Key principle of the efficient running, swimming, and flying

V. B. Kokshenev(a)

Departamento de Física, Universidade Federal de Minas Gerais, Instituto de Ciências Exatas - Caixa Postal 702, CEP 30123-970, Belo Horizonte, Brazil

received 16 April 2010; accepted in final form 18 May 2010
published online 17 June 2010

PACS 87.85.G– Biomechanics
PACS 87.19.ru– Locomotion
PACS 04.20.Fy – Canonical formalism, Lagrangians, and variational principles

Abstract – Empirical observations indicate striking similarities among locomotion in terrestrial animals, birds, and fish, but unifying physical grounds are lacking. Being coherent in displacements, velocities and forces, the body appendages of animals are tuned to the natural propagation frequency through elastic muscle moduli. When applied to efficient locomotion, the analytical mechanics principle of minimum action yields two patterns of biomechanical similarity via two explicit spatiotemporal coherent states. In steady-locomotion states, the slow muscles, determining maximal optimum speeds, maintain universal intrinsic muscular pressure. In transient states, maximal speeds are due to fixed mass-dependent stiffness of fast muscles generating a uniform force field, exceeding gravitation.

Copyright © EPLA, 2010

Introduction. – Although evolutionary biologists and comparative zoologists make wonderful generalizations about the movements of terrestrial animals, birds, and fish of different size [1–12], the fundamental physical principles underlying striking similarities in distinct types of movement for organisms remain a challenge [13]. Within the scope of the simplest pendulum model (stiff-legged approximation), it has been demonstrated [14] that humans and other animals, in contrast to human-made engines, accomplish efficient propulsion (maximum power output at minimum power consumption) by tuning the musculoskeletal system to the resonant propagation frequency. Storing mechanical energy in elastic oscillations of body parts and in pendulum oscillations of legs or other appendages, animals thereby reduce the energy consumption [1,3]. In this study, instead of searching for uncovered principles of body mass effects in biology [5], or doing in-depth analysis of equations of motion in pendulum [14], spring [7,8], or vortex [15] approximations and other engineer constructive approaches, e.g., [9], I address the key principle of mechanics.

In analytical mechanics, the requirement of minimum action between two fixed points of the conceivable trajectory of an arbitrary isolated mechanical system determines Lagrangian \( L(q,v) \), the function of time-dependent coordinates \( q(t) \) and instant velocities \( v(t) = dq/dt \). One of the most pronounced properties of a closed freely moving system is the preservation of total energy and momentum, arising respectively from the temporal and spatial homogeneity of \( L(q,v) \), e.g., [16]. Since the multiplication of Lagrangian on an arbitrary constant does not affect the equations of motion, the property of spatiotemporal homogeneity of frictionless closed systems results in the mechanical similarity [16] that establishes the major mechanical constraints without consideration of equations of motion. More specifically following Landau and Lifshitz [16], let us consider the uniform transformation of mechanical trajectories due to linear changing of all coordinates \( q \rightarrow aq \) and times \( t \rightarrow bt \), and hence velocities \( v \rightarrow (a/b)v \), via arbitrary coefficients \( a \) and \( b \). Let the potential energy change consequently through a certain exponent \( \mu \), i.e., \( U(aq) = a^\mu U(q) \). Being a quadratic function of velocities, the kinetic energy scales as \( K(av/b) = (a/b)^2 K(v) \). The requirement of homogeneity of \( L(q,v) = K(v) - U(q) \) is self-consistent when both the energies change similar, i.e., \( (a/b)^2 = a^\mu \) or \( b = a^{1-\mu}/2 \). Thereby, the frictionless propagation of a classical system obeys the scaling relations imposed on the overall-system dynamic characteristics (period \( T \), speed \( V \)) and mechanical characteristics (force amplitude \( F \), energy \( U \)), namely [16]

\[
T \sim L^{1-\mu/2}, \quad V \sim L^{\mu/2}, \quad F \sim L^{\mu-1}, \quad \text{and} \quad U \sim L^{\mu},
\]

where \( L \) is a characteristic linear size of the trajectory. Known examples are the uniform gravitational (\( \mu = 1 \))\(^{(a)}\)

---

\(^{(a)}\)E-mail: valery@fisica.ufmg.br
and elastic-strain ($\mu = 2$) force fields. The seminal case
$\mu = -1$ introduces Newtonian’s intertrajectory coupling
force $F \sim M^2 L^{-2}$, where mass $M$ emerges in eq. (1) as
the dimensional coefficient of proportionality.

It will be demonstrated below how the mechanical
principle of minimum action applied to musculoskeletal
system of animals involved in the resonant (efficient)
locomotion provides the basic patterns of biomechanical
similarity.

**Minimum action in biomechanics.** – During animal
locomotion, the chemical energy released by muscles and
the mechanical elastic energy stored in the body system
are transformed into external and internal work and
partially lost as heat caused by frictional effects. In steady
locomotion (walking, running, flying, or swimming), the
permanent metabolic energy consumption, which is
locomotion (walking, running, flying, or swimming), the
chemical energy released by muscles and
are transformed into external and internal work and
partially lost as heat caused by frictional effects. In steady
locomotion (walking, running, flying, or swimming), the
permanent metabolic energy consumption, which is
minimal at the resonance conditions [14,15].

As can be exemplified by the resonant steady human
walking [17], the weak velocity-dependent frictional effects
are accounted for as a special perturbation theory, exclud-
ing resonance effects near the natural frequency of prop-
gagation ($\omega_0$). Such a framework suggests a generalization
of the Lagrangian formalism over weakly open systems
driven by non-conservative forces. As a result, the steady
locomotion tuned to the resonant frequency (and resonant
phase) via harmonic and anharmonic parts of the body
driving force emerges as a free body’s center-of-mass prop-
gagation (forward translation and backward rotations) that
justifies the application of the mechanical similarity [16],
raising from the principle of minimum action in the freely
moving systems, at least in the narrow frequency domain
near $\omega_0$ (further details can be found in the appendix).

During the muscle-forced resonant locomotion, the
maximum stride length $\Delta L$ for terrestrial steady loco-
motion, e.g., [1,17], or stroke amplitude $\Delta L$ of steadily
flying and swimming animals, e.g., [4], establishes the
characteristic dynamic length of the body’s center-
mass trajectory and the propagation speed $V = \Delta L/T$,
through the period $T = 2\pi/\omega_0$. As common in bio-
mechanics [1,7,8,17–19], the *force change* $\Delta F$ for the body
force output $F$, driving through the environment a given
animal (of characteristic body length $L$, cross-sectional
area $A$, and body mass $M$) is characterized through the
effective body rigidity, or stiffness $K = \Delta F/\Delta L$, which
determines the *natural cyclic frequency* $\omega_0 = \sqrt{K/M}$.

Since the animal locomotion is substantially muscu-
lar [1,3,18], the *muscle stiffness* $K_m = E_m A_m / L_m$ (of an
effective muscle of length $L_m$ and cross-sectional area
$A_m$) controlled by the geometry-independent muscle
rigidity or *elastic modulus* $E_m$ (ratio of *stress* $\sigma_m$
onto *strain* $\varepsilon_m$, i.e., $\sigma_m/A_m(\varepsilon_m/\varepsilon_m)$) [7,18], is also
under our consideration.

Using very simple physical ideas [20], the *scaling
biomechanics* [1,2,7,9,18,19] introduces similarities on
the body-size scale, relating the dynamic (trajectory)
motion parameters to animal’s size and mass, e.g.,
$\Delta L \propto L \propto M^{1/3}$. To advance the integrative approach
to animal locomotion [1–18], had been elucidated by geometrical
[1,2,7,20], mechanical [19] and elastic-strain
[7,19,21,22] similarities, let us determine a
force field $g_m \equiv F_m/m$, where the *muscle mass* $m$
(or *motor mass* [6]) plays the role of a source (or fuel [6])
in the generation of the *active* elastic-force output $F_m$.

The principle of mechanical similarity shown in eq. (1)
is now applied to different-sized *elastic* body systems
and muscle subsystems, moving at resonance along similar trajectories. When combined with the known
body mass scaling relations (hereafter distinguished by
symbol $\propto$) taken in the linear-displacement approximation
($L \propto \Delta L \propto \Delta L_m \propto L_m$), the resulted minimum action in
biomechanics yields

$$ T^{-1} = 1/T_{ms} \propto \sqrt{E_{ms}L_m^{-1}}, \quad V \propto V_{ms} \propto \sqrt{E_{ms}}; $$

$$ \Delta L \propto L \propto M^{1/3}, \quad \Delta L_m \propto L_m \propto m^{1/3}; $$

$$ F \propto \Delta F \propto \Delta F_m = \varepsilon_m A_m E_m \propto F_m \propto m E_m L_m^{-1}; $$

$$ \text{with } E_m \propto (L_m)^s \text{ and } g_m \propto (L_m)^{s-1}. \quad (2) $$

The shown here scaling relations arise from the equations
provided above for all physical quantities and the
constrains imposed by the invariable [1,7,9,18,20] *body
density* $\rho (M/AL)$ and *muscle density* $\rho_m (m = A_m L_m)$. Thus, combining the knowledge of modeling
of animals and muscle subsystem [1,2,7,8,12,14,15,18,20]
with the mechanical principle [16], eq. (2) eventually
introduces the intrinsic muscle characteristics $E_{ms}$ as
a hidden dynamic degree of freedom. Such a characteri-
ization is attributed to the ability of muscular tuning to
the efficient locomotion in a certain mode distinguished
by the single *dynamic-state exponent* $s$. More specifically,
a bridge between the active-force elastic muscular
fields, underlying body systems of the elastic energy
$U_{elast}$, and common “passive-force” elastic systems with
$\mu = 2$ discussed below eq. (1), is suggested through
eq. (2) via the evident relations: $U_{elast} \propto K \Delta L^2 \propto
m E_{ms} (\Delta L / L_m)^2 \propto m (L_m)^s \propto ML^s$. One can see
that the dynamic exponent $s$ of the active-force bio-
mechanical systems plays the role of the exponent $\mu$
in eq. (1).

**Results and discussion.** –

**Steady-speed modes.** For the flight mode, the steady-
speed locomotory pattern was first recognized by Hill: “the
frequencies of hovering birds are in inverse proportionality
to the cube roots of the weights, *i.e.*, to the linear size” [2].
The corresponding natural propagation frequency $T^{-1} \propto\sqrt{E_{ms}/\rho L}$, following from eq. (2) with $s = 0$, lucidly
indicates that muscle forces drive this locomotory regime
instead of the gravitational field $g$, resulting in the rigid-
pendulum modeling with $T_{pend}^{-1} \propto \sqrt{gL^{-1/2}}$ [7,14]. Hill’s
observation therefore plays the role of Kepler’s observation
of third law for planets $T^2 \propto L^3$ anticipated Newton’s
theory, as discussed below eq. (1) taken with $\mu = -1$. 

48005-p2
Table 1: Mechanical characteristics of animal’s body system and slow individual muscles moving in steady dynamic states $s = 0$ prescribed by the principle of minimum muscular action in eq. (2). All calculations are made on the basis of the provided above relations using four invariants: $\rho \propto M^0$, $\rho_m \propto E_0 \propto \varepsilon_m \propto m^0$. Abbreviation: $E_0 = E_{\text{mod}}^{(\text{max})} = E_{\text{mod}}^{(\text{max})}\varepsilon_{\text{mod}}$.

| $s = 0$ | Frequency | Speed | Force | Mass |
|---------|-----------|-------|-------|------|
| $T^{-1}$ | $T^{-1}$ | $\rho^{-\frac{1}{2}} E_0^{\frac{1}{2}} \cdot L^{-1}$ | $\rho^{-\frac{1}{2}} E_0^{\frac{1}{2}} \cdot V^{-\frac{1}{2}}$ | $F^0$ | $\rho^{-\frac{1}{2}} E_0^{\frac{1}{2}} \cdot M^{-\frac{1}{2}}$ |
| $\Delta L, L$ | $\rho^{-\frac{1}{2}} E_0^{\frac{1}{2}} \cdot T$ | $L$ | $\rho^{-\frac{1}{2}} E_0^{\frac{1}{2}} \cdot V^{-\frac{1}{2}}$ | $F^0$ | $\rho^{-\frac{1}{2}} E_0^{\frac{1}{2}} \cdot M^{-\frac{1}{2}}$ |
| $V^{(\text{max})}$ | $\rho^{-\frac{1}{2}} E_0^{\frac{1}{2}} \cdot T^0$ | $1$ | $\rho^{-\frac{1}{2}} E_0^{\frac{1}{2}} \cdot V^{-\frac{1}{2}}$ | $L^{-1}, F$ | $\rho^{-\frac{1}{2}} E_0^{\frac{1}{2}} \cdot M^{-\frac{1}{2}}$ |
| $K^{(\text{max})}_{\text{body}}$ | $\rho^{-\frac{1}{2}} E_0^{\frac{1}{2}} \cdot A \cdot T^{-1}$ | $E_0 A \cdot L^{-1}$ | $\rho^{-\frac{1}{2}} E_0^{\frac{1}{2}} \cdot V^{-\frac{1}{2}}$ | $L^{-1}, F$ | $\rho^{-\frac{1}{2}} E_0^{\frac{1}{2}} \cdot M^{-\frac{1}{2}}$ |
| $\varepsilon_{\text{mod}}^{(\text{max})}$ | $\varepsilon_m E_0 \cdot T^0$ | $\varepsilon_m E_0 \cdot L^0$ | $\varepsilon_m E_0 \cdot V^0$ | $\varepsilon_m E_0 \cdot F^0$ | $\varepsilon_m E_0 \cdot m^0$ |
| $E_{\text{mod}}^{(\text{max})}$ | $\varepsilon_m E_0 A \cdot m^0 T^0$ | $\varepsilon_m E_0 A \cdot m^0 L^0$ | $\varepsilon_m E_0 A \cdot m^0 V^0$ | $\varepsilon_m E_0 A \cdot m^0 F^0$ | $\varepsilon_m E_0 \cdot m^0$ |

Hence, when the animal travels or cruises slowly for long distances [4] with the constant optimum speed $V_{\text{body}}^{(\text{max})} \propto \sqrt{\frac{E_{\text{mod}}^{(\text{max})}}{\rho}}$, invariant with body weight and frequency, or moves throughout the terrestrial, air, or water environment resisting drag forces, the legs, wings, and tails are adjusted to maintain constant elastic modulus $E_{\text{mod}}^{(\text{max})}$ in slow muscles responsible for the steady locomotion [23]. Consequently, the universal (speed-, period-, and mass-independent) functional intrinsic muscle stress $\varepsilon_m E_0$, predicted in eq. (2) with $s = 0$, provides constant safety factor (ratio of muscle strength to peak functional stress), also foreseeing by Hill [2]. These and other relevant constraints of steady-speed locomotion are displayed in table 1.

The constant maximum propulsive force $F_{\text{body}}^{(\text{max})} \propto E_{\text{mod}}^{(\text{max})} A$, equilibrating all drag forces by slow muscles, i.e., $F_{\text{drag}}^{(\text{max})} \propto F_{\text{mod}}^{(\text{max})}$ (table 1), was first documented by Alexander via the peak body force $F_{\text{body}}^{(\text{exp})} \propto M^{2/3}$ [10] exerted on the environment by running, flying, and swimming animals ranged over nine orders of body mass. More recently [6], the slow-fiber force output $F_{\text{mod}}^{(\text{max})} \propto m^{2/3}$ (table 1) was revealed by statistical regression method in both biological and human-made slow motors. The underlying muscle longitudinal field “caused by intrinsic muscle quantity (here associated with $E_{\text{mod}}^{(\text{max})}$), equally stimulated electrically and by the nervous system” [2] decreases linearly with the distance $r$: $g_{\text{mod}}^{(\text{max})}(r) \approx E_{\text{mod}}^{(\text{max})} \varepsilon_m^{(\text{max})} / \rho_m r$, where $\varepsilon_m^{(\text{max})}$ is nearly “isometric” strain [7,18], also following from eq. (2) with $s = 0$.

The efficient locomotion emerges as a concerted behavior of the body’s appendages synchronized in time and coordinated in displacements. Consequently, the muscle duty factor $\beta_m = \Delta T_m / T$ ($\Delta T_m$ is the timing of the muscle lengthening or shortening displacement $\Delta L_m$) [1,11] must be constant, besides the body mass invariable Strouhal number $St = \Delta L / VT$, explaining the role of tail and wing oscillations in steady swimming and flying [24]. The universal number $St_{\text{cruis}} \approx 0.3$ was remarkably established [4] for dolphins, birds, and bats, cruising at maximum propulsive efficiency.

The steady-speed-locomotion state also was established in hovering flying motors via the wing frequencies $1/T_{\text{exp}} \propto M^{-1/3}$ [25] (see table 1). However, departures from Hill’s findings rationalized here by the dynamic state $s = 0$ were debated [26]. For example, it was claimed [7] that Hill’s maximal optimum speeds are in sharp disagreement with the peak trot-gallop crossover speeds $V_{\text{cross}}$ measured in quadrupeds [12]. The same could refer to the bipeds [11]. As can be seen from the proper empirical data $1/T_{\text{exp}} \propto M^{-0.178}$ [11] and $1/T_{\text{exp}} \propto V_{\text{cross}}^{-1} \propto M^{-0.145}$ [7,12], the measured stride frequencies indicate observations of another kind of biomechanical similarity attributed to the transient-mode dynamic state $s = 1$, prescribed by eq. (2) through the mass-dependent muscle modulus $E_{\text{mod}}^{(\text{max})} \propto L_m \propto m^{1/3} \propto M^{1/3}$.

**High-speed transient-mode steady states.** The minimum muscle action of leg muscles in fast running rats, wallaby, dog, goat, horse, and human was indirectly revealed through the biomechanical similarity derived on the basis of leg spring model [8]. The realistic modeling provided the observation of scaling relations for the stride frequency $T_{\text{mod}}^{-1} \propto \Delta T_m^{-1} \propto M^{-0.19}$, stride length $L_{\text{mod}}^{(\text{max})} \propto M^{0.30}$, characteristic model-body (leg) length $L_{\text{mod}} \propto M^{0.34}$, justifying the scaling rule $\Delta L \propto L \propto M^{1/3}$ employed in eq. (2), as well as the model-body stiffness $K_{\text{mod}}^{(\text{max})} \propto M^{0.67}$ and force output $F_{\text{mod}}^{(\text{max})} \propto M^{0.97}$, all predicted in table 2. Thereby, the modeled scaling relations are unified by the dynamic steady state $s = 1$, also found above as the crossover state between two fast modes.

In accord with table 2, the equilibration of the air drag by wings of flapping birds is manifested by the observed wing frequencies $1/T_{\text{exp}} \propto M^{-1/6}$ [25]. Moreover, the biomechanical similarity between animals resisting air, ground, and water friction forces was demonstrated via the energy cost minimization [9], though the dynamic scaling relation $V \propto L^{1/2}$ prescribed by the minimum action in table 2, was critically involved in the constructal theory on ad hoc basis.

When the physiologically equivalent, transient equilibrated states [19] are associated with $s = 1$ steady state
of the individual fast-twitch-fiber muscles, controlling fast modes [23], the muscle field is apparently uniform and likely universal [6]. Indeed, the body force field \( F\) of fast motor individual muscles in running, flying, and swimming animals. One therefore infers that the gravitational field \( g \) is not crucial in fast running modes, as proposed in [9]. Moreover, the principle of minimum muscular action suggests that fast muscles in the state \( s = 1 \) may generate force in the whole muscle bulk [27] maintaining velocity-independent body stiffness (table 2). In other words, the fast muscles are not simple passive-force springs, acting in parallel with the length-independent period (see eq. (1) with \( \mu = 2 \)), but are complex systems [3,28], being able to activate fibres in both parallel and series. Maintaining the uniform muscle force field \( g_{m1} \) in fast muscles, the Froude number \( (Fr = V/\sqrt{gL} [1]) \) must be therefore mass-invariable at \( V_{cross} \), for both body systems and muscle subsystem (with \( F_{cross} = g_{m1}(\rho g) \), apart from the corresponding Strouhal number \( S_{cross} \)). Examples are \( Fr_{run} = 1.5 \) and \( S_{cross} \approx 0.4 \) established [8] for animals running with maximal speeds.

**Conclusion.** – The main goal of this letter is to demonstrate how the complex biological phenomenon of biomechanical similarity in animal locomotion allows to be rationalized and formulated as a predictive, quantitative framework. It has been shown how the fundamental physical principle of minimum action applied to locomotory muscles tunes to the natural cyclic frequency via intrinsic elastic moduli quantifies amazing similarities established empirically via dynamic and mechanical characteristics for different-sized animals, moving in similar gaits. Naturally operating the softness of legs, wings, and tails, the efficient runners, flyers, and swimmers are shown to maintain constant Strouhal number via the universal muscular pressure (table 1), when traveling or cruising at steady speeds. When acting quickly at higher speeds, escaping from predators, or when hunting, the successful runners, flyers, and swimmers appear to maintain the universal field in the whole body via fast muscles (table 2).

The uniform muscular field results in the bodyweight-depending muscle stiffness, maintaining the universality of Froude and Strouhal numbers. The study provided from first principles illuminates and supplements a wide spectrum of reliable empirical data on walking and running bipeds [3,11], trotting and gallopping quadrupeds [6–9,12], hovering and flapping birds [2–4,10,11], bats, and insects [3,4,9], undulating and tail-beating fish [2–4,9,10], dolphins [2,4], sharks [4], and whales [2].

On the other hand, the study of muscle characteristics, including obtained scaling relations to muscle and body mass, is limited by the linear-displacement approximation. It can be shown that the top speeds attributed to limiting animal performance [19,26] cannot be achieved by linear strains. The consequences of application of the minimum action to specific fast locomotory muscles structurally adapted to a certain mechanical activity, such as motor, brake, or strut functions [3] prescribed by non-linear elastic effects [27] will be discussed elsewhere.

***

Thanks are due to anonymous referees for helpful critical comments. Financial support by the national agency CNPq is also acknowledged.

**Appendix: moving at resonance.** – Following the principle of superposition of the motion, the longitudinal propagation for the center of mass (c.m.) of a given animal of mass \( M \), moving with a steady speed \( V \), can be described by \( X(t) = Vt + x(t) \). Separating the translational degree of freedom [17], the cyclic c.m. rotations of frequency \( \omega \) obey the Newtonian equation

\[
\ddot{x} + 2\lambda \dot{x} + \omega_0^2 x = a_0 \cos \omega t. \tag{A.1}
\]

Here \( \lambda = \gamma/2M, \omega_0 = \sqrt{K/M}, \) and \( a_0 = \Delta F/M \) are parameters determined by the body friction coefficient \( \gamma \), body stiffness \( K \), and the driving force amplitude \( \Delta F \) (for further details see [17]). The steady-state \((t \gg \lambda^{-1})\) solution to eq. (A.1)

\[
x(t) = \frac{a_0 \cos(\omega t - \varphi)}{[(\omega_0^2 - \omega^2) + 4\lambda^2 \omega^2]^{1/2}}, \quad \varphi = \arctan \frac{2\lambda \omega}{\omega_0^2 - \omega^2}, \tag{A.2}
\]
can be found in standard manuals on analytical mechanics. One can see that the friction i) modifies the original resonant frequency $\omega_0$, reducing it to $\tilde{\omega}_0 = \sqrt{\omega_0^2 - \lambda^2}$, and ii) makes to be finite the c.m. displacement amplitude, achieving maximum at $\sqrt{\omega_0^2 - 2\lambda^2}$, also lower $\omega_0$. The resonant solution to eq. (A.2) $x_0(\omega_0 t) = a_0(2\lambda \omega_0)^{-1}\sin(\omega_0 t)$, obtained at $\omega = \omega_0$ and $\varphi = \varphi_0 = \pi/2$, removes the friction term from eq. (A.1), thereby providing free c.m. rotation, besides free translation. In order to describe such an almost frictionless locomotion beyond the resonant frequency, let us consider eq. (A.1) at $\omega = \omega_0(1 - \epsilon)$, namely

$$\ddot{x} + \omega_0^2 x = \Lambda[\omega_0(1 - \epsilon)t], \tag{A.3}$$

within the resonant domain $\omega_0 \geq \omega > \tilde{\omega}_0$, treating $\epsilon$ as a small parameter. The frictional effects are now described by a function $\Lambda(\omega t)$, found with the help of eq. (A.2). Using the evident relation $\omega_0^2 - \omega^2 = 2\omega_0\epsilon(1 - \epsilon/2)$, one introduces the standard perturbation scheme via the phase $\varphi$ of the form $\varphi(\epsilon) = \pi/2 + \epsilon\varphi_1 + \epsilon^2\varphi_2$, which coefficients readily follow from eq. (A.2). However, one can see that the resonant solution $x(t) = x_0(\omega_0 t) + \epsilon x_1(\omega_0 t) + \epsilon^2 x_2(\omega_0 t)$ has divergent-amplitude terms $x_1(\omega_0 t)$ and $x_2(\omega_0 t)$.

As shown in [17], the problem of the divergency could be avoided, if the driving force was improved self-consistently, with account for the cycle-symmetry and temporal-inversion-symmetry conditions. Specifically, the right part of eq. (A.1) should be completed by additional terms, arising from the anharmonic parts of both potential and kinetic energies, cycling near the double resonant frequency $2\omega_0$ (see eq. (4) in [17]). As a result, the improved near-resonance solution has the form $\tilde{x}(t) = x_0(\omega_0 t) + \epsilon\tilde{x}_1(2\omega_0 t) + \epsilon^2\tilde{x}_2(2\omega_0 t)$, following from eq. (6) in [17] taken with the above found phase $\varphi(\epsilon)$, with $\epsilon \omega_0 \ll \lambda < \omega_0$.

REFERENCES

[1] Alexander R. McN., Principles of Animal Locomotion (Princeton University Press, Princeton and Oxford) 2002, pp. 53–67.
[2] Hill A. V., Sci. Prog., 38 (1950) 209.
[3] Dickinson M. H., Farley C. T., Full J. R., Koehl M. A. R., Kram R. and Lehman S., Science, 288 (2000) 100.
[4] Taylor G. K., Nudds R. L. and Thomas A. L., Nature, 425 (2003) 707.
[5] Darveau C. A., Suarez R. K., Andrews R. D. and Hochachka P. W., Nature, 417 (2002) 166.
[6] Marden J. H. and Allen L. R., Proc. Natl. Acad. Sci. U.S.A., 99 (2002) 4161.
[7] McMahon T. A., J. Appl. Physiol., 39 (1975) 619.
[8] Farley C. T., Glasheen J. and McMahon T. A., J. Exp. Biol., 185 (1993) 71.
[9] Bejan A. and Marden J. H., J. Exp. Biol., 209 (2006) 238.
[10] Alexander R. McN., J. Exp. Biol., 115 (1985) 231.
[11] Gatez S. M. and Biewener A. A., J. Zool. Lond., 224 (1991) 127.
[12] Heglund N., McMahon T. A. and Taylor C. R., Science, 186 (1974) 1112.
[13] Cressey D., Moving forward together, Nat. News, 1 December 2008, doi:10.1038/news.2008.1268.
[14] Ahlborn B. K. and Blake R. W., Zoology, 105 (2002) 165.
[15] Ahlborn B. K., Blake R. W. and Megill W. M., Zoology, 109 (2006) 43.
[16] Landau L. D. and Lifshitz E. M., Mechanics, 3rd edition (Pergamon Press, Oxford) 1976, Sect. 10.
[17] Kokshenev V. B., Phys. Rev. Lett., 93 (2004) 208101.
[18] McMahon T. A., Muscles Reflexes, and Locomotion (Princeton University Press, Princeton, NJ) 1984.
[19] Kokshenev V. B., J. Biomech., 40 (2007) 2911.
[20] Lin H., Am. J. Phys., 50 (1981) 72.
[21] Rubin C. T. and Lanyon L. E., J. Theor. Biol., 107 (1984) 321.
[22] Hokkanen J. E. I., J. Theor. Biol., 120 499.
[23] Rome L. C., Funke R. P., Alexander R. McN., Lutz G., Aldridge H., Scott F. and Freedman M., Nature, 335 (1988) 824.
[24] Whitfield J., One number explains animal flight, Nat. News, 16 October 2003, doi:10.1038/news031013-9.
[25] Ellington C. P., J. Exp. Biol., 160 (1991) 71.
[26] Jones J. H. and Lindstedt S., Annu. Rev. Physiol., 55 (1993) 547.
[27] Kokshenev V. B., J. Biomech., 41 (2008) 912.
[28] Lindstedt S. L., Reich T. E., Keim P. and LaStayo P. C., J. Exp. Biol., 205 (2002) 2211.