A theory of physiological similarity in muscle-driven motion

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Muscle contraction is the primary source of all animal movement. I show that the mechanical output of such contractions is constrained by a characteristic dimensionless number, the "effective inertia", Γ. Contractions with equal Γ may be considered *physiologically similar*, in the sense that they involve equal fractions of the muscle's maximum strain rate, strain capacity, work and power density; there exists a unique musculoskeletal geometry which enables a unit volume of muscle to deliver maximum work and power simultaneously, corresponding to Γ close to unity. External forces truncate the accessible mechanical performance space by introducing parasitic losses, and fundamentally alter how musculoskeletal anatomy modulates muscle performance, challenging canonical notions of skeletal force-velocity trade-offs. Γ varies systematically under isometric transformations of musculoskeletal systems, with profound consequences for our understanding of muscle mechanics and animal locomotion.

Muscle, the "prime mover" of the animal kingdom, is used for acts of tender kindness, devastating brutality and astonishing grace. By conversion of chemical into mechanical energy, it enables contractions long-lasting and cyclical, actions fast and forceful, movements precise and reflexive. Whether an animal swims, runs, crawls or flies; whether it is smaller than the tip of a sharp pencil or heavier than 15 school buses; whether it first appeared millions or only thousands of years ago — muscle is what gets it about [1–4].

Juxtaposed to this diversity stands the observation that many functional, physiological and ultrastructural features of muscle vary remarkably little [1, 5, 6], suggesting the existence of general limits to what it can achieve. Identification of these limits, and assessment of their consequences for locomotor performance and musculoskeletal anatomy, has a long history in biomechanics and muscle physiology [e. g. 7–24]. A particularly successful and thus popular approach in comparative studies of animal locomotion has been the notion of similarity indices, derived via dimensional analysis, and introduced to biology in the hope to replicate the success it afforded in the physical sciences [e. g. 11, 13, 14, 25]. Remarkably, the two dominant similarity indices for animal movement — the Froude and the Strouhal number — consider elastic and gravitational forces instead of muscle forces as the primary agents of motion [3]. The scarcity of similarity theories which make explicit reference to muscle [see e. g. 16, 17, 21, 22] may be partially explained by the complexity of muscle as a motor: the force, work and power output of muscle depend in non-trivial fashion on its strain rate [26], strain [27], and contractile history [28]. Appropriate assessment of muscle performance thus requires coupling these characteristic properties with both internal and external forces, in order to avoid results that are mechanically possible, but physiologically prohibited [29–31]; a task rarely addressed and so challenging that it typically requires numerical resolution [e. g. 15, 19, 32–34].

In this text, I investigate how the interaction between physical constraints, muscle physiology, and the anatomy of musculoskeletal systems places bounds on the mechanical performance space accessible to muscle. I demonstrate analytically that the maximal mechanical output of every muscle contraction is governed by the competition between two distinct limits which arise from physiological and anatomical constraints. The relative importance of these constraints characterises the degree of 'physiological similarity' of muscle contractions, a metric defined by a dimensionless number that enables direct comparison of musculoskeletal systems across size, and physiological and anatomical make-up.

Two speed limits in muscle-driven motion

Consider the seemingly simple example of a muscle with constant gear ratio G, capable of exerting a maximum constant force F_{max}. What is the maximum speed it can impart to an object of mass m in a single contraction?[1] Mass, force and gear ratio together determine the net acceleration, $a = F_{max}Gm^{-1}$, of dimension [L t^{-2}]. Identifying a maximum a speed v of dimension [L t^{-1}] thus requires to specify either a time, $v_t \sim at$, or a displacement, $v_\delta \sim \sqrt{a\delta}$. These results may be recognised as the first time- and displacement-integrals of Newton's 2nd law, respectively, which link the speed imparted to the delivered impulse, $mv \sim p \sim \int F_{max}Gdt$, or the work done, $mv^2 \sim W \sim \int F_{max}Gd\delta$. Unfortunately, this analysis does not yet yield the resulting speed, for Newtonian mechanics alone provides no information about what the appropriate displacement or time might be. Because no muscle can contract in perpetuity, both boundary conditions may be identified through introduction of appropriate physiological and anatomical constraints.

In order to develop some intuition for how such constraints enter the problem, consider the joyful if simplistic analogy of riding a bicycle: If the gear is much too small, it is impossible to increase speed, because the muscle cannot contract quickly enough to accelerate the pedals; the best it can do is to keep them spinning at their current speed. If the gear is much too large, in turn, the muscle will accelerate the pedals rather slowly, so that the speed imparted at the end of a single contraction cycle will be miniscule. Both scenarios are manifestations of two limits to the speed of muscle-driven motion: How fast a muscle can contract, and by how much it can shorten. The axiomatic limit on muscle strain rate, $\dot{\varepsilon}$, and the anatomical limit on muscle strain, ε, can inform the mechanical analysis, for they each impose a distinct limit on the maximum impulse muscle can deliver, and the maximum work that it can do.

The maximum distance available for acceleration must be some fraction of the muscle fibre length l_m, $\delta_{max} = l_m\varepsilon_{max}G^{-1}$, where I consider ε_{max} to be independent of the gear ratio. This distance is covered in a time $t \sim \sqrt{2\delta_{max}a^{-1}}$ (the factor two arises from integration). Where work and impulse are limited by the strain capacity of muscle, the speed imparted then follows from either maximum distance or time as:

$$v_{\text{Bo}} = \sqrt{2\frac{W_{max}}{m}} = \sqrt{\frac{2}{m}V_m\sigma\varepsilon_{max}} \tag{1}$$

where V_m is the muscle volume, σ is the muscle stress, and $W_{max} = F_{max}l_m\varepsilon_{max}$ is the work done in a contraction to ε_{max}. In recognition of the pioneering work of GA Borelli, who first derived an equivalent result [7], I will refer to eq. 1 as the Borelli-limit to speed, and define the Borelli-number, $\text{Bo} = \sqrt{2Wm^{-1}}v^{-1}$.

Consider next the case where muscle work and impulse are limited by the maximum shortening speed of muscle instead. Let this maximum shortening speed be $v_{max} = l_m\dot{\varepsilon}_{max}$, where $\dot{\varepsilon}_{max}$ is the maximum strain rate in units muscle lengths per second. Reaching v_{max} requires accelerating the mass over a distance $\delta_{max} \sim 1/2v_{max}^2a^{-1}G^{-2}$, which takes a time $t_{max} \sim v_{max}a^{-1}G^{-1}$. The speed imparted then follows from either as:

$$v_{\text{Hi}} = \frac{v_{max}}{G} = \frac{l_m\dot{\varepsilon}_{max}}{G} \tag{2}$$

which I will call the Hill-limit to speed, with associated Hill-number $\text{Hi} = l_m\dot{\varepsilon}(Gv)^{-1}$, in recognition of AV Hill's groundbreaking contributions to our understanding of the force-velocity properties of muscle [26].

The Borelli- and Hill-number are dimensionless numbers which identify two possible conditions for dynamic similarity in muscle-driven motion: where muscle does equal amounts of mass-specific work, movements will have equal Borelli-numbers; equality of Hill-numbers, in turn, implies equal ratios between the muscle contraction speed and the musculoskeletal gear ratio. But which number is appropriate to assess the limit which binds maximum speed?

To answer this question, I once more borrow from the versatile toolbox of dimensional analysis: the ratio between a characteristic speed and a characteristic displacement depends on the acceleration via $v^2\delta^{-1} \sim a$. Thus, for vanishing acceleration, the speed gained per unit displacement is negligible, and the muscle will have shortened maximally long before it has reached its maximum shortening speed; the contraction is quasi-static *relative to the maxi-*

[1] An exact analysis would need to consider separately the mass of the object and of the muscle. For simplicity, I here lump both into one term. This lumping will introduce an error in calculations where the muscle mass is comparable to the external mass that is moved by the muscle, but this error will only change the result in magnitude, and not in principle, because the distributed mass of the muscle can be taken into account with an "effective mass"-term which is a fixed fraction of the total muscle mass [35].

mum strain rate. If the acceleration is large, in turn, the maximum speed is reached with minimum length change of the muscle, and within miniscule time; the contraction is quasi-instantaneous. Thus, in general, a muscle which contracts against a sufficiently small mass is bound by the Hill-limit (Fig. 1 A & B); the impulse and work it can deliver, and thus the speed it can impart, are limited by its maximum strain rate. In contrast, a muscle which contracts against a sufficiently large mass is Borelli-limited (Fig. 1 A & D); the impulse, work and speed it can deliver are limited by its strain capacity.

This dimensional argument is simple, but unsatisfying – how large is a sufficiently large, and how small is a sufficiently small mass? To render the qualitative argument quantitative, I next normalise the mass with the relevant physiological properties of muscle, with the aim to find the reduced mass, or "effective inertia" of the musculoskeletal system.

The effective inertia of a muscle contraction

The Borelli- and Hill-limit are absolute: a muscle limited by its strain capacity cannot increase the mass's kinetic energy further, even if it could contract faster still; a muscle contracting with its maximum strain rate can no longer increase the momentum of the mass, even if it has not yet shortened by the maximum possible amount. The maximum speed muscle can impart is thus determined by whichever of the two speeds is lower (Fig. 1 A); the relevant limit can be identified by consideration of the ratio between the Hill- and the Borelli-number:

$$\Gamma = \left[\frac{\mathrm{Hi}}{\mathrm{Bo}}\right]^2 = \frac{1}{2}\left[\frac{l_m^2}{G^2}\right]\left[\frac{\dot{\varepsilon}_{max}^2}{\sigma\varepsilon_{max}}\right]\left[\frac{m}{V_m}\right] \qquad (3)$$

I squared the ratio for convenience; the effective inertia Γ may then be interpreted as the ratio between the maximum kinetic energy muscle can impart, and the maximum work that it can do [see below, and also the supplementary information (SI) in 33]. The bracketed terms identify three key contributors to the effective inertia: the geometry of the musculoskeletal system, represented by the gear ratio and the allocation of a unit volume of muscle into fibre length versus cross-sectional area; the physiology of the muscle, represented by the strain rate, stress and strain capacity; and a characteristic density m/V_m. For $\Gamma < 1$, the muscle uses a fraction $\varepsilon = \Gamma\varepsilon_{max}$ of its strain capacity to reach its maximum strain rate, and thus operates in the Hill-limit (Fig. 1 A & B). For $\Gamma > 1$, in turn, the muscle uses its entire strain capacity to accelerate to a fraction $\dot{\varepsilon} = \Gamma^{-1/2}\dot{\varepsilon}_{max}$ of its maximum strain rate, and thus operates in the Borelli-limit (Fig. 1 A & D). An effective inertia of unity corresponds to the unique special case for which a constant force muscle operates simultaneously in both limits.

The equations of motion landscape and the Hill-Borelli transition for real muscle

If muscle were to generate a constant force, the above analysis would be exact. However, muscle is more complex a motor. The force it generates is, in general, a function of both its shortening speed and its length [26, 27]: muscle produces maximum force during an isometric contraction at "optimal" length, and less force for any deviation from these conditions. Unfortunately, as the muscle contracts, it must change both its length and contractile speed. As a result, the net force it generates — and thus the acceleration the mass experiences — varies dynamically throughout a contraction. In order to assess the effect of this dynamic complexity on the effective inertia, I now introduce the force-length (FL) and force-velocity (FV) properties of muscle. I make three simplifying assumptions to aid this analysis: the muscle activation time constant, t_{act}, is much smaller than the characteristic acceleration time, $t_{act} << t^* \sim v_m m F_m^{-1} G^{-2}$, so that the muscle can be considered fully activated throughout; I consider a single contraction from rest; and the FV and FL functions are independent. The muscle force then may be written as $F_m = F_{max} f(v_{rel}) f(l_{rel})$, where the normalised FV and FL functions express the muscle force as a fraction of the peak muscle force, and thus take a maximum value of unity, and a minimum value of (or close to) zero (dashed lines in Fig. 1 B & D).

In order to develop some intuition for the effect of FV and FL properties on muscle contraction dynamics, I briefly return to the simpler case of a muscle which generates a constant force throughout the contraction. The contraction dynamics — that is the change of speed and displacement with time — are governed by the equation of motion (EoM), $a = F_{max} G m^{-1}$. All possible solutions of this EoM can be visualised in a single plot of the normalised net force against the normalised displacement and velocity, respectively. Because the net force is constant, all such solutions lie in one single plane (grey plane at the top of Fig. 1 C). Consider now the path inscribed onto this plane by contractions with differ-

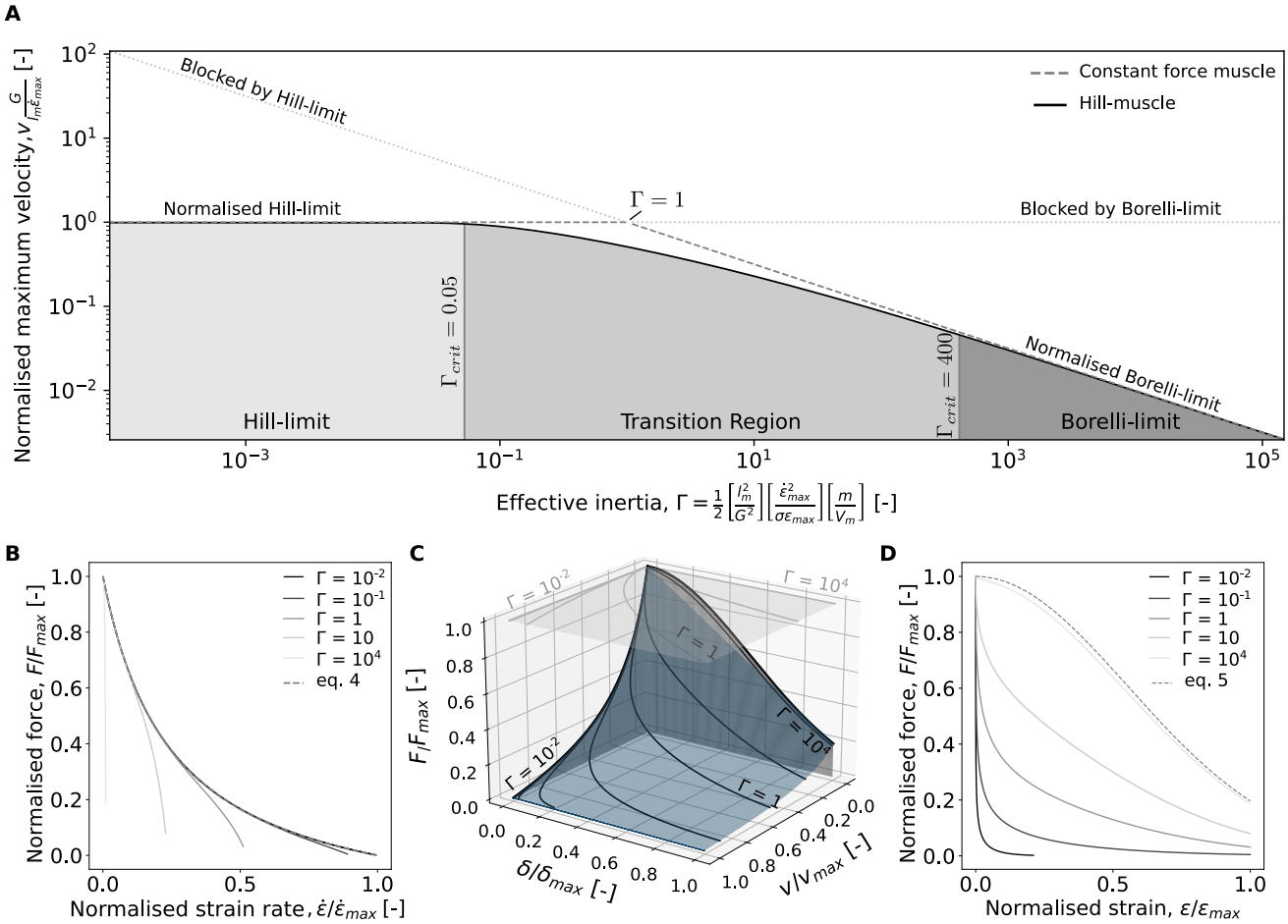

Figure 1 | (**A**) The maximum speed muscle can impart in a single contraction depends on the effective inertia, Γ, of the mass-musculoskeletal system. For $\Gamma < 1$, the speed is bound by the Hill-limit (eq. 2), which arises because muscle has a finite maximum strain rate. For $\Gamma > 1$, the speed is bound by the Borelli-limit (eq. 1), which arises because muscle can only shorten by a fraction of its length. For a constant force muscle, the Hill- and the Borelli-limit are exact expressions for the maximum speed (dark grey dashed line), and the transition between both occurs abruptly at $\Gamma = 1$. For a Hill-muscle (solid line), where the force depends both on muscle strain rate and strain, the Hill- and the Borelli-number are asymptotic solutions, exact only in the limit of vanishing and diverging Γ; they are however close approximations for $\Gamma_{crit} < 0.05$ and $\Gamma_{crit} > 400$, so defining a large transition region (see text). (**B**) The effective inertia controls the fraction of the maximum strain rate muscle can access. For vanishing Γ, the contraction may be considered quasi-instantaneous, and the relation between force and velocity is described solely by the FV relationship of the muscle (cf. to (**D**)). (**C**) The solutions of all possible equations of motion can be visualised on a 3D landscape which relates the normalised force to normalised displacement and velocity. For a constant force muscle, the resulting contractile landscape is a single plane (grey, on top), but for a Hill-type muscle, it describes a complex 3D envelope (blue), shaped by the projections of the FV and FL relations, respectively. A muscle with small Γ operates in the Hill-limit and contracts close to the FV plane; a muscle with large Γ operates in the Borelli-limit and contracts close to the FL plane. (**D**) The effective inertia determines the fraction of the maximum strain over which muscle can accelerate. For diverging Γ, the relation between force and displacement approaches the FL relationship (dashed line), and the contraction may thus be considered quasi-static with respect to the maximum relative speed (cf. to (**B**)).

ent effective inertias; as illustrative example, let the very same muscle contract against different masses. For any specific mass, the contraction describes a unique trajectory onto the EoM plane: If the mass is very small, Γ vanishes and the mass thus gains normalised speed rapidly, and with minimum normalised displacement; the contractile trajectory is almost parallel to the FV-line. If the mass is large, in turn, Γ diverges and the normalised speed remains small throughout the displacement; the contractile trajectory is almost parallel to the FL-line. For intermediate masses and Γ close to unity, the contraction involves significant changes in both normalised speed and displacement, and thus describes a more com-

plex FVL trajectory. For a constant force muscle, the Hill- and the Borelli-limit are exact expressions for the maximum speed muscle can impart; the transition between both is sharp, and occurs at $\Gamma = 1$, where the muscle reaches its maximum contraction velocity exactly when it has contracted by its maximum length (Fig. 1 C).

Consider next the more complex case of a Hill-muscle with FV and FL properties, yielding the EoM, $a = F_{max} G m^{-1} f(v_{rel}) f(l_{rel})$. For a constant force muscle, the FV- and FL-functions take a constant value; an EoM-plane is thus span by two straight lines. For a muscle where force changes with length and velocity, these lines become curves, and the EoM-plane is thus transformed into a complex EoM landscape, shaped by their projection (Fig. 1 C). The principal logic and interpretation, however, remain the same: If muscle contracts against a vanishing mass, Γ is small, the acceleration is large, and the muscle reaches its maximum velocity with a small change in length. The EoM of the contraction is defined solely by the muscle's FV properties, $f(l_{rel}) \approx$ constant, so that the contractile trajectory is approximately equal to the FV-curve (Fig. 1 B-C). If muscle contracts against a diverging mass, in turn, Γ is large and the acceleration is small, and the muscle will have shortened by its maximum amount long before it reached its maximum strain rate. The EoM of the contraction is defined solely by the muscle's FL properties, $f(v_{rel}) \approx 1$, so that the contractile trajectory is approximately equal to the FL-curve (Fig. 1 C-D). The relative FV and FL functions may thus be interpreted as the sole contributors to the EoMs of two contractions which represent unphysical extremes: a quasi-instantaneous contraction which reaches the maximum strain rate with vanishing strain; and a quasi-static contraction, during which a muscle shortens by its maximum strain with a vanishing increase in strain rate. Between these two extremes, across a large range of intermediate masses, both strain rate and strain change significantly during a contraction, as indicated by the more complex contractile trajectory on the EoM-landscape (Fig. 1 A-C); the contraction dynamics are then influenced by both the FV and the FL relationship. The Hill- and the Borelli-limit are now asymptotic, exact only for a vanishing or diverging mass, respectively; the transition between both is no longer sharp, but instead occurs across a transition region around an effective inertia of unity (Fig. 1 D).

The above analysis is agnostic to the exact form of the FV and FL functions. However, in order to quantify the maximum speed for effective inertias close to unity, to estimate the size of the transition region, and to determine the FVL trajectory of muscle across the EOM landscape, an explicit EoM must be solved. There are no accepted first principle forms for the FV and FL functions of striated muscle [but see 36, for exciting recent developments], but ample empirical candidates. I choose two common forms, not to proclaim their superiority, but merely by way of example; the procedure laid out here may be followed just as well for any other choice. I describe the FV relationship with a normalised Hill-equation [1, 26, See dashed line in Fig. 1 B]:

$$F_m = F_{max} \frac{1 - v_{rel}}{1 + K v_{rel}} \tag{4}$$

Here, $v_{rel} = v_m / v_{max}$ is the shortening speed relative to the maximum speed, and K is a dimensionless constant of order unity [for vertebrate muscle, $K \approx 4$, which I use for all calculations in this manuscript. See 3].

The FL relationship, in turn, may be written as [e. g. 37, See dashed line in Fig. 1 D]:

$$F_m = F_{max} \exp\left[-\beta \varepsilon^2\right] \tag{5}$$

where β is a dimensionless shape parameter [a reasonable value is 6.5, which I use for all calculations in this manuscript, see e. g. 38], and I have used the simplifying assumption that the optimal length is equal to the length of the muscle fibres at the start of the contraction.

Combination of both functions results in an EoM akin to that for a fully activated Hill-type muscle:

$$\ddot{x} = \frac{F_{max} G}{m} \underbrace{\left[\frac{1 - \dot{x}\frac{G}{v_{max}}}{1 + \dot{x}\frac{KG}{v_{max}}}\right]}_{f(v_{rel})} \underbrace{\exp\left[-\beta \left(x \frac{G}{l_m}\right)^2\right]}_{f(l_{rel})} \tag{6}$$

Eq. 6 is a first order non-linear differential equation which must be solved numerically, and for which I chose two termination criteria: when the strain rate is within 0.1% of its maximum (the Hill-equation is asymptotic, i. e. the maximum strain rate is reached only in the limit $t \to \infty$), or when muscle has shortened by its maximum amount. The solution reveals the exact variation of the maximum speed with Γ, and demonstrates that for sufficiently large or small Γ, the Hill- and the Borelli-limit are satisfying ap-

proximations of the achievable speed (Fig. 1 A). Because eq. 6 has, to the best of my judgement, no analytical solution, I do not think it possible to derive a general closed-form expression for the size of the transition region, i. e. values for the effective inertia below and above which the maximum speed deviates by more than a few percent, say, from the Hill- and the Borelli-limit, respectively. A suitable approximation, provided that neither the FL or FV functions are very steep, may be found by calculating the values for Γ at which a muscle with constant force would reach (i) the Hill-Limit while using only a small percentage of its strain capacity, and (ii) the Borelli-Limit with only a small percentage of its contractile speed capacity. As illustrative example, setting this percentage to 5% yields a lower bound $\Gamma_{crit} \approx \varepsilon/\varepsilon_{max} = 0.05$; and an upper bound $\Gamma_{crit} \approx (\dot{\varepsilon}_{max}/\dot{\varepsilon})^2 = 400$, in robust agreement with the exact numerical result (Fig. 1 A).

Finding an expression for the maximum speed muscle can impart is, at first glance, a simple problem in Newtonian mechanics. But the simplicity of the governing equations is deceiving. No muscle can contract by more than ε_{max} or faster than with $\dot{\varepsilon}$. Because these boundary conditions compete and dynamically couple to the mass that is driven, and because muscle is a rather peculiar motor with complex FV and FL functions, the problem acquires considerable subtlety. I have demonstrated that the resulting complexity is suitably captured by a single characteristic dimensionless number: the effective inertia, Γ.

The effective work and power density of muscle, and the "optimal" geometry of musculoskeletal systems

Equipped with a first order understanding of the relevance of the effective inertia in muscle contractions, we may next interrogate musculoskeletal "design". A classic concept in the analysis of muscle performance is the notion of a characteristic energy and power density; each unit mass of muscle can at most deliver an ostensibly fixed maximum amount of work and power, and these maxima represent putatively suitable metrics to characterise muscle performance limits [4, 7, 9, 10, 22, 33, 39]. What determines whether a mass-musculoskeletal system operates close to these limits?

By definition, muscle operates with maximum work density, W_ρ, in the Borelli-limit, where it contracts over the largest possible distance with the smallest possible increase in strain rate [Fig. 2 A and 3]; W_ρ is a sole function of the muscle's FL-properties, the muscle density, ρ, and the maximum strain, $W_\rho \sim \hat{\sigma}(\varepsilon_{max})\varepsilon_{max}\rho^{-1}$, where the hat indicates that a quantity is averaged over time or displacement as appropriate (see SI). As may be expected by analogy, muscle operates with maximum average power density in the Hill-limit, where it reaches its maximum shortening speed with a minimum loss in force due to length changes (Fig. 2 B); P_ρ is a sole function of the muscle's FV-properties, its density, and a characteristic strain rate, $P_\rho \sim \hat{\sigma}(\dot{\varepsilon}_c)\dot{\varepsilon}_c\rho^{-1}$. For a muscle which generates constant force, maximum average power is delivered in contractions to $\dot{\varepsilon}_{max}$, but for a muscle with FV-properties, average power is maximised when the contraction is terminated at a lower strain rate [about half of $\dot{\varepsilon}_{max}$ for $K = 4$; see SI for a detailed calculation and 40, 41, for related results].[2]

To explore the implications of these observations for musculoskeletal design, I again return first to the simpler case of a constant force muscle: A unit volume of muscle operates with maximum W_ρ in the Borelli-limit, and with maximum P_ρ in the Hill-limit. It can thus only operate with maximum W_ρ and maximum P_ρ if $\Gamma = 1$; the unique effective inertia at which the musculoskeletal system is simultaneously in both limits (Fig. 2 C). For $\Gamma < 1$, muscle only delivers a fraction of its work density, equal to $W_{\rho,\%} = \Gamma$; and for $\Gamma > 1$, it delivers only a fraction of its power density, equal to $P_{\rho,\%} = \Gamma^{-1/2}$ (see SI, and Fig. 2 A-C). The product of the relative power and work densities thus takes a maximum value of unity at $\Gamma = 1$, and is equal to Γ for $\Gamma < 1$, and to $\Gamma^{-1/2}$ for $\Gamma > 1$. Somewhat fortuitously, Γ can thus also be interpreted as the fraction of the maximum work and average power density muscle can deliver. Indeed, Γ may be interpreted as the ratio between the power and work density of the contracting muscle, $P_\rho W_\rho^{-1} = \dot{\varepsilon}_{max}\varepsilon_{max}^{-1}$, which defines a characteristic physiological time scale; normalisation of this time scale with the time it takes to accelerate to the maximum possible strain rate, $t_c = m\dot{\varepsilon}_{max} l_m F_{max}^{-1} G^{-2}$, yields the effective inertia.

For a muscle with FV and FL properties, these results are no longer exact, but the implicit scaling relations hold in the limit of small and large Γ, i. e. outside the approximate transition region (Fig. 2 A-C). Although there no longer exists an effective inertia at which the muscle is simultaneously in both the Hill-

[2] In fact, the power density goes to zero as the strain rate approaches $\dot{\varepsilon}_{max}$, because the Hill-equation is asymptotic, see SI.

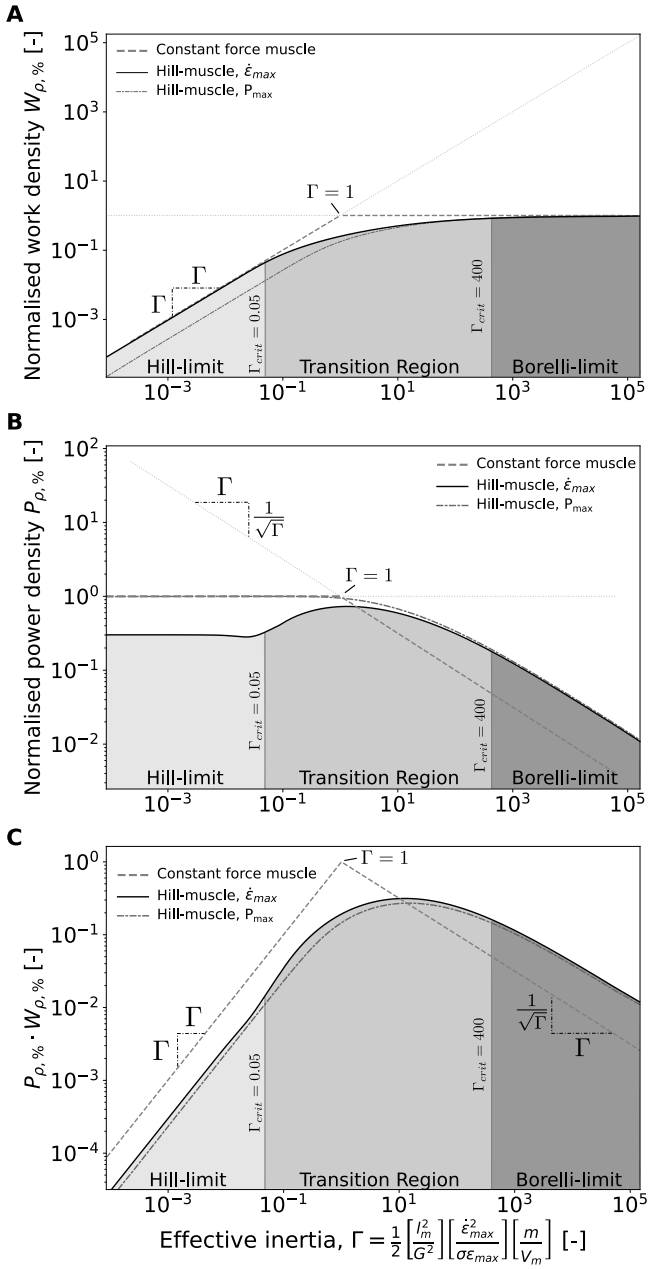

Figure 2 | A muscle delivers its maximum work density, W_ρ, in the Borelli-limit (**A**), and its maximum power density, P_ρ, in the Hill-limit (**B**). The effective inertia Γ is directly related to the fractions $W_{\rho,\%}$ and $P_{\rho,\%}$ delivered in the Hill- and the Borelli-limit, respectively, as indicated by the slopes. (**C**) Maximising the product between $W_{\rho,\%}$ and $P_{\rho,\%}$ may be considered a design objective: A constant force muscle operating at $\Gamma = 1$ can deliver both its maximum work and power density simultaneously. For a Hill-muscle, the maximum product is less than unity and occurs at $\Gamma > 1$. Dark grey lines show contractions which result in maximum average power output, P_{max}, as opposed to close to maximum strain rate, $0.99\dot{\varepsilon}_{max}$ (for details, see main text and SI).

and the Borelli-limit, an equivalent optimum may be still be defined as the value of Γ which maximises the product between $W_{\rho,\%}$ and $P_{\rho,\%}$. This maximum product is now smaller than unity, and occurs at an effective inertia larger than unity (Fig. 2 C). An exploration of the exact value of Γ which corresponds to this putative optimum as a function of the FL and FV properties of muscle is beyond the scope of this work. However, the implication is clear: operation with small or large Γ means operation with suboptimal work- or power-density, respectively (Fig. 2 A-C).

It is instructive to note that although neither W_ρ nor P_ρ depend on the geometry of the musculoskeletal system, or on the mass muscle contracts against, the ability of muscle to deliver either depends on both (see Fig. 2 A-B and eq. 3). In the classic literature, the influence of mass on the ability of muscle to deliver maximum W_ρ or P_ρ has rarely been explicitly considered [but see e. g. 19, 20, 22, 24], and variations in musculoskeletal anatomy are typically interpreted as controlling a trade-off between force and velocity. The above result demonstrates that this popular interpretation is correct only if muscle operates in the Hill-limit (i. e. $\Gamma < 1$), where musculoskeletal geometry determines the extent to which a unit power is split into force versus velocity (see eq. 2). In sharp contrast, in the Borelli-limit (i. e. $\Gamma > 1$), the maximum velocity is independent of the musculoskeletal geometry (see eq. 1), which instead merely determines the extent to which a unit amount of work is split into force and displacement, respectively; changing the gear ratio in the Borelli-limit changes the force, but leaves the maximum velocity unaffected. Consider as illustrative example a muscle operating close to an effective inertia of unity: Increasing the gear ratio results in a reduction of both the maximum achievable speed, and the time it takes to reach this maximum speed; the power remains constant but the work done decreases. Decreasing the gear ratio, in turn, leaves the maximum speed unchanged, but increases the time it takes to reach it; the work remains constant but the power decreases [see 20, 23, for other results indicating a work-power trade-off modulated by musculoskeletal geometry]. At an effective inertia of unity, the musculoskeletal system imparts the maximum possible speed in the shortest possible time.

On the basis of these remarks, it is tempting to consider an effective inertia close to unity as the "optimal design" for a musculoskeletal system. This may well

be so, but the notion of a maximum speed and maximum effective power and work densities as sole design objective is likely overly simplistic for at least two reasons. First, where muscle is expected to move a range of masses in stereotypical scenarios, muscle performance is not suitably characterised by a single-valued effective inertia, and will thus deviate by necessity from any putative optimum. Second, delivering the same amount of muscle-mass specific work or power in a different time may well be associated with a variation in efficiency, that is the amount of metabolic energy required to deliver a unit amount of mechanical energy. Such variation may then favour effective inertias smaller or larger than unity.

Parasitic forces and the truncation of the EoM landscape

The above analysis is vulnerable to the reasonable criticism that it is concerned with a case of seemingly limited practical relevance – muscle is never the sole contributor to the net force acting on the driven mass. I will next demonstrate that the initial development, though restricted to a special case, constructed an analytical framework strong enough to carry the burden of further complexity.

The net force is the vector sum of all external forces. Where such forces oppose the muscle force, they will influence muscle dynamics in two distinct ways, distinguished in their generality by their dependence on the FV and FL relationships. Let a muscle contract against an opposing force P. The opposing force is "parasitic", in the sense that it does negative work; it consumes part of the work done by muscle, redirecting it from kinetic energy to other forms of energy – heat, gravitational potential energy, what have you. To evaluate the partitioning of muscle work into kinetic versus parasitic energy, I derive from conversation of energy:

$$\frac{E_{kin}}{W_m} = 1 - \frac{E_{para}}{W_m} = 1 - \hat{\kappa} \tag{7}$$

where W_m is the work done by muscle. The reduced parasitic energy $\hat{\kappa} = \hat{P}\hat{F}_m^{-1}G^{-1}$ is the fraction of muscle work consumed by the parasitic force, with the immediate consequence that $1-\hat{\kappa}$ represents the fraction of muscle work which flows into kinetic energy. Because $\hat{\kappa}$ is the ratio of the work done by the parasitic and the driving force, which both act over the same displacement, it is, in general, a ratio of *average* forces. For $\hat{F}_m G = 10\hat{P}$, 90% of the work done by muscle flows into kinetic energy, and for $\hat{F}_m G = 2\hat{P}$ it is half. For $\hat{F}_m G = 20\hat{P}$, the error in neglecting the parasitic forces in the energy balance is less than 5%, and for $\hat{F}_m G = \hat{P}$, muscle can do zero work; no acceleration is possible at all, and the system is in equilibrium. The reduced parasitic energy can be related to familiar dimensionless numbers, such as the Froude, Strouhal or Reynolds number for gravitational, elastic or viscous parasitic forces, respectively, via $E_{kin}E_{para}^{-1} = \hat{\kappa}^{-1} - 1$ (note that these then differ from their definition in Alexander's sense, as gravitational and elastic energy are no longer the source of kinetic energy, but a sink for muscle work). I submit that their definition via a ratio of forces is preferable in problems of muscle dynamics, because it places the focus on the cause instead of the final result of the total change in energy which resulted from muscle contraction.

For a constant force muscle, $\hat{\kappa}$ fully captures the influence of parasitic forces on muscle performance. The Hill-number remains unchanged, but the Borelli-number and thus the effective inertia gain an additional term, defined by eq. 7. The net effect of the parasitic force is thus an increase of the effective inertia by a factor $\Gamma_\kappa\Gamma^{-1} = (1-\hat{\kappa})^{-1}$; as P approaches $F_m G$, the constant force muscle is increasingly likely to be Borelli-limited (see Fig. 3 A), and reaching a unit speed takes longer. The interpretations developed above remain valid, but now refer to the work that flows into kinetic energy, rather than the total muscle work.

For a Hill-muscle, the influence of parasitic forces is more complex, which I illustrate by returning to the notion of the EoM landscape. For a constant force muscle, the presence of a constant parasitic force manifests itself in a downward shift of the EoM plane (Fig. 3 A). The net force is reduced, but the maximum possible relative speed and displacement remain unchanged, because the muscle force is independent of muscle strain and strain rate; the relative FL and FV functions are equal and constant. For a Hill-muscle, the FL and FV functions are curves. As a consequence of the downward shift of the normalised net force, these curves may now intersect with the zero-plane at a shortening velocity smaller than $l_m\dot{\varepsilon}_{max}$, and at a finite displacement smaller than $l_m\varepsilon_{max}$; parasitic forces truncate the EoM landscape [Fig. 3 B and 30, 31, 42–46]. The extent of this truncation can, in principle, be quantified through an exercise in equilibrium mechanics [see 30, 42, 45, 46]: the maximum relative displacement over which the muscle can ac-

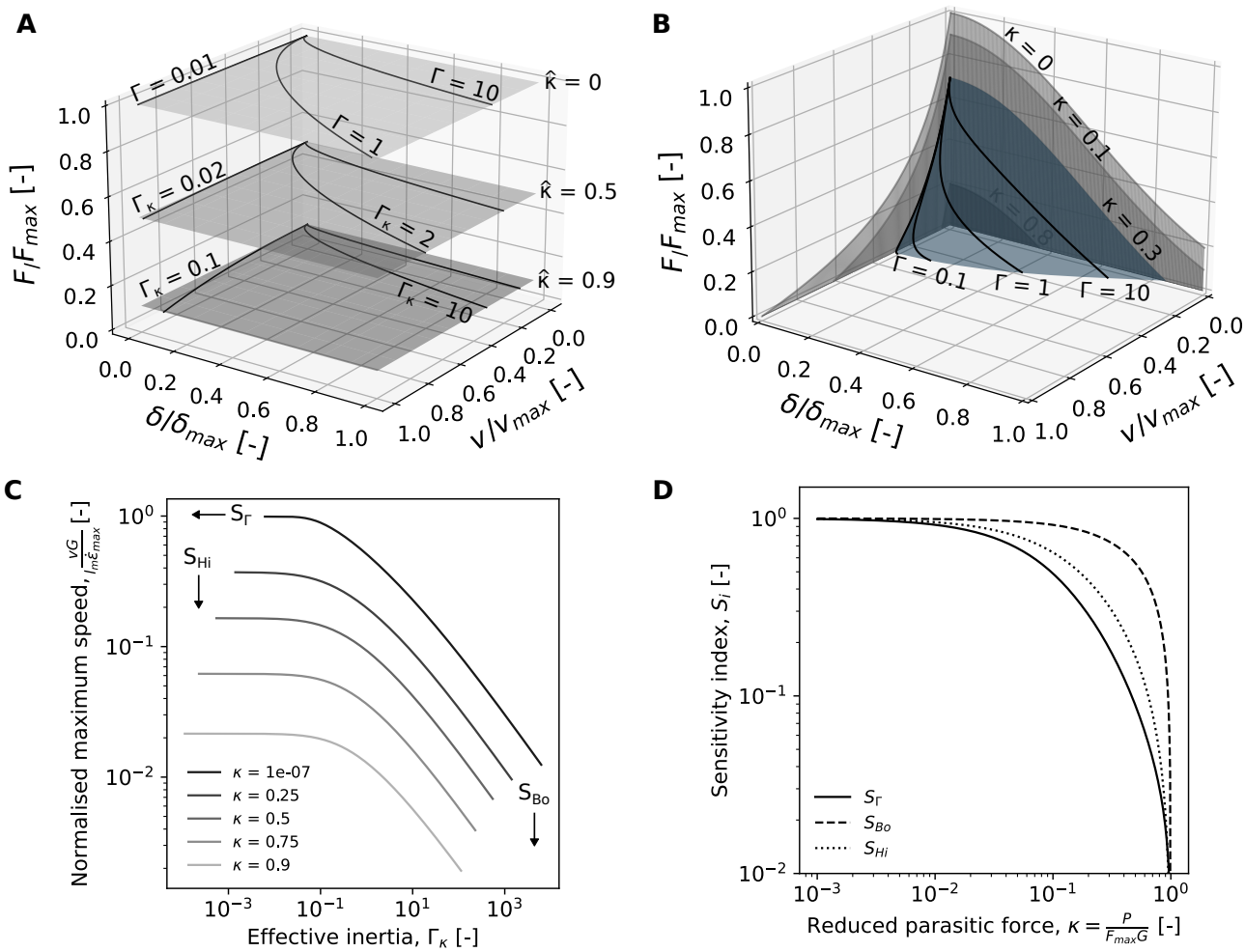

Figure 3 | External forces which oppose motion influence muscle dynamics in two distinct ways, distinguished in their generality by their dependence on the force-length (FL) and force-velocity (FV) relationships. (**A**) A constant opposing force, P, manifests itself via a downward shift of the equation-of-motion (EoM) plane. P consumes part of the work done by muscle and may thus be considered 'parasitic'. The amount of muscle work which flows into parasitic instead of kinetic energy is quantified by the reduced parasitic energy, $\hat{\kappa} = P\hat{F}_m^{-1}G^{-1}$. The effective inertia increases with κ, as illustrated by the contractile trajectories on each EoM plane. (**B**) For a Hill-muscle, the influence of parasitic forces is more complex. Because the FL and FV functions are now curves, the downward shift of the EoM plane results in a truncation of the accessible speed and displacement range. The extent of this truncation depends on the magnitude of the reduced parasitic force, $\kappa = PF_{max}^{-1}G^{-1}$, as illustrated by the FL and FV planes, and the EoM plane for $\kappa = 0.3$. (**C**) The net effect of a constant parasitic force is a decrease in both the maximum relative speed and the effective inertia. (**D**) The magnitude of these changes can be described by proportionality constants, S_i, which depend on κ and may thus serve as sensitivity indices which quantify the importance of external forces: For $\kappa < 0.005$, $\kappa < 0.01$ and $\kappa < 0.05$, all $S_i \geq 0.95$, i. e. Γ_κ, Hi_κ and Bo_κ are within 5% of Γ, Hi, and Bo, respectively, and the parasitic force may be neglected. The asymptote at $\kappa = PF_{max}^{-1}G^{-1} = 1$ is a force limit to muscle-driven motion. *En route* to this asymptote, all S_i decline steeply. For typical FL and FV functions, the Hill-number is more sensitive to parasitic forces than the Borelli-number, as the muscle force declines more sharply with strain rate than with muscle strain.

celerate, and the maximum speed it can contract with, are reached when the net force is zero, i. e. when the muscle force balances the parasitic force. For constant P, analytical evaluation of the fraction of the strain rate and strain that are accessible is straightforward. Setting P equal to the FV and FL functions defined by eqs. 4 and 5 yields:

$$\varepsilon_\kappa = \begin{cases} \varepsilon_{max} \text{ if } \sqrt{\log(\kappa)(-\beta)^{-1}} \geq \varepsilon_{max} \\ \sqrt{\log(\kappa)(-\beta)^{-1}} \text{ otherwise} \end{cases} \tag{8}$$

$$\frac{\dot{\varepsilon}_\kappa}{\dot{\varepsilon}_{max}} = \frac{1-\kappa}{1+K\kappa} \tag{9}$$

where I introduced the reduced parasitic force,

$\kappa = PF_{max}^{-1}G^{-1}$. Because the parasitic force truncates both the strain rate and strain range, both the Hill- and Borelli-limit are altered, and follow from combination of eqs. 8 and 9 with eqs.1 and 2, respectively:

$$v_{\mathrm{Hi},\kappa} = v_{\mathrm{Hi}} \underbrace{\left[\frac{1-\kappa}{1+K\kappa}\right]}_{S_{\mathrm{Hi}}} \tag{10a}$$

$$v_{\mathrm{Bo},\kappa} = v_{\mathrm{Bo}} \underbrace{\left[C\left(\sqrt{\frac{\pi}{4\beta}}\mathrm{erf}\left(\sqrt{\beta}\varepsilon_\kappa\right) - \kappa\varepsilon_\kappa\right)\right]^{0.5}}_{S_{\mathrm{Bo}}} \tag{10b}$$

Here, erf is the error function, C is a constant which depends on β and ε_{max} (see SI), and S_i are sensitivity indices which quantify the importance of the parasitic force (see below and Fig.3 D). Both the Hill- and the Borelli-limit now approach an asymptote of zero speed at a critical reduced parasitic force $\kappa = 1$; a "force limit" to muscle-driven motion. Close to this limit, both the Hill- and the Borelli-limit drop rapidly (see Figs. 3 C-D). The effective inertia follows immediately as the squared ratio of the Hill- and the Borelli-number:

$$\Gamma_\kappa = \Gamma \underbrace{\left[\frac{(1-\kappa)^2}{(1+K\kappa)^2 C\left(\sqrt{\frac{\pi}{4\beta}}\mathrm{erf}\left(\sqrt{\beta}\varepsilon_\kappa\right) - \kappa\varepsilon_\kappa\right)}\right]}_{S_\Gamma} \tag{11}$$

For $G = 4$, $\beta = 6.5$ and a not unreasonable maximum strain of $\varepsilon_{max} = 0.5$, eq. 11 is a decreasing function of κ (see Figs. 3 C & D).

The integration of parasitic forces into the definition of the effective inertia, and the visualisation of its effect via the EoM landscape, are conceptually simple. But even for the most simple case of a constant parasitic force, the increase in mathematical complexity is noticeable. Indeed, analytical evaluation of the Hill- and the Borelli-number in the presence of parasitic forces will only rarely be possible, first because of the complex form of the FV and FL relationships, and second because parasitic forces may depend on speed (viscous dissipation), or displacement (structural dissipation), resulting in non-trivial interactions with muscle contraction dynamics. A thorough evaluation of the above results, and their generalisation to characteristic non-constant forces will have to await further work. However, from the cursory analysis presented here emerge two points of note.

First, for a given reduced parasitic force, Γ_κ, Hi_κ and Bo_κ are constant multiples of Γ, Hi and Bo. The proportionality constants, S_i, which link both definitions (see bracketed terms in eqs. 10a-11), are thus suitable indices for the sensitivity to parasitic forces: For $\kappa < 0.005$, $\kappa < 0.01$ and $\kappa < 0.05$, all $S_i \geq 0.95$ (see Fig 3 D). In other words, Γ_κ, Hi_κ and Bo_κ are within 5% of Γ, Hi, and Bo, respectively, and the parasitic force may be neglected in leading order analyses. To illustrative the utility of this simple analysis, I address briefly a long-standing observation in comparative biomechanics: small animals are seemingly untroubled by the presence of gravity, and only change locomotor speed slightly, if at all, between running on horizontal or vertical surfaces. In contrast, larger animals generally slow down significantly when moving up inclines [47–49]. The relevant parasitic force is the gravitational force, $F_g = mg$, with an associated reduced parasitic force $\kappa_g = mgF_{max}^{-1}G^{-1}$, and a ratio between kinetic and parasitic energy — the Froude number of the contraction — $Fr = \kappa_g^{-1} - 1$. An upper bound $\kappa_g \leq 0.05m^{1/3}$, where m is the body mass in kilogram, was estimated from published data by Alexander [50]. Thus, animals with a body mass $m < 1$ g, $m < 10$ g and $m < 1$ kg may be considered 'gravitationally indifferent' in terms of their effective inertia, their Hill- and their Borelli-number, respectively, in robust agreement with the scarce experimental data [47–49]. The work done by the muscle of small animals against the gravitational force is negligible compared to the total muscle work, because the reduced parasitic force is small, and the muscle Froude number is large [see also 18].

Second, the role of musculoskeletal anatomy, represented by the ratio between fibre length and gear ratio, $l_m G^{-1}$, needs careful re-interpretation. In the absence of parasitic forces, the Borelli-number is agnostic to musculoskeletal anatomy, because all work flows into kinetic energy, irrespective of whether it is done by displacing a large force over a small distance, or a small force over a long distance (see above and eq. 1). Musculoskeletal anatomy does however control the speed in the Hill-limit, which is maximal for maximum values of $l_m G^{-1}$ (see eq. 2). In the presence of parasitic forces, both results change fundamentally (see eqs. 10a-10b). In the Borelli-limit, the split of a unit work into force *versus* dis-

placement now matters, because it controls the partitioning into parasitic *versus* kinetic energy; minimising $l_m G^{-1}$ minimises the reduced parasitic energy, $\hat{\kappa} = \hat{P}\hat{\sigma}^{-1}V_m^{-1}l_m G^{-1}$. In the Hill-limit, in turn, maximising $l_m G^{-1}$ will now minimise speed, because it increases the reduced parasitic force, $\kappa = P\sigma^{-1}V_m^{-1}l_m G^{-1}$, so amplifying the truncation of the accessible contractile speed range [43, 45, the analogous result holds for the truncation of the strain range in the Borelli-limit]. Thus, in both the Hill- and the Borelli-limit, increasing the gear ratio or decreasing the muscle fibre length at constant muscle volume may now increase not only the force, but also the maximum possible velocity and displacement, in noteworthy contrast to their canonical interpretation as parameters which control putative force-velocity or force-displacement trade-offs [see above and 51–53, for a recent controversial discussion of this topic]. This force-velocity trade-off is now more complex: if $l_m G^{-1}$ is too small, the muscle can only reach a fraction of its theoretical maximum possible speed, and only has access to a fraction of its work density; if it is too large, in turn, muscle performance is reduced by parasitic losses instead (see Fig. 3 C–D). The optimum anatomy thus likely corresponds to intermediate values of $l_m G^{-1}$ which result in effective inertias close to the transition between the Hill- and the Borelli-limit; around this transition, the absolute speed, and relative effective work and effective power density are all close to their theoretical maximum (see Fig. 1 & 2). Realising this optimum will require a different anatomy for a physiologically identical muscle contracting against varying parasitic force (see Fig. 3 C and D). Some reduced parasitic forces, for example those due to gravity, will vary systematically with animal size, $\kappa_g \propto m^{1/3}$ (assuming isometry). It follows at once that there now exists an incentive to depart from isometry via systematic variation of musculoskeletal anatomy, for example due to posture variation [20, 54], in order to remain close to the putative optimum; a systematic increase of gear ratio with size can attenuate the decrease in the Froude number of the muscle contraction predicted from isometry, and keep a larger fraction of the dynamic muscle performance space accessible.

A theory of physiological similarity in muscle-driven motion

Muscle is a motor with a complexity to baffle any mind; but its operation must be restricted to a space bound by the laws of physics. In the above, I have made an attempt to analyse how these laws interact with some of the key physiological and anatomical idiosyncrasies of muscle, in an effort to delineate fundamental limits to its mechanical performance. From this analysis emerged three key dimensionless parameters — the effective inertia Γ, the reduced parasitic energy $\hat{\kappa}$ and the reduced parasitic force κ — which quantify the relative importance of different physiological and physical constraints on a continuous scale.

The effective inertia, Γ, provides a direct measure of the extent to which a unit volume of muscle is limited by its strain rate versus strain capacity, and thus of the degree to which it can deliver maximum power and work, respectively. Analogous to how seemingly different problems in fluid dynamics are considered hydrodynamically similar if they occur with equal Reynolds number, problems in muscle-driven motion may be considered *physiologically similar* if they involve equal Γ: the involved muscles will operate with comparable fractions of their maximum strain rate and strain capacity, follow similar contractile trajectories along the EoM landscape, and deliver a similar fraction of their maximum power and work density. A unit volume of muscle has access to its maximum performance space if the musculoskeletal geometry is such that contractions occur with an effective inertia close to unity. For much smaller or much larger Γ, muscle contractions may be considered quasi-instantaneous or quasi-static, and are governed dominantly by the power or work density of muscle, or – equivalently – its FV and FL relationships, respectively. Analytical expressions for the asymptotic maximum speed in these limits are available in form of the Hill- and the Borelli-number, which shed light on the distinct relevant "design" features of the musculoskeletal system in each regime.

The reduced parasitic energy and force, $\hat{\kappa}$ and κ, quantify the relative importance of parasitic forces which oppose muscle motion. Parasitic forces consume muscle work, and truncate the accessible mechanical performance space. As a consequence, the Hill- and the Borelli-number, and thus the effective inertia, gain additional terms which may serve as quantitative indices of sensitivity to parasitic forces. For $\kappa < 0.005$, parasitic forces may be ignored to first order; for $\kappa > 0.005$, they alter the dynamics by more than a few percent. Large parasitic forces can decrease both the effective inertia of the contraction and the maximum speed muscle can impart, resulting in a

fundamental change in how musculoskeletal anatomy modulates canonical trade-offs between force and velocity or force and displacement. It stands to reason that any investigation of muscle performance, and any assessment of musculoskeletal design, ought to explicitly consider Γ, κ and $\hat{\kappa}$ of characteristic contractions; ignoring them is to accept considerable risk of erroneous conclusions.

Up to this point, the text may have been heavy in theoretical thought, but arguably light in demonstrated practical consequence. Contractions at different Γ and κ may well be governed by rather different physiological and physical constraints, but what range of Γ and κ does real muscle find itself in? I note that both Γ and typical κ such as κ_g for the gravitational force are size-dependent: Under the parsimonious assumption of isometry, all lengths scale as $L \propto m^{1/3}$, all areas as $A \propto m^{2/3}$, and all volumes as $V \propto m$. It follows that, for an isometric musculoskeletal system moving an isometric mass, $\Gamma \propto m^{2/3}$ and $\kappa_g \propto m^{-1/3}$. Evolution has thus involuntarily conducted a control experiment in one of the world's largest laboratories: the animal kingdom. Animals which use muscle to move vary by at least 13 orders of magnitude in mass, so that, assuming isometry, Γ should vary by a factor about $(10^{13})^{2/3} \approx 10^8$, and $1/\kappa_g$ should vary by a factor of $(10^{13})^{1/3} \approx 10^4$. Without allowing for non-trivial departures from isometry, or systematic changes in muscle physiology, it is hard to avoid the conclusion that muscle of animals of different size operates in most substantially different physiological regimes, and with markedly different gravitational sensitivity.

The immediate implications of the influence of Γ and κ on muscle performance and their size-dependence are profound and diverse: characterisation of the maximum intrinsic muscle shortening speed via experiments on isolated muscle fibres is only sound if the contraction occurs in the Hill-limit [see also 35]; extrapolation of such single-fibre experiments to whole muscle or indeed *in vivo* performance can be misleading as it is typically associated with changes in Γ; musculoskeletal geometry plays a more complex role than its canonical interpretation as a parameter which controls a force-velocity or force-displacement trade-off would have one believe, so that conclusions from previous comparative analyses of musculoskeletal functional morphology across species may need to be carefully reconsidered [see also 51, 53]; isometric animals of different sizes neither have access to the same (maximum) work density, nor to the same (maximum) power density per unit volume of muscle, and are suffering to different extents from parasitic losses to gravitational potential energy — three assertions which challenge the classic scaling theories in animal locomotion [3, 4, 7–9, 17, 21, 22, 33, 55, but see [24]]; and extrapolation of data on extant animals to infer muscle-driven locomotor performance of larger extinct animals may have to explicitly introduce the size-dependence of Γ and κ, and assess their influence on the EoM landscape to avoid physically possible but physiologically prohibited inference. Analyses framed in terms of Γ and κ may also provide inspiration for the design of legged robots and in sports biomechanics: electrical motors have characteristic torque-rounds-per-minute relationships, akin to a FV function; many sports may be characterised by specific κ, which interacts with the muscle anatomy and physiology of the competing athlete. Some sports may provide dynamic control over κ, for example gears in bicycles or oars in rowing, suggesting the possibility of optimal athlete-specific configurations [see 45, for a similar suggestion]. Whether future work verifies or rejects what at this point are mere hypotheses is immaterial to their potential to advance our understanding of muscle-driven motion, and of the design of musculoskeletal systems.

The insights provided by the similarity theory developed in this text should not belie the fact that the list of tasks which need to be completed before it can be considered comprehensive is rather long indeed. It includes the appropriate consideration of activation and deactivation times and the degree of muscle activation [56]; the propagation velocity of muscle excitation [35]; contraction history effects; non-constant parasitic forces and gear ratios [e. g. 23, 57]; muscle pennation [e. g. 58]; series compliance and the associated storage of strain energy in muscle and in tendons [e. g. 16, 57, 59]; multi-segment motion [e. g. 19]; and instances where muscle is lengthened, acts as a break and does negative work – to name but a few. I am under no illusion that the simplistic account of physiological similarity presented here will often be inadequate, and fail to produce a convincing account of phenomena across the breathtaking diversity of tasks performed by muscle. However, it is my hope that identifying the origin of these shortcomings will push us further in our understanding of the mechanical, physiological, neurological, developmental and phylogenetic constraints that govern the operation of muscle across the animal tree of life.

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