbations. These mechanics represent a continuum of all limb motion, allowing us to show how the leg movements of stick insects and the leg movements of horses, while looking extremely different from a neural perspective, are just two ends of a size and speed mediated spectrum of movement.
Figures:

Figure 1 – Formulation of the model. A) Humans, stick insects, and many animals possess rotary joints actuated by antagonistic muscle groups. B) We model this configuration by a rigid massive tibia segment rotating about a fixed point, moved by a pair of actuators that can only generate active tension and possess intrinsic viscoelasticity. Furthermore, gravity pulls the center of mass of the tibia (white and black circle) downward. C) The equation of motion can be written in terms of $x$, the actuator stretch. In this case, the active muscle force is equal to the tibia’s mass times acceleration plus the actuators’ damping times velocity plus stiffness times displacement. However, this formulation does not incorporate the rotary, pendulum-like dynamics of the tibia, so we can consider the rotary form of this equation by calculating the moment of each force about the joint. Now, gravity applies a restoring moment like a spring, introducing an additional term into the equation of motion. Finally, to understand how energy is exchanged throughout this system, the moments are integrated over the angular displacement $\theta$. In each equation, terms are color coded based on whether they represent kinetic (yellow), viscous (orange), or potential (red) energy. This color code is continued throughout the manuscript. D) Each term in the equation of motion scales with length differently (see Supplemental materials for details). Each linear motion parameter has a rotary analogue. The relative scaling between the linear parameters is preserved in the rotary analogues. Note that gravitational stiffness scales with a higher exponent than does elastic stiffness, meaning that large animals possess pendular dynamics, but small animals do not.
Figure 2 – **Muscle work is converted into kinetic, potential, or viscous energy depending on the length- and time-scales of an appendage’s movement.** A. Depending on the length scale ($L$) and cycle period ($T$) of a motion, muscle work is transformed into a different form of energy: Kinetic energy (yellow), viscous energy (orange), or potential energy (red). Black lines indicate where the balance between these terms shifts (see Supplemental materials for analytical derivation of the lines). The solid black line is the boundary between the kinetic energy and quasi-static (i.e. potential energy) regions; the dashed black line is the boundary between the quasi-static and viscous energy regions; the dash-dotted line is the boundary between the viscous energy and kinetic energy regions. The dotted black line indicates the length scale at which motions transition from overdamped to underdamped. In total, five combinations of $T$ and $L$ are identified: B. Kinetic underdamped, in which kinetic energy dominates and perturbations cause the limb to oscillate (see Figure 3, B-F); C. Quasi-static underdamped, in which potential energy dominates and perturbations cause the limb to oscillate; D. Quasi-static overdamped, in which potential energy dominates and perturbations do not cause the limb to oscillate; E. Viscous overdamped, in which viscous effects dissipate most energy and perturbations do not cause the limb to oscillate; and F. Kinetic overdamped, in which kinetic energy dominates and perturbations do not cause the limb to oscillate. For each, the actuation moment ($M$) acting about the limb is plotted against the rotation of the joint ($\theta$) in black. The area inside the loop represents energy transferred from the limb to the environment through viscous loss. The area under the loop represents energy contained in the limb, either as kinetic (yellow) or potential (red). The colors on the surface plot match the colors of the work loops.
Figure 3 – How an appendage removes unwanted energy from perturbations depends on its length-scale. A. Perturbations decay differently with respect to time ($T$) depending on length ($L$). Black lines represent boundaries between different responses to perturbations. The dotted black line indicates the length scale at which motions transition from overdamped to underdamped. The solid black line is the boundary between the kinetic energy and quasi-static (i.e. potential energy) regions; the dashed black line is the boundary between the quasi-static and viscous energy regions; the dash-dotted line is the boundary between the viscous energy and kinetic energy regions. Perturbation force of 20% the driving force was applied for one cycle, signified by the black horizontal bar in B-F. This perturbation caused the motion to deviate from the unperturbed amplitude (indicated by a dashed black line in each plot). To track how the amplitude varies from cycle to cycle, the maximum angle reached during each cycle is traced with a spline (solid black line in each plot). Small appendages have more damping and naturally remove unwanted energy from the system. However, depending on the cycle time ($T$), energy may be removed at an impractically slow rate. B. In the kinetic underdamped region, a small perturbation alters the motion in a highly erratic way for many subsequent cycles because the energy cannot be easily dissipated. C. In the quasi-static underdamped region, the mass is so small relative to the other parameters that the system rapidly returns to its previous oscillatory pattern. D. In the quasi-static overdamped region, the system does not vibrate because it is overdamped. E. In the viscous overdamped region, a perturbation does not cause erratic vibration as in B, but it does alter the mean angle of the ongoing motion. F. In the kinetic overdamped region, a perturbation substantially alters the mean angle of the ongoing motion, but does not cause erratic oscillation as in B because it is overdamped.
Figure 4 – Periodic animal motions fall into separate dynamic region depending on the appendage’s length scale and the motion’s time scale. Thick black horizontal lines indicate cycle periods for a given animal and its length scale (elephant (5), horse (46), emu (47), human (45), red kangaroo (48), rock wallaby (48), cat (35) spring hare, rat kangaroo (48), human finger tapping (49, 50), rat (36), stick insect (51), hopping mouse (52), mouse (37), sea slug grasp during feeding (41), discoid cockroach (43), American cockroach (39), tiger beetle (42), mite (44), fruit fly (53).

Black lines indicate barriers between muscle work and perturbation energy removal regions. The solid black line divides the inertial energy and quasi-static regions; the dashed black line divides the quasi-static and viscous energy regions; the dash-dotted black line divides the viscous energy and inertial energy regions. The space above the dotted black line is underdamped and the area below is overdamped. The dashed gray line represents a line of constant, maximum bone stress (100 MPa). The dotted gray line represents a line of constant, maximum muscle stress (300 kPa). Red lines indicate cycle periods for a given genus and its length scale. Muscle force appears to limit the speed of biological motions.
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