Thermodynamics of animal locomotion

E. Herbert,1 H. Ouerdane,2 Ph. Lecoeur,3 V. Bels,4 and Ch. Goupil4

1Laboratoire Interdisciplinaire des Energies de Demain (LIED), CNRS UMR 8236, Université Paris Diderot, 5 Rue Thomas Mann, 75013 Paris, France
2Center for Energy Science and Technology, Skolkovo Institute of Science and Technology, 3 Nobel Street, Skolkovo, Moscow Region 121205, Russia
3Institut d’Electronique Fondamentale, Université Paris Sud CNRS, 91405 Orsay, France, CNRS, UMR 8622, 91405 Orsay, France
4Institut de Systématique, Evolution, Biodiversité, ISYEB, CNRS/MNHN/EPHE/UA UMR 7205, Muséum national d’Histoire naturelle, Sorbonne Universités, 45 rue Buffon, 75005 Paris, France

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Muscules are biological generators of mechanical power. They have been extensively studied in the frame of Hill’s classic empirical model as isolated biomechanical entities, which hardly applies to a living body subjected to internal and environmental constraints. Here we elucidate the overarching principle of a living muscle action for a specific purpose such as locomotion, considering it as an assembly of chemical-to-mechanical energy converters (muscle units) connected in parallel, under mixed boundary conditions. Introducing the energy cost of effort, $COE_e$, as the generalization of the well-known oxygen cost of transport, $COT$, in the frame of our compact locally linear nonequilibrium thermodynamics model, we analyze oxygen consumption measurement data from a documented experiment on energy cost management and optimization by horses moving at three different gaits. Horses adapt to a particular gait by mobilizing a nearly constant number of muscle units minimizing waste production per unit distance covered; this number significantly changes during transition between gaits. The mechanical function of the animal is therefore determined both by its own thermodynamic characteristics and by the metabolic operating point of the system.

Introduction

The ability to move is a fundamental characteristic of animal life [1], the study of which dates back to Aristotle [2]. Whether in the air, under water or on the ground, animal locomotion in its rich variety of modes and purposes, rests on the active association of three of the main systems that compose the animal body: the skeleton, the nervous system, and the muscles [3, 4]. By active association, we mean that to set the whole body or part of it in motion, the somatic nervous system sends control signals that trigger chemical reactions in the skeletal muscles, which in turn act mechanically on the bones. Notwithstanding the rather detailed understanding of some essential aspects of animal locomotion, a complete holistic physics description of its mechanisms, including the couplings between the body actors (nerves, muscles, bones) and boundary conditions (environment), is yet to be achieved: outstanding questions concerning, e.g., neuromuscular control, notably considering overload and fatigue problems, biomechanics and sex-specific patterns, and energetics to name just a few, remain to be addressed [6, 12].

Physiological properties of living organisms such as, e.g., temperature, pressure, chemical species concentrations in fluids, which can be described as thermodynamic variables, are maintained within certain ranges by homeostatic mechanisms to ensure steady-state internal working conditions [13]. Further, since the thermodynamic description of the energy conversion process permitting muscle motion does not require consideration of all the intricate biochemical processes at the heart of the complex body’s regulatory system, Onsager’s close-to-equilibrium force-flux formalism [14] is very well suited for the study of metabolism under muscle load. In a recent work, we developed such a nonequilibrium thermodynamics model to understand the chemical-to-mechanical energy conversion process under muscular effort [15], considering living organisms as open thermodynamic systems that exchange energy and matter with their environment. We derived Hill’s widely used empirical muscle equation [16] from the principles of thermodynamics, provided the description of the response of the muscle in terms of active impedance, and critically discussed the so-called maximum power principle [18], which was formulated after Lotka’s theory of energy optimal consumption based on the energy/efficiency trade-off and exergy [19]. We also showed that for a generic energy conversion engine, living or not, power maximization [19, 20], entropy minimization [21], efficiency maximization, or waste minimization states are only specific operation modalities [15, 22].

Animals manage their energy expenditure as their movement is constrained both by needs and availability of metabolic resources. Broadly speaking, the most efficient systems minimize energy dissipation and entropy production at the cost of being also the most constrained in terms of working conditions and use, while systems that do not boast high efficiency or power, may have a wider range of use and therefore marked robustness. The fundamental difference between a living energy conversion engine and a non-living one being the existence of an energy (basal) flow at rest, the core question is then
how to deduce the constraints due to energy conversion specific to living systems [15] [22]. Further, as animals may change gaits or more generally their locomotor behavior, the questions of energy efficiency and oxygen consumption variations on the one hand, and of the specific muscular mechanisms permitting transition, are yet to be precisely answered. Indeed, though Hill’s muscle model [16] is extensively used in biomechanics, it is important to remind that Hill’s studies of muscles were performed using dissected muscles extracted from dead animals, while for energy efficiency and oxygen consumption economy, knowledge of the actual oxygen cost of transport (COT) is needed, meaning the study of a living muscle and its boundary conditions.

In this work, we address the generic question of thermodynamic constraints applied to an animal, assessing their impact on the animal’s effort production, using instantaneous oxygen consumption experimental data. Building on [15] [22], we develop an integrated framework for animal locomotion, which may also bridge calorimetric measurements of muscles [17], the dynamic energy budget phenomenological approach based on balance and conservation laws [23] [24], and biological studies based on the analysis of proxies such as oxygen consumption. We thus establish: (i) the link between oxygen consumption during muscular effort of moderate intensity and our thermodynamic formalism for metabolism [15], to use oxygen consumption to characterize and compare the modes of movement [25] and as a proxy of the output flux of low-grade waste energy; (ii) a basic model describing a complex organism as an association of muscle fibers, in light of which we discuss experimental data [26], providing insights from which we can draw general conclusions on animal locomotion from the energetic viewpoint.

**Animal activity and oxygen COT** An animal has to arbitrate between several operating points, depending on the desired optimization, say, e.g., maximum efficiency, maximum power production, or minimum waste flow per unit of power produced. The constitutive metabolic force ($F_M$)-flux ($I_M$) equations describing an organism’s overall energy balance, considering an assembly of $N$ (identical) muscle units connected in parallel to chemical energy source and sink, read [15] [27]:

$$\Phi_+ = N \varphi_+ = \alpha \mu M_+ I_M + \Delta \mu M / R_E$$  \hspace{1cm} (1)

$$\Phi_- = N \varphi_- = \alpha \mu M_- I_M + R_M I_M^2 + \Delta \mu M / R_E$$  \hspace{1cm} (2)

$$P_M = N P_M = F_M I_M = \Phi_+ - \Phi_-$$  \hspace{1cm} (3)

where $\Phi_\pm$ are the incoming from the source/outgoing to the sink energy fluxes, $\Delta \mu M = \mu M_+ - \mu M_-$ is the chemical potential difference across the conversion zone, which has efficiency $\eta = P_M / \Phi_+$, and the resistances $R_M$ and $R_E$ characterize dissipation and entropy production due to the coupled (a) transport of energy and matter. Note that the zero intensity configuration $I_M = 0$ describes the organism globally at rest with a nonzero basal residual energy consumption $B \equiv Nb \approx \Delta \mu M / R_E$ [27].

For aerobic efforts, i.e. of limited duration and intensity, that the respiratory chain is involved at the end of the Krebs cycle, via cytochrome oxidases, shows that the measured oxygen consumption is a proxy of the power fraction rejected $\Phi_-$ [28]. One can then define the energy cost of effort index $COE_-$ as a measure of the energy required per unit of muscular effort, i.e. $COE_- \equiv \Phi_- / I_M$, which in the framework of [15] [22], reads:

$$COE_- = a_0 + R_M I_M + \Delta \mu M / (R_E I_M)$$  \hspace{1cm} (4)

with $a_0 = \alpha \mu M_-$ being Hill’s constant parameter [15]. The term $\Delta \mu M / (R_E I_M) \approx B / I_M$ is only dominant in situations where the metabolic intensity $I_M$ is low.

![FIG. 1. Four-quadrant plot of COE- (North direction), $\eta$ (West), $I_M$ (East) and $P$ (South): (a) COE- vs $\eta$, (b) COE- vs $I_M$, (c) $P$ vs $\eta$, (d) $P$ vs $I_M$. The arrows show the direction along which $I_M$ increases. The red star symbol (resp. blue squares and green dots) indicates the position of $P_{max}$ (resp. $COE_{-}^{max}$).]

The relevant quantities for the energetic description of an animal’s muscular activities are summarized in the reduced set: $\{P; \eta; COE_-; I_M\}$, which can be put together in a single four-quadrant chart as shown in Fig. 1. The overall observed behavior resembles that of a thermodynamic system with the two usual optimum working points, namely the maximum efficiency $\eta_{max}$ and the maximum power $P_{max}$, which can be readily identified. However, a third optimum working point is also evidenced here, which corresponds to the minimization of the waste flux $\Phi_-$ per unit of metabolic intensity $I_M$, leading to a minimal value for $COE_-$, denoted $COE_+^*$. These three optima correspond to three different values of the metabolic intensity $I_M$ shown in Fig. 1 (c): the organism first sees its efficiency and power increase linearly with $I_M$ before the points of maximum efficiency, minimum $COE_-$, and finally maximum power are successively reached. Beyond the latter point, the organism is in a physiologically unfavorable situation, which can, at the extreme, lead to exhaustion.
The oxygen COT, which quantifies the total amount of energetic waste required by a unit mass of animal to perform a unitary displacement, is a tool routinely used for categorizing animal species with respect to their motion efficiency [25, 29–33]. We now write \( COT \equiv \Phi_{v/v} \), with \( v \) being the animal’s velocity, assuming a linear relationship \( P_M = kv \) (with \( k > 0 \)) between the metabolic intensity and the animal displacement velocity [24]. The mechanical power \( P_M \) produced by the organism is necessarily equal or higher than the power \( P_r \) required to enable the displacement under various experimental conditions: ascent or descent, headwind or back-wind, load carried or assistance with the motion; hence the number of fibers involved \( N \) and the metabolic intensity \( i_M \) increase with the required mechanical power, which drives the growth of the metabolic power. Here, assuming that \( N \) varies linearly with \( i_M \) [27] and hence with \( v \), we get:

\[
COT = \frac{N}{N_H} \left( a_0 k + R_M k^2 v + \frac{B}{v} \right) = k \frac{N}{N_H} COE,
\]

from Eq. (4), with \( N_H \) being the maximum (fixed) number of muscle units that can be mobilized for an effort, as for a Hill-type of effort [13, 16]. The system’s response thus is characterized by only three parameters: \( a_0 k, R_M k^2 \) and \( B \), the latter two being dependent on \( N \), unlike the former, which is directly related to the “extra heat” term in Hill’s equation [13, 27]. The speed for which the \( COT \) is minimum, is \( v \equiv v^* = \frac{N}{N_H} \sqrt{\frac{b}{R_M}} \), from which we get the \( COT \) minimum value for a fixed \( N \):

\[
COT^* = a_0 k + 2 k \sqrt{r_M b}
\]

which remarkably turns out to be independent of the number \( N \) of muscle units put in action during the effort. \( COT^* \) is therefore an intrinsic characteristic of the organism, independent of the imposed experimental configuration; and \( B_v = \frac{N}{N_H} B, R_v = \frac{N}{N_H} R_M \) and \( a_v = \frac{N}{N_H} a_0 \) thus become experimentally directly accessible.

**Gaits modeling; the case of horse motion** We now focus on the documented case of horse motion studied by Hoyt and Taylor [29]. Three main modes of displacement are usually adopted by a horse: walk, trot and gallop; the related measurement data are reported in Fig. 2a. Walk is chosen as the reference gait and the related quantities are all denoted with the subscript \( w \), e.g.: \( N_H \equiv N_{H_w} \) for the walk. When the animal was let free to run on the ground, some ranges of speeds were naturally never used by the horse, for any sustained period, as shown in the histograms Fig. 2c. Whichever gait was adopted, the speeds chosen by the animal were systematically close to the speed corresponding to minimal \( COT \), i.e. close to the point of minimal waste rejection per unit of displacement. Increasing the animal motion velocity while maintaining a constant metabolic intensity per fiber requires increasing the number of muscle units: this is achieved only by a change of gait. Interestingly, a similar behavior was reported in the case of robots aimed at mimicking walking bipeds or quadrupeds [35]. As robots do not need basal consumption, energy optimization is therefore based on a trade-off between the number of limbs for motion and the energy consumption of their motorization. The fitting curves obtained with Eqs. (4) and (6) are in remarkable qualitative agreement with all the experimental data of Hoyt and Taylor [29] as shown in Fig. 2. As the metabolic intensity increases, the number of muscle units involved in the motion is likely not be conserved, both within a gait and between gaits; so it is important to determine whether the intra-gait variation remains small or not compared to the inter-gait variation: if the former is small, one can then assume that the fitting parameters within a same gait can be taken as constants. The oxygen flux fitting curve \( \Phi_{O_2} \), in Fig. 2b in good quantitative agreement with the experimental data, is simply a polynomial of degree 2; this justifies in what follows the use of constant fitting parameters, thus neglecting higher order contributions [27].

As \( COT^* \) is a constant independent of the number of muscle units involved, the law governing the modulation of the number of muscle units \( N \) remains the same for all gaits. When the number of fibers is fixed, \( a_0 \) is expected to be the same for all gaits; varying the number of fibers within the same gait should lower the value of \( a_0 \). We observe that the metabolic intensity \( i_M \) is found to be slightly negative but essentially the same for all gaits. It is therefore legitimate to consider that: (i) the variation in the number of intra-gait units remains moderate, i.e. of the order of 10 % [27], though we cannot quantify it more accurately; (ii) this variation is identical for each gait. We may then safely assume that \( a_v \approx a_0, R_v \approx R_M \), and \( B_v \approx B \). We can also consider that Eq. (4) giving \( COT^* \) at a constant \( N \), is a quite accurate approximation, with fitting parameters \( R_v \) and \( B_v \), also assumed constant within the same gait, linked to the intrinsic parameters \( r_M \) and \( b \). One can find, in particular, that \( k \sqrt{R_v B_v} = k \sqrt{r_M b} \approx 9 \text{ ml m}^{-1} \) is indeed constant.

If we now consider the inter-gaits behavior, we find as
expected that the resistance \( R_v \approx v_M/N \) decreases when the gait increases, as in this case a growing number of muscle units are put to work. From a thermodynamic viewpoint, this amounts to increasing the number of thermodynamic engines operating in parallel, rather than increasing the intensity of operation of each of them. As a result, the unit metabolic intensity is not unduly increased, thus limiting the influence of the quadratic dissipative terms; and the multiplication of the units put in action leads to a basal power value \( B_v \approx M/N \), which establishes a linear relationship between \( V = v/v^* \approx \sqrt{\frac{v_M}{b}} \times i_M \) and the proportionality coefficient \( \sqrt{\frac{v_M}{b}} \) being entirely determined by the metabolism of a single muscle unit.

Let us now evaluate more precisely the number of muscle units involved during displacement. The actual number \( N_{H_v} \) of muscle units involved for walk is of course not known in the experiment. However, from Eq. (5), one can derive the relative number of muscle units, \( N/N_{H_v} \), put in action in the two other gaits: \( N_{H_v}/N = v_{v^*}/v^* \), with \( N_{H_v}/\sqrt{\beta/v_M} = v_{v^*}/v^* \sqrt{B_v/R_v} \). The parameters \( N, v^*, B_v \) and \( R_v \) are connected through the identities: \( N_{H_v}/N = v_{v^*}/v^* = R_v/R_{v^*} = B_v/B_{v^*} \). The ratio \( N_{H_v}/N \) is shown in the inset of Fig. 2 (e) as a function of \( v^* \). For a given metabolic intensity \( i_M \), the horse can increase its speed when changing its gait from walk to trot and from trot to gallop, mainly by increasing the number of muscle units put in action, by a factor \( N/N_{H_v} \), respectively 2.59 ± 0.04 and 4.95 ± 0.06. From Eq. (4), we also recover the waste energy output flux \( N_{H_v}/N \) as shown in Fig. 2 (c). As expected, all curves collapse into a master curve, and including the scaled velocity \( V \) in Eq. (5) finally yields \( COT \), which depends on only two adjustable factors:

\[
COT = a_0k + k\sqrt{\frac{r_M}{b}}(V + 1/V)
\]  

The dark thick line of Fig. 2 (e) represents the fitting curve, Eq. (8), for the all aggregated data from which we extract: \( a_0k = -0.37 \pm 0.08 \) N·kg\(^{-1}\) and \( k\sqrt{r_M/b} = 1.284 \pm \)
0.004 \text{ N-kg}^{-1}. Each COT curve can be described using a minimal set of 3 parameters: $B$, $R_M$ and $a_0$. Note that $a_0k$ is found to be slightly negative as a result of the modulation of the number of fibers involved in the displacement within the same gait; but as the feedback resistance $R_0 \propto a_0$ [15], feedback therefore appears as a positive contribution to the available power $P_M$.

**Conclusion** An animal left free to choose its locomotion speed, operates at minimum waste production per unit distance covered. A muscle may be divided in muscle units connected in parallel, the number of which in action varies little in time for the same gait, but substantially changes during transition to a different gait, thus showing from a thermodynamic viewpoint how an animal’s muscles operate in concert to sustain a particular effort [26]. The master curve of the number of muscle units put in action clearly confirms this result. Our model may apply to the description of the locomotion of all living organisms using a reduced set of physiological parameters, easily extractable from the literature or from experiments, allowing systematic comparison across species. It constitutes also a bridge between studies of animal locomotion and robot locomotion in terms of COT and gait adaptation [37–39], as adaptability, acquired by an increase of the number of limbs, competes with the need to minimize energy consumption. Hence, an adopted solution cannot be simultaneously adapted and adaptable: the more efficient the solution, the narrower the optimal operating range, implying that optimization in the sense of adaptability to changing environments and, on the contrary, adaptability to a stable environment, results in differing evolutionary strategies [22].

**SUPPLEMENTAL MATERIAL**

Recap of the thermodynamics of metabolism [15]

We consider a system composed of an assembly of muscle bundle fibers that we shall refer to as a *muscle unit*. For simplicity, we assume that these units produce an effort of limited duration, which prevents any saturation effect due to the presence of waste, including secondary metabolites production.

In our approach, a living muscle or even a complete organism, is a system composed of a source and a sink, both connected to a locus where energy conversion actually occurs as depicted in Fig. 3. The coupled transport of energy and mass fluxes through the conversion zone is characterized by the resistance $r_E$, associated to the energy flux, and the resistance $r_M$, associated to the mass flux, thus yielding dissipation and entropy production. The source reservoir (at potential $\mu_+$) includes the resource, in the form of chemical energy, and the sink (at potential $\mu_-$) is the receiving zone for energetic, chemical and thermal wastes, rejected after completion of the conversion process. Two resistive dipoles, which ensure the connection of the conversion zone to both reservoirs, define the boundary conditions for the access to the resource with resistance $r_+$, and the waste rejection with resistance $r_-$. The construction of our model thus requires solely the chemical potential as a thermodynamic potential, which is perfectly justified inasmuch the chemical potential is a physical quantity that can be absolutely measured. As for other thermodynamic systems, the modification of the boundary conditions generate feedback loops that largely govern the overall behavior of the system [40–43]. Note that our approach is quite similar to that for thermoelectricity where heat (microscopic-scale energy) is directly converted into electric – usable, at the macroscale – work [44].

![FIG. 3. Schematic force-flux representation of the complete thermodynamic system: a) general configuration; b) simplified configuration for low duration efforts.](image-url)
We now turn to the constitutive equations describing an animal’s overall energy balance considering an assembly of 
N separated (identical) muscle units connected in parallel, and contributing to the production of the total mechanical
power. On this large scale, the total incoming and outgoing energy fluxes are \( \Phi_+ = N \varphi_+ \) and \( \Phi_- = N \varphi_- \), and the
resistances are \( R_E = \frac{\varphi_+}{N} \), \( R_M = \frac{\varphi_-}{N} \), \( R_+ = \frac{\varphi_+}{N} \) and \( R_- = \frac{\varphi_-}{N} \). The forces produced by these parallel elements add
up, as well as the total metabolic intensity, \( I_M = N i_M \), which characterizes the effort produced by the animal. The
power and potentials thus satisfy [15]:

\[
\begin{align*}
\Phi_+ &= N \varphi_+ - \alpha M_+ I_M + \Delta M_/R_E \\
\Phi_- &= N \varphi_- - \alpha M_- I_M + R_M P^2_M + \Delta M_/R_E \\
P_M &= N p_M = \Phi_+ - \Phi_-
\end{align*}
\]

where \( \Delta M_/M_+ - \Delta M_/M_- \) is the chemical potential difference across the conversion zone, and \( \alpha \) is the strength of
the energy-matter coupling characterizing also the energy conversion efficiency. Since we assume efforts of limited
duration, waste production is small and its rejection to the sink not hindered by its accumulation; hence we may
consider the limit \( r_\rightarrow 0 \) without loss of generality. Note that the zero intensity configuration \( I_M = 0 \) corresponds
to the situation with an organism at rest and a nonzero basal residual energy consumption \( B = Nb = \frac{\mu_- - \mu_+}{R_E + R_+} \) that
sustains basic biochemical processes, so that the whole power \( \Phi_+ = \Phi_- \) consumed by the organism is used to keep
it alive, without production of any (macroscopic) work. From [15], we obtain the power delivered by a single muscle
unit as the product of the extensive metabolic intensity \( I_M \), and the intensive metabolic force per muscle unit, \( F_M \):

\[
p_M = F_M i_M = \left[ F_{iso} - \left( 1 + \frac{r_H}{r_M} \right) r_M i_M \right] i_M
\]

where \( F_{iso} \) is the isometric force for a given muscle unit. Note the presence of the additional dissipative term
\( R_H = \frac{F_{iso} - R_{iso}}{r_M} \) in Eq. (12), which stems from feedback effects \( R_{iso} = \frac{\alpha M_+ - \alpha M_-}{r_M} \); the term \( r_T = N r_T = \frac{1}{\alpha R_E + R_+} \)
refers to a threshold of metabolic intensity beyond which the available power collapses. In the case of a Dirichlet-type
coupling with the reservoirs, i.e. \( R_+ = R_- = 0 \), \( R_H(I_M) = 0 \), there is no feedback effect. As such, the metabolic
intensity characterizes the operating point of the system, i.e., the intensity of the effort produced, either in a static
situation or when setting in motion.

Experimental conditions of Hoyt’s work

It is customary, as Hoyt and Taylor did in [26], to tilt the treadmill slightly to prevent the subject from working
without any effort, which is a situation experienced as unpleasant for the limbs. At constant speed, this experimental
treadmill configuration corresponds to a constant average resistive force stress \( F_r = f \) exerted on the animal. From
an experimental point of view Hoyt and Taylor state that no change in blood lactate levels was detected in the animal
up to speeds of 10 m s\(^{-1}\) [26]. It is therefore reasonable to consider that no significant anaerobic contribution is to be
expected in these measurements, which places them within the limits of validity for the model. The horse is placed
on a treadmill, the running speed of which is imposed. It is therefore immobile in relation to the laboratory frame
of reference, and even at high speed, there is no external viscous contribution to the force deployed by the animal to
move. It can be noted (see Fig. 2 in the main text of the article) that the COT seems to show a discrepancy, and a
deviation from the model, for the highest values of speed in the case of walking. This can be understood considering
that the animal is in this case in close proximity to the maximum power it can produce when walking, and therefore
to its maximum speed for this mode of movement. The linear approximation \( I_M = kv \) described in Eq. (17) and
Fig. 4 is then no longer valid, which explains why the points no longer follow the model. Concretely, the animal is in
pain, as a walker would be during an exaggeratedly fast walk. This is a physiological state beyond the scope of the
model, so we have chosen not to include these points when processing the data.

Relationship between the number of muscle units \( N \) and the metabolic intensity \( i_M \)

In the most general case where only the required power is imposed, neither \( N \) nor \( i_M \) are fixed a priori, and
any increase in the power and/or speed setpoint results in an increase of both \( N \) and \( i_M \); \( N \) can thus vary from
\( N_0 = N(i_M = 0) \) to \( N_H = N(i_M = I_H) \), i.e. the maximum metabolic intensity explored when all the muscle units
are activated. The latter case corresponds to the protocol for an isolated muscle in which all fibers are activated
simultaneously, typically force/speed experiments. As a first approximation, let us consider that the relation linking \( N \) to \( i_M \) can be approximated by a first-order polynomial in \( i_M \) for values between \( i_M = 0 \) and \( i_M = i_H \),

\[
N(i_M) = N_0 \left[ \left( \frac{N_H}{N_0} - 1 \right) \frac{i_M}{i_H} + 1 \right] \tag{13}
\]

Rewriting the expression of the waste rejection flux \( \Phi_- \) as follows, makes its dependency on \( N \) appear:

\[
\Phi_- = N(a_0 i_M + r_M i_M^2 + b) = a_0 I_M + \frac{N_H}{N} R_M I_M^2 + \frac{N}{N_H} B, \tag{14}
\]

with \( R_M = r_M/N_H \), \( B = N_H b \) and \( I_M = N i_M \). The power is then written

\[
P_M = (\alpha \Delta \mu M - R_M I_M) I_M \tag{16}
\]

As expected the driving force term \( \alpha \Delta \mu M - R_M I_M \) is intensive, i.e. it does not depend on \( N \). Increasing the power \( P_M \) can be obtained by multiplying the number of muscle fibers by or increasing the metabolic intensity (up to a certain point).

![Graph](image_url)

**FIG. 4.** In the top panel \( \Phi_- \), represented by the solid thick line, is shown as a function of \( i_M \propto v \), for a constant muscle units number \( N \); it is also shown as a red dotted-dashed line and a green dotted line for \( N \) increasing linearly from \( N(i_M = 0) = 0.90N_H \) to \( N(i_M = I_H) = N_H \), and from \( N(i_M = 0) = 0.75N_H \) to \( N(i_M = I_H) = N_H \) with \( I_H = 2 \), respectively. In the bottom panel, the corresponding \( COT = \varphi_- / v \) is shown as a function of \( i_M \propto v \) (with the same same color code). The dots indicate the minimum of each curve. The ratio \( B/v \) is represented by the decreasing black dashed curve, while the increasing black dashed line that shows \( a_0 + R i_M \) (see Eq. (5) in the main text) characterizes the dissipation process.

Considering a muscle unit that contracts at the frequency \( f \) over a length \( L \), the metabolic intensity \( i_M \) can be approximated using a linear relationship \( i_M \propto fL = kv_1 \), with \( v_1 \) being the global velocity obtained using a single muscle unit and \( k \) a coupling constant. Thus, the speed \( v \) associated with \( N \) fibers is written \( I_M = N i_M = N kv_1 = kv \), where \( v \) is the observed velocity (the horse forward motion). For an animal moving on an inclined slope, modulating the angle of this slope while keeping constant \( v \) is equivalent to increase \( N \) keeping \( f \) constant. Conversely, modulating \( f \) at constant \( N \) is equivalent to a classical force/speed experiment. For any displacement the metabolic power \( P_M \)
and the external required power are related via $P_r = F_r v$, where $F_r$ is the required force and $P_r \leq P_M$. Of course $F_r$ depends directly on the experimental conditions, i.e. the viscous friction due to the air, the slope, the transported load. In the case of horizontal movement on a conveyor belt, it is reasonable to assume that $F_r$ is constant. Thus it comes from Eq. (4) in the main text that the general expression for $v(I_M) = \frac{F_{iso} I_M}{P_{iso}}$ may read:

$$v = \left[ F_{iso} - \left( 1 + \frac{R_H (I_M) I_M}{R_M} \right) R_M I_M \right] \frac{I_M}{F_r}$$

(17)

from which we then derive the COT:

$$COT = \frac{N}{N_H} \left( a_0 k + R_M k^2 v + \frac{B}{v} \right)$$

(18)

$$= k \frac{N}{N_H} \text{COE}_-$$

(19)

Contrary to the situation when all the muscle units are stimulated, both the effective basal and effective viscosity depend on the operating point. The basal is modulated downwards by a factor $\frac{N}{N_H} < 1$ while the effective viscosity is increased by the inverse of this factor, $\frac{N_H}{N} > 1$. When $N = N_H$ is constant, it comes that the speed associated with the minimum of COT reads:

$$v^* = \sqrt{\frac{r_M b}{I_M}}$$

(20)

which, in a scaled version, can be written:

$$V = \frac{R_M I_T^2}{F_r v^*} I_M^2 \left[ \left( \frac{F_{iso}}{a_0} + 1 \right) r_M z - I_M + 1 \right]$$

(21)

where $I = i_M / I_T$ and $V = v / v^*$ indicate the scale (dimensionless) for intensities and velocities respectively; $z$ is the figure of merit of the underlying thermodynamic process, which is a generalization of the figure of merit usually encountered in Onsager-type developments: $z = \frac{F_{iso} R_M B}{R_{iso} B^2}$. Note that in the case of a strict Dirichlet type boundary condition, i.e. $R_+ = 0$, the above equation is reduced to

$$V = \frac{R_M I_T^2}{F_r v^*} I_M^2$$

(22)

The flux $\Phi_-$ and the corresponding COT are shown in Fig. 3, where the number of muscle units varies by 10% and 25%, between $i_M = 0$ and $i_M = i_H$. As expected, the overall behavior is preserved and, in particular, the hyperbolic behavior when $i_M \rightarrow 0$ as well as the linear growth beyond the minimum of COT. It is further expected that the coordinates of the minimum $(v^*, COT^*)$ decrease as $N$ increases. Regarding the term $a_v$, it is important to note that the intercept at the origin of the COT curve is such that when $v \gg 1$ then $a_v < a_0$. On the other hand, since $a_0 = \alpha_- \mu_-$ is a priori small, $a_v$ can possibly become negative; $a_v$ is essentially proportional to $\mu_-$, so a modulation by $N$ can lead to $\mu_-$ being identified as a negative potential when fitting the curves. This question remains unresolved, due to the lack of Hill type measurements that would remove the uncertainty on the determination of $a_0$.

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