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Physical Insights Into Dynamic Similarity in Animal Locomotion. I. Theoretical Principles and Concepts

Valery B. Kokshenev

*Departamento de Física, Universidade Federal
de Minas Gerais, Belo Horizonte
Brazil*

1. Introduction

Comparative zoologists, evolutionary biologists, experimental biologists, and mechanical engineers make wonderful generalizations about the movements of different-sized running bipeds and quadrupeds (Heglund et al., 1974; McMahon, 1975; Alexander, 1976; Hoyt & Taylor, 1981; Garland, 1982; McMahon et al., 1987; Rome et al., 1988; Gatesy & Biewener, 1991; Farley et al., 1993; Cynthia & Farley, 1998; Bullimore & Burn, 2006), flying birds and swimming fish (Hill, 1950; Alexander, 2003; Taylor et al., 2003). The dynamic similarity across body mass and taxa of animals maintaining a certain gait in locomotion has been thoroughly investigated (Alexander, 1976, 1985, 1989, 2005; Alexander & Bennet-Clark, 1976; Alexander & Jayes, 1983; Marden & Allen, 2002; Biewener, 2005; Bejan & Marden, 2006a, b; Bullimore & Donelan, 2008). Based on integrative approach to animal locomotion (e.g., review by Dickinson et al., 2000) and using simple physical ideas (e.g., reviews by Lin, 1982 and Alexander, 2003), many cited above researches have demonstrated the importance of scaling biomechanics via reliably established scaling relations for gait characteristics with changes of speed and body mass. Among well known empirical findings of the dynamic similarity in animals observed across body mass are scaling relations established for stride (or stroke) speed and/or frequency (Hill, 1950; Heglund et al., 1974; Greenewalt, 1975; Garland, 1982; Heglund & Taylor, 1988; Gatesy & Biewener, 1991; Farley et al., 1993; Bullen & McKenzie, 2002; Bejan & Marden, 2006a), duty factor and relative stride length (Alexander & Jayes, 1983; Gatesy & Biewener, 1991), body force output (Alexander, 1985; Marden & Allen, 2002; Bejan & Marden, 2006a), limb stress and stiffness (Rubin & Lanyon, 1984; McMahon & Cheng, 1990; Farley & Gonzalez, 1996; Biewener, 2005; Bullimore & Burn, 2006).

Although the concept of *mechanical similarity*, well known in analytical mechanics (e.g., Duncan, 1953; Landau & Lifshitz, 1976), was accurately re-formulated in application to the *dynamic similarity* (Alexander, 1976, 1989, 2003, 2005; Bullimore & Donelan, 2008), its exploration in biomechanics is often controversial. For example, Hill's seminal observation of dynamic similarity through the optimal speeds of birds in flight gaits (Hill, 1950) was found in sharp disagreement (McMahon, 1975) with that revealed through transient (trot-to-gallop) speeds in quadrupeds (Heglund et al., 1974). Then, comparing anatomic consequences of McMahon's elastic similarity (McMahon, 1975) for the stride length, Alexander noted

the conceptual inconsistency between the elastic and dynamic similarities (Alexander, 1989, p.1212). Biewener (2005) also claimed confusing biomechanical consequences of McMahon's scaling relations. More recent example is the observation of a new kind of similarity in running humans, simulated on the basis of spring-mass model, no matching the dynamic similarity in running animals (Delattre et al., 2009), reliably established by the same biomechanical model (Farley et al., 1993).

Another example of conceptual controversy concerns the long term standing problem of the origin of empirical scaling laws in biomechanics. The constructal theory by Bejan & Marden (2006a), unifying running, flying, and swimming animals suggested fundamental explanations of intriguing statistically established universal scaling relations for the optimal speed and stride frequency. As a matter of fact, the authors have clearly demonstrated that their principle of minimum useful energy does not provide unifying scaling laws. Instead of searching for new principles, exemplified by recently rediscovered "least-action principle" in human walking (Fan et al., 2009), the design principle of flow systems (Bejan & Marden, 2006a, b), and the basic theorem of dimensional analysis (Bullimore & Donelan, 2008), seemingly resolving the origin of scaling laws in biomechanics, I have addressed the fundamentals of classical analytical mechanics.

In theoretical physics, the mechanical similarity arises from the key principle of minimum mechanical action closely related to Lagrangian's formalism. Examples of successful applications of Lagrangian's method to the dynamics of human walk and the dynamic similarity in animals are explicit descriptions providing, respectively, (i) the conditions of dynamic instability during a walk-to-run crossover obtained regardless of inverted-pendulum modeling (Kokshenev, 2004) and (ii) the whole spectrum of observable scaling laws inferred without recourse to equations of motion (Kokshenev, 2010).

In biomechanics, the dynamic similarity hypothesis (Alexander, 1976; Alexander & Jayes, 1983; Alexander, 1989) stands that similarly in running terrestrial animals should equal their *Froude numbers* (the squared speeds divided by hip heights times the gravitation constant) when tend to change locomotion modes at certain "equivalent speeds" (Heglund et al., 1974) or maintain a certain gait at "preferred speeds" (Heglund & Taylor, 1988). In contrast to *in vivo* established dynamic similarity in the horses trotting at equal Froude numbers (Bullimore & Burn, 2006), the spring-mass model analysis has indicated that the Froude number alone does not yet guarantee the observation of dynamic similarity in the running animals (Donelan & Kram, 1997; Bullimore & Donelan, 2008). Such kind of controversial findings begged a number of questions: whether the sole Froude number (Alexander & Jayes, 1983; Vaughan & O'Malleyb, 2005; Bullimore & Burn, 2006; Delattre et al., 2009), or the sole *Strouhal number* (the limb length, or wing length divided by the speed times stride period, or stroke period) as hypothesized by Whitfield (2003), Taylor et al. (2003) and, likely, Bejan & Marden (2006a), or both the numbers (Delattre et al., 2009), when taken in a certain algebraic combinations (Delattre & Moretto, 2008), e.g., presented by the Groucho number (Alexander, 1989), may warrant the dynamic similarity in animal locomotion? Moreover, when other dimensionless parameters are chosen as the determinants of dynamic similarity, what is the minimal set of independent physical quantities underlying the principle of similarity (Bullimore & Donelan, 2008)?

In this research, a model-independent theoretical framework basically employing Lagrangian's method suggests to establish the validation domains, conditions of observation, criterion, and the minimal set of determinants of dynamic similarity empirically established in different-sized animals.

2. Theory

2.1 Similarity in analytical mechanics

According to the key variational principle of Hamiltonian's classical mechanics, the requirement of minimum mechanical action between two fixed points of the conceivable trajectory of an arbitrary mechanical system determines the Lagrangian function $L(q, v)$ through time-dependent coordinates $q(t)$ and instant velocities $v(t) = dq/dt$. One of the most pronounced properties of the *closed* mechanical systems is preservation of the total energy and momentum, arising respectively from the temporal and spatial homogeneities of the Lagrangian function. The *mechanical similarity* between frictionlessly moving systems also arises from the property of spatiotemporal homogeneity (e.g., Duncan, 1953; Landau & Lifshitz, 1976). Since the property of homogeneity guarantees that the multiplication of Lagrangian on an arbitrary constant does not affect the resulting equations of motion, the *scaling laws* of mechanical similarity can be established without consideration of equations of motion.

More specifically, let us consider the uniform transformation of mechanical trajectories due to linear changing of all coordinates $q' = aq$ and times $t' = bt$ performed via arbitrary in amplitude (positive) linear-transformation factors a and b , resulting in changed velocities $v' = (a/b)v$. The overall-system basic mechanical characteristics, *period* T and *speed* V change as $T' = bT$ and $V' = (a/b)V$, whereas the kinetic energy \mathcal{K} , as a quadratic function of velocities, and potential energy \mathcal{U} scale as

$$\mathcal{K}'(v) = \mathcal{K}\left(\frac{a}{b}v\right) = \left(\frac{a}{b}\right)^2 \mathcal{K}(v) \text{ and } \mathcal{U}'(v) = \mathcal{U}(aq) = a^\lambda \mathcal{U}(q), \quad (1)$$

where the *dynamic exponent* λ is introduced to distinguish distinct cases of mechanical similarity.

The self-consistency of exploration of the property of homogeneity, determining the property of similarity, requires the proportionality in changes of both the energies of the Lagrangian $\mathcal{L}'(q, v) = \mathcal{K}'(v) - \mathcal{U}'(q)$, i.e., $\mathcal{K}' \sim \mathcal{U}'$, thus, $(a/b)^2 = a^\lambda$, or $b = a^{1-\lambda/2}$, as follows from Eq. (1). Hence, the frictionless propagation of a classical system obeys the *scaling rules* imposed on the overall-system dynamic characteristics (T and V) and mechanical characteristics (*force amplitude* F and \mathcal{U}), namely

$$T_\lambda \propto L^{1-\lambda/2}, V_\lambda \propto L^{\lambda/2}, F_\lambda \propto L^{\lambda-1}, \text{ and } \mathcal{U}_\lambda \propto L^\lambda, \quad (2)$$

where L is a characteristic linear size of the *trajectory*, as suggested by Landau & Lifshitz (1976, Eqs. (10.2) and (10.3)).

The well known examples of distinct mechanically similar systems distinguished by dynamic exponent readily follow from Eq. (2): (i) $\lambda = -1$; the case resulting in the third law for planets $T^2 \propto L^3$ that anticipated Newton's theory through interplanetary coupling force $F \propto M^2 L^{-2}$; (ii) $\lambda = 2$; the system is driven by the elastic-strain field and has the elastic energy $\mathcal{U}_{elast} = K\Delta L^2$ with $\Delta L \sim L$, and (iii) $\lambda = 1$; the system moves in the uniform *gravitational field* $g = F_g/M$ and has the potential energy $\mathcal{U}_g = MgH$, with $H \sim L$. The dimensional factors of proportionality M and K , required by the scaling relations, are analyzed below by dimensional method.¹

¹ Hereafter I distinguish two symbols of proportionality: \sim and \propto , supporting and not supporting dimensional units that should be read as "is proportional to" and "scales as", respectively.

2.2 Similarity in biomechanics

The exploration of the concept of dynamic similarity generally assumes model-independent relations validated for slow and fast gaits and supporting linear transformations in changing dynamic and mechanical characteristics, namely

$$\Delta L \sim L \sim H \sim L_b \text{ and } \Delta T \sim T, \Delta F = K\Delta L_b. \quad (3)$$

Here ΔL is a change of the amplitude of *dynamic length* L , e.g., stride length L , or the maximum vertical displacement H of body's center of mass that may be chosen for periodic terrestrial locomotion, or the stroke amplitude of flying and swimming animals (e.g., Alexander, 2003). The dynamic length and its change should be distinguished from the *static length* L_b and its change ΔL_b , that may be also chosen either as of the body length L_b or the corresponding limb, wing, or tail length. Respectively, T^{-1} is the stride, wingbeat, or tailbeat rate attributed to the *frequency* of locomotion. The dynamic length is commonly determined by the measured speed V (*mean cycle forward velocity*) and frequency, i.e., as $L = V/T^{-1}$, whereas the body *propulsion force* ΔF introduces the *body stiffness* $K = \Delta F/\Delta L_b$.²

2.2.1 Dimensional analysis

Broadly speaking, the mechanical similarity may be tested by two uniform linear transformations, scaling simultaneously all spatial and temporal characteristics. Extending these two degrees of freedom of *biomechanical mechanical systems* by their *body masses* M , let us introduce the corresponding *ltm class of units* through the independent dimensions $[L] = l$, $[T] = t$, and $[M] = m$, in accord with the standard scaling theory (e.g., Barenblatt, 2002). One can show that the three body-system mechanical quantities

$$\Delta F \sim LT^{-2}M, V \sim LT^{-1}, \text{ and } K \sim T^{-2}M \quad (4)$$

are mutually independent. Indeed, following the method of dimensional analysis (e.g., Barenblatt, 2002), let us assume the converse, i.e., that numbers x and y exist such that $F \sim V^x K^y$. Substituting F, V , and K from Eq. (4) and equating exponents in the *ltm class*, one finds the solutions $x = 1$ and $y = 1$ not matching with $2x + y = 2$. This proves that the considered set $(\Delta F, V, K)$ consists of three physically independent quantities.

The application of the mathematical concept of geometric similarity (Hill, 1950; Rashevsky, 1948; McMahon, 1975; Lin, 1982) introduced between cylindric-shape bodies through the constraint $\rho_b A L_b = M$ (A is body's *cross-sectional area*), where ρ_b is the invariable *body density* (McMahon, 1975, 1984; Alexander, 2003; Bejan & Marden, 2006a, b), allows one to suggested another equivalent set of candidates to the mutually independent *determinants of mechanical similarity*, namely

$$T^{-1} \sim \sqrt{\frac{\Delta F}{A}} L_b^{-1}, V \sim \sqrt{\frac{\Delta F}{A}}, \text{ and } \Delta F \sim K L_b, \quad (5)$$

chosen in the *ltf class* of unites and also depending neither on locomotor gaits nor biomechanical models.

2.2.2 Unifying constructal theory revisited

For the case of a running (or flying) animal of mass M with the *constant horizontal speed* $V = L/t$, the constructal law calls for the minimization of the total destruction of work W per stride

² These last two and other similar model-independent equations play the role of the definitive basic equations in the scaling theory.

(and stroke) length L , represented as

$$\frac{W}{L} = \frac{W_1}{L} + \frac{W_2}{L} = \frac{MgH}{Vt} + C_D \rho_a V^2 L_b^2. \quad (6)$$

Here W_1 is the vertical loss of energy associated with fall from the height H in the gravitational field and W_2 is the horizontal loss of energy related to the friction with air of density ρ_a (for further details see Eqs. (1)-(4) in Bejan & Marden, 2006a). The minimization procedure of the total loss function results in the optimal speed $V_{opt} \sim \sqrt[3]{MH/L_b^2 t}$, clearly leaving uncertain a choice of the dynamic variables t and H . Using the linear relation $H \sim L_b$ discussed in Eq. (3) and postulating for the frictionless vertical motion that

$$t = t_{opt} = \sqrt{\frac{2H}{g}} \sim \sqrt{\frac{L_b}{g}} \propto M^{1/6}, \quad (7)$$

the constructal theory suggests relations

$$V_{opt} \approx \left(\frac{\rho_b}{\rho_a}\right)^{1/3} g^{1/2} \rho_b^{-1/6} M^{1/6} \text{ and } T_{opt}^{-1} \approx \left(\frac{\rho_b}{\rho_a}\right)^{1/3} g^{1/2} \rho_b^{1/6} M^{-1/6} \quad (8)$$

for the optimal speed and frequency, in the case of fast running and flying animals, as shown, respectively, in Eqs. (5) and (22) and Eq. (23) in Bejan & Marden (2006a). Likewise, the frictionless vertical motion has been postulated in the case of optimal swimming, for which the energy loss $W_1 \sim MgL_b$ was adopted in Eq. (6). For further details, see Eq. (26) in Bejan & Marden (2006a).

2.2.3 Minimum muscular action

Aiming to apply the principle of mechanical similarity formulated for closed inanimate systems to musculoskeletal systems of different-sized animals, one should consider conditions of the observation of effectively frictionless propagation of almost-closed (weekly open) animate systems. These are all cases of *efficient locomotion* (maximum useful work at minimum power consumption) realized at the *resonant propagation frequency*.

Since the animal locomotion is substantially muscular (e.g., McMahon, 1984; Rome et al., 1988; Dickinson et al., 2000; Alexander, 2003), the body-system relations shown in Eqs. (4) and (5) can be generalized to the muscle subsystem presented by a synergic group of locomotory muscles of the *effective muscle length* L_m and cross-sectional area A_m . In the approximation of fully activated muscle states, the maximum muscle stiffness $K_m = E_m A_m / L_m$ is controlled by the geometry-independent muscle rigidity, i.e., the elastic modulus amplitude E_m , defined by ratio of the peak muscle stress $\sigma_m = \Delta F_m / A_m$ to the peak muscle strain $\varepsilon_m = \Delta L_m / L_m$ (e.g., McMahon, 1975, 1984). Let us treat the mass specific muscular (or relative) force output defined by $\mu_m \equiv \Delta F_m / M_m$ as the *muscular field* generating active force ΔF_m through the *muscle mass* M_m , which being a source of the force field μ_m plays the role of the motor mass (Marden & Allen, 2002).

Dynamic motion parameters of the trajectory of body's center of mass are linked to the characteristic static body's and muscle's lengths via the common in biomechanics *linear* relations, namely

$$\frac{\Delta L}{L} \sim \frac{\Delta L_b}{L_b} = \varepsilon_b \sim \frac{\Delta L_m}{L_m} = \varepsilon_m, \quad \frac{\Delta T}{T} = \frac{\Delta T_m}{T_m} = \beta, \text{ and } \Delta F \sim \Delta F_m. \quad (9)$$

Dynamic regime $\lambda = 0$	Frequency	Length	Speed	Force	Mass
$T_{res}^{-1}, T_m^{-1} = T^{-1} \sim (K/M)^{1/2}$	T^{-1}	$\rho_b^{-\frac{1}{2}} E_0^{\frac{1}{2}} \cdot L_b^{-1}$	$\rho_b^{-\frac{1}{4}} E_0^{\frac{1}{4}} \cdot V^{-\frac{1}{2}}$	F^0	$\rho_b^{-\frac{1}{6}} E_0^{\frac{1}{2}} \cdot M^{-\frac{1}{3}}$
$L_{dyn}^{(max)} \sim L_b, L = VT$	$\rho_b^{-\frac{1}{2}} E_0^{\frac{1}{2}} \cdot T^1$	L^1	$\rho_b^{-\frac{1}{4}} E_{m0}^{\frac{1}{4}} \cdot V^{\frac{1}{2}}$	F^0	$\rho_b^{-\frac{1}{3}} \cdot M^{\frac{1}{3}}$
$V_{b-slow}^{(max)} = \rho_b^{-\frac{1}{2}} E_0^{\frac{1}{2}}, V_{m-slow}$	T^0	L^0	$\rho_b^{-\frac{1}{2}} E_0^{\frac{1}{2}}$	F^0	M^0
$K_{b-slow}^{(max)} \sim K_{m-slow}^{(max)}$	$\rho_b^{\frac{1}{2}} E_0^{\frac{1}{2}} A \cdot T^{-1}$	$E_0 A \cdot L_b^{-1}$	$\rho_b^{\frac{1}{4}} E_0^{-\frac{1}{4}} \cdot V^{-\frac{1}{2}}$	$L^{-1} \cdot F$	$\rho_b^{-\frac{1}{3}} E_0 \cdot M^{\frac{1}{3}}$
$\sigma_{m-slow}^{(max)} = \varepsilon_m E_{m0}^{(max)}$	T^0	L_m^0	V_m^0	F_m^0	M_m^0
$F_{b-slow}^{(max)} \sim \varepsilon_b A E_{b-slow}^{(max)}$	T^0	L^0	V^0	F^0	$\rho_b^{-\frac{2}{3}} \varepsilon_b E_0 \cdot M^{\frac{2}{3}}$
$St_{slow} = T^{-1} L_b / V = L_b L^{-1}$	T^0	$L_b \cdot L^{-1}$	V^0	F^0	M^0
$Fr_{slow} = V^2 / g L_b$	$g^{-1} \rho_b^{-\frac{1}{2}} E_0^{\frac{1}{2}} \cdot T^{-1}$	$g^{-1} \rho_b^{-1} E_0 \cdot L_b^{-1}$	$g^{-1} \rho_b^{-\frac{3}{4}} E_0^{\frac{3}{4}} \cdot V^{-\frac{1}{2}}$	F^0	$g^{-1} \rho_b^{-\frac{2}{3}} E_0 \cdot M^{-1/3}$

Table 1. The scaling rules of dynamic similarity in different-sized animals moving in the *stationary dynamic regime*, associated with the activation of *slow locomotor muscles*. The calculations are made on the basis of Eqs. (11) and (12) for muscular subsystem taken at $\lambda = 0$ and then extended to the body system via Eq. (5). The abbreviations $E_{m0} = E_{m-slow}^{(max)}$ and $E_0 = E_{b-slow}^{(max)}$ for, respectively, muscle subsystem and body system are adopted.

Here ΔT is the limb ground contact time or the timing ΔT_m of an activated effective locomotory muscle during maximal shortening (or lengthening) resulted in the *duty factor* β . Considering effective muscles and bones (e.g., Kokshenev, 2007) of the musculoskeletal system as whole, one may ignore the relatively small effects in scaling of muscle and bone masses to body mass and thus introduce in Eqs. (3) and (9) the simplified (isometric) approximation by scaling relations

$$L \sim L_b \sim L_m \propto M^{1/3} \sim M_m^{1/3}. \tag{10}$$

When the principle of mechanical similarity is applied to the different-sized *elastic* body musculoskeletal systems, including muscles, tendons, and bones, and moving at resonance in a certain regime λ along geometrically similar body’s center of mass trajectories, the following three scaling relations, namely

$$T_{m\lambda}^{-1} = T_{\lambda}^{-1} \propto \sqrt{E_{m\lambda}} L_m^{-1}, V_{m\lambda} \sim V_{\lambda} \propto \sqrt{E_{m\lambda}}, \text{ and } \Delta F_{m\lambda} \propto M_m E_{m\lambda} L_m^{-1}, \tag{11}$$

are suggested as the three possible determinants of dynamic similarity discussed in Eq. (5). One can see that the self-consistency between the body system, including locomotor muscle subsystem, activated in the same dynamic regime λ , and the principle of mechanical similarity formulated in Eq. (2), requires the dynamic elastic modulus of locomotory muscles in Eq. (11) to be adjusted with the muscle length L_m and body length L_b through the scaling relations

$$E_{m\lambda} \propto (L_m)^{\lambda} \propto (L_b)^{\lambda} \text{ and } \mu_{m\lambda} \propto (L_m)^{\lambda-1} \sim \mu_{\lambda} \propto (L_b)^{\lambda-1}. \tag{12}$$

Thereby, the dynamic process of generation of the active force $\Delta F_{m\lambda} = \mu_{m\lambda} M_m$ during muscle contractions at the resonant frequency $T_{m\lambda}^{-1}$ and the optimized contraction velocity $V_{m\lambda}$ is patterned by the single dynamic exponent λ . In Tables 1 and 2, the scaling rules prescribed by the minimum muscular action in efficiently moving animals are provided for two well distinguished patterns of the dynamic similarity regimes $\lambda = 0$ and $\lambda = 1$.

Dynamic regime $\lambda = 1$	Frequency	Length	Speed	Force	Mass
$T_{opt}^{-1}, T_{res}^{-1}, T^{-1} \sim (K/M)^{1/2}$	T^{-1}	$\mu_1^{\frac{1}{2}} \cdot L_b^{-\frac{1}{2}}$	$\mu_1 \cdot V^{-1}$	$(\rho_b \mu_1^2 A)^{\frac{1}{2}} \cdot F^{-\frac{1}{2}}$	$\rho_b^{\frac{1}{6}} \mu_1^{\frac{1}{2}} \cdot M^{-\frac{1}{6}}$
$L_{opt}^{(max)}, L_{trans}^{(max)}, L$	$\mu_1 \cdot T^2$	L	$\mu_1^{-1} \cdot V^2$	$(\rho_b \mu_1 A)^{-1} \cdot F$	$\rho_b^{-\frac{1}{3}} \cdot M^{\frac{1}{3}}$
$V_{opt}^{(max)}, V_{trans}^{(max)}, V = LT^{-1}$	$\mu_1 \cdot T^1$	$\mu_1^{\frac{1}{2}} \cdot L^{\frac{1}{2}}$	V^1	$(\rho_b A)^{-\frac{1}{2}} \cdot F^{\frac{1}{2}}$	$\rho_b^{-\frac{1}{6}} \mu_1^{\frac{1}{2}} \cdot M^{\frac{1}{6}}$
$K_{b-fast}^{(max)} \sim \rho_b \mu_{fast}^{(max)} A$	T^0	L^0	V^0	F^0	$\rho_b^{-\frac{1}{3}} \mu_1 \cdot M^{\frac{2}{3}}$
$\sigma_{m-fast}^{(max)} = \Delta F_m / A_m$	$\rho_m \mu_{m1} \cdot T^2$	$\rho_m \mu_{m1} \cdot L_m$	$\rho_m \cdot V_m^2$	$A_m^{-1} \cdot F_m$	$\rho_m^{\frac{2}{3}} \mu_{m1} \cdot M_m^{\frac{1}{3}}$
$F_{fast}^{(max)} / gM \sim \mu_1 / g$	T^0	L^0	V^0	F^0	M^0
$St_{fast} = T^{-1} / V L_b^{-1} = L_b L^{-1}$	T^0	$L_b \cdot L^{-1}$	V^0	F^0	M^0
$Fr_{fast} = V^2 / g L_b \sim \mu_1 / g$	T^0	$L_b^{-1} \cdot L$	V^0	F^0	M^0

Table 2. The scaling rules of dynamic similarity between animals moving with gradually changing speeds within the dynamically similar fast gaits. The corresponding dynamic regime $\lambda = 1$ include optimal-speed stationary states and continuous transient dynamic states, all associated with activation of the fast locomotory muscles. The calculations are provided through Eqs. (11), (12), (5), and some other definitive basic equations discussed in the text, all taken at $\lambda = 1$. The abbreviations $\mu_{m1} = \mu_{m-fast}^{(max)}$ and $\mu_1 = \mu_{b-fast}^{(max)}$ for, respectively, muscle subsystem and body system are adopted.

3. Results and discussion

3.1 Minimum useful energy

Bejan & Marden (2006a, b) employed the principle of generation of the turbulent flow structure to unify gait patterns of running, swimming, and flying. Specifically, the dynamic similarity between animals across taxa is suggested as an optimal balance achieved between the vertical loss of useful energy (lifting the bodyweight, which later drops) and the horizontal loss caused by friction against the surrounding medium. Broadly speaking, the minimization procedure of total energy losses, being consistent with the concept of minimum cost of locomotion (e.g., Alexander, 2005), is underlaid by the minimization of energy consumption, treated here in terms of the efficient locomotion required by resonance conditions. Consequently, it is not surprising that the contrsuctal theory has demonstrated its general consistency with scaling rules attributed to the special case of dynamic similarity (Table 2). On the other hand, the optimization approach exemplified in Eq. (6), clearly demonstrating that the empirical scaling relations for speed and frequency should be hold in optimal running, flying and swimming, suggests that solely the gravitational field may explain scaling factors in scaling rules shown in Eq. (8). Therefore, a delicate question on the origin of basic scaling rules in the dynamic similarity remains unanswered in contrsuctal theory.

However, the major disadvantage of the proposed principle is that the proper scaling relations for optimal speed V_{opt} and frequency T_{opt}^{-1} were in fact incorporated into contrsuctal theory regardless of the minimization procedure. Indeed, the desired relations

$$V_{opt}^{(max)} \propto T_{opt} \propto \sqrt{L} \sim \sqrt{L_b} \propto M^{1/6}, \tag{13}$$

underlying the theoretical findings in Eq. (8) could straightforwardly be derived from the postulate adopted in Eq. (7), without recourse to the principle of minimum useful energy.

Strictly, the postulated basic equation $t_{opt} = \sqrt{2H/g}$ discussed in Eq. (7) has been borrowed from frictionless Newtonian's mechanics, arising from the spatiotemporal homogeneity of the gravitational field. Indeed, one can see that Eqs. (7) and (13) is the special case discussed in Eq. (2) at $\lambda = 1$. The proposed theory of dynamic similarity explains that instead of the gravitational field, in fact adopted on *ad hoc* basis in Eq. (7), the muscular field determines spatiotemporal homogeneity through the universal scaling exponents established for dynamic characteristics of animals naturally tuned to the dynamic similarity regime $\lambda = 1$ (Table 2).

Without doubts, the gravity is important in terrestrial locomotion and the Froude number related to potential gravitational energy ($Fr = MV_{opt}^{(max)2}/MgL_b$) plays important role in understanding of dynamic similarity in animate and inanimate systems (e.g., Vaughan & O'Malleyb, 2005). After Alexander & Jayes (1983), it is widely adopted that instead of scaling relations shown in Eq. (13) the dynamic similarity between fast moving animals may be determined by the requirement for Froude numbers to be constants. Indeed, the universality of Froude numbers, i.e., $Fr \propto M^0$, straightforwardly provides the basic scaling rule for optimal speed, namely

$$V_{opt}^{(max)} = (Fr \cdot gL_b)^{1/2} \propto L_b^{1/2} \propto M^{1/6}. \quad (14)$$

With regard to the second basic scaling rule shown in Eq. (13), it follows from the definitive basic equation for dynamic length $L = VT$ and Eq. (14) providing

$$T_{opt}^{-1} = V_{opt}^{(max)} L_{opt}^{-1} \propto (Fr \cdot gL_b^{-1})^{1/2} \propto M^{-1/6}, \text{ with } L_{opt}/L_b \propto M^0. \quad (15)$$

It is noteworthy that the optimal frequency is obtained under an additional requirement of the relative dynamic length to be invariable with body mass, as shown in Eq. (15).

3.2 Maximum muscular efficiency

3.2.1 Realization of resonant states

During animal locomotion, *chemical energy* released by muscles in the form of muscular force field and *potential energy* of the gravitational field, both being able to be stored in body's system in the corresponding forms of active-force and reactive-force *elastic energy*, are eventually transformed into useful external body work and partially lost as a heat due to internal work and external frictional effects. In a constant-speed walk, run, flight, and swim, attributed to the dynamic similarity regime $\lambda = 0$, the total mechanical energy is almost unchanged and the animate mechanical system is almost closed. In the non-stationary dynamic similarity regime $\lambda = 1$ characteristic of the gradual change in speeds caused by the steady muscular field, the total mechanical energy may be also unchanged because of the permanent consumption of metabolic energy. The efficient propulsion of humans and other animals, in contrast to human-made engines, is accompanied by the tuning of musculoskeletal system to natural (resonant) propagation frequency (McMahon, 1975; Ahlborn & Blake, 2002), resulted in the reduction to minimum the oxygen (Hoyt & Taylor, 1981) and metabolic energy (e.g., Ahlborn & Blake, 2002; Ahlborn et al., 2006) consumption. It has been demonstrated above, that the requirement of minimum action of musculoskeletal system in animals provides the major constraint in realization of dynamically equivalent (similar) states. Nevertheless, the applicability of the key principle in analytical mechanics, driving frictionless systems, to real animate systems characteristic of non-conservative muscle forces required a special physical analysis. In the special case of the stationary ($\lambda = 0$) human walking (Kokshenev, 2004), the speed-dependent frictional effects were shown to be weak and therefore effectively excluded within the scope of a special dynamic perturbation theory. Likewise, the case of efficient locomotion $\lambda = 1$, including *moderate run* and *fast run* modes in the fast gaits of animals, has

required a generalization of Lagrangian's formalism from the closed mechanical systems to the weakly open, moving at resonance biomechanical systems (Kokshenev, 2010).

As the outcome of analytical study, the *slow-walk* and *fast-walk* modes in bipeds emerge as the free-like body's center of mass propagation composed by the forward translation and the elliptic-cyclic backward rotations (Kokshenev, 2004). The optimal-speed stationary regime ($\lambda = 0$) has been found to be consistent with a slow-walk-to-fast-walk *continuous mode transition* between the two walk modes indicated by the highest symmetry (circular) trajectory of body's center of mass (Kokshenev, 2004, Fig. 2). In contrast, the discontinues in humans *fast-walk-to-slow-run* transition is indicated by the absolute instability of the walk-gait trajectory (Kokshenev, 2004, Fig. 2), signaling on the muscular field amplitude exceeding gravitation, i.e., $\mu_{run} > g$. The formal condition $\mu_{walk-run}^{(mod)} = g$, completed by that for the limb duty factor $\beta_{walk-run}^{(mod)} = 0.5$, discussed by Ahlborn & Blake (2002) on the basis of the data for humans started run (Alexander & Bennet-Clark, 1976), may be treated as two *indicators* of the model-independent walk-to-run continuous transition, generally uncommon to terrestrial animals. Hence, the provided above estimates for the transient muscle field amplitude suggest the walk-to-run transition as a smoothed crossover between the slow-regime and the fast-regime dynamic resonant states.

The natural ability of muscles to be tuned to various dynamic regimes is incorporated in animate mechanical systems through the elastic active-force muscle modulus $E_{m\lambda}^{(max)}$, as shown in Eqs. (11) and (12). Thereby, the muscle modulus, most likely sensitive to the intrinsic dynamic muscle length (Kokshenev, 2009), establishes an additional dynamic degree of freedom, not existing in skeletal bone subsystem and other inanimate elastic mechanical systems. Conventionally, the stationary slow-speed dynamics ($\lambda = 0$) and optimal and transient fast-speed dynamics ($\lambda = 1$) are attributed to the activation of the slow-twitch-fiber muscles and fast-twitch-fiber muscles respectively recruited by animals during slow and fast locomotion (Rome et al., 1980). As illustrative example in animal swimming, the studies of gait patterns in fish (Videler & Weihs, 1982) revealed that slowly swimming and quickly swimming fish exploit, respectively, red (slow fibre) muscles or white (fast fibre) muscles, showing those contraction velocities at which recruited muscles work most efficiently (Alexander, 1989).

3.2.2 Mechanical similarity against geometric similarity

Broadly speaking, the dynamic similarity observed through the universal scaling exponents in scaling biomechanics is intimately related to the geometric similarity that can directly be observed in animals of the same taxa through the body shape, including body's locomotor appendages, i.e., limbs, wings, and tails or fins. Mathematically, the geometric similarity in animals is due to adopted spatial uniformity, preserving body shapes under arbitrary linear transformations of linear dimensions of animals (Rashevsky, 1948; McMahon, 1975; Lin, 1982). Mechanically, the dynamic similarity between animals across taxa arises from the similarity established between the geometric and kinematic parameters of the body's point-mass trajectories and driving forces.

Following the formalism of analytical mechanics discussed in Eq. (2), the concept of mechanical similarity has been discussed in physics (e.g., Duncan, 1953) and biomechanics (Alexander & Jayes, 1983; Alexander, 1989, 2005) in terms of the three arbitrary linear-transformation factors (a , b , and, say, c) preserving the homogeneity of all spatial (L), temporal (T) and force (F) mechanical characteristics of animals moving in a certain fashion or gait. Although no conceptual gap exists between the similarities in classical mechanics and biomechanics, the fundamental constraints imposed on the initially chosen arbitrary factors

of linear transformation, i.e., $b = a^{1-\lambda/2}$ and $c = a^{\lambda-1}$, underlying Eq. (2) and providing basic scaling rules of the dynamic similarity, namely

$$T_{\lambda}^{-1} \propto L_b^{\lambda/2-1}, V_{\lambda} \propto L_b^{\lambda/2}, \text{ and } \Delta F_{\lambda} \propto L_b^{\lambda-1}, \text{ with } L/L_b \propto M^0, \quad (16)$$

are generally ignored in experimental biology and even violated in some theoretical studies mentioned in the Introduction. This analysis shows how the spatial uniformity, achieved via the stabilization of dynamic length in relation to static length, determines the observation of dynamic similarity in any dynamic regime λ .

The provided analysis explains why the model-dependent requirements of strict geometric similarity, e.g., the requirement of the equality of joint angles in running animals (Alexander, 1989) or swinging angles in dynamically similar pendulums (Alexander, 2005), do not reduce the dynamic similarity concept to the so-called *strict dynamic similarity* (Alexander, 1989, 2005). First, one can see that both the angles may be expressed in terms of the *swept angle* $\Theta = \arcsin(\beta/2St)$ introduced in biomechanics of animal locomotion as a relative angle between the leg spring and vertical (see, e.g., Fig. 1 in Farley et al., 1993), which is also known as the maximum *compass angle* (Cynthia & Farley, 1998), modeling in turn the *protraction-retraction angle* in bipeds (Gatesy & Biewener, 1991, Fig. 1). Second, the requirement of observation of the dynamic similarity through scaling laws of the mechanical similarity reproduced in Eq. (16) implies that the Strouhal number $St (= L_b/L)$, as well as some other dimensionless numbers, including the duty factor $\beta (= \Delta T/T)$, should be invariable across different-sized animals, i.e., $St \propto \beta \propto M^0$. One may infer that a rigorous requirement of the strict geometric similarity on that the swing or other related angles (as well as relative stride lengths) must be equal constants is the overestimated constraint of the dynamic similarity concept. In other words, the requirement of dynamic angles to be mass independent, i.e., $\Theta \propto M^0$, arising from the the requirement of stabilization of relative dynamic lengths, i.e., $St \propto M^0$, unambiguously determines observation of the *perfect* dynamic similarity (Alexander, 1989).

3.2.3 Criterion, determinants, and indicators of dynamic similarity

Being the major requirement in realization of both universal dynamic regimes unifying animals in a certain gait, the high mechanical efficiency of the musculoskeletal system prescribed by minimum muscular action plays the role of the unique *criterion* of observation of dynamic similarity.

The concept of mechanical similarity in biomechanics, consistent with that in analytical mechanics, allows linear transformations of two dynamic (spatial and temporal) and one mechanical (force or mass) characteristics through the three independent scaling factors. Hence, the set $(T^{-1}, V, \Delta F)$ of mutually independent and model-independent quantities, chosen in Eq. (5) in the *ltf* class of units, can be treated as tentative candidates for the determinants of dynamic similarity. The optimization of muscle-field interactions by the minimum mechanical action (i) introduces new state-dependent scaling relations for T_{λ}^{-1} , V_{λ} , and ΔF_{λ} , which determine three scaling rules of the dynamic similarity, and (ii) reduces the number of independent determinants from three to one, as discussed in Eq. (16). Since the choice of the optimal speed V_{λ} by an animal is accomplished by the resonant frequency T_{λ}^{-1} , the suggested principal set of determinants $(T_{\lambda}^{-1}, V_{\lambda})$ does not generally excludes another set, including the uniform muscular field or the uniform relative dynamic length, both required by the high level mechanical efficiency. However, the observation of just only one of the two basic scaling rules guarantees the observation of other features of dynamic similarity in animals. Indeed, the observation of the scaling rule for stride frequency $T_{\lambda}^{-1} \propto L_b^{\lambda/2-1}$

indicates stabilization of the relative dynamic length, as shown in Eqs. (15) and (16). Hence, experimental observation of the constant Strouhal number in animals moving efficiently in any similar gaits determines them as dynamically similar. When solely the fast gaits are considered, the universal Strouhal number should be revealed along with the universal Froude number Fr , whose stabilization in animals across body mass is equivalent to the observation of scaling rule for the maximum amplitude of optimal and transient speeds $V_{opt}^{(max)} \propto L_b^{1/2}$, as follows from Eqs. (14) and (16). If the principal determinants St or Fr , each may play the role of the dynamic similarity criterion, are chosen for the corresponding cases $\lambda = 0$ and $\lambda = 1$, other universal determinants, such as muscle stress, speed, in the first case, and the Strouhal number and relative muscular field, in the second case, play the role of the indicators of stabilization of the universal similar dynamic states. Moreover, in both cases the *indicators of dynamic similarity* can be extended by the universal duty factors $\beta \propto M^0$ and swept angles $\Theta \propto M^0$.

3.2.4 Mechanically efficient slow and fast flyers

The stationary-state mode patterns of flight gaits were likely first noted by Hill (1950). He had established that the wing frequencies of *hovering birds* are in inverse proportionality with the linear size, that corresponds to the predicted frequency $T_{hover}^{(pred)-1} \sim \sqrt{E_{m0}^{(max)} / \rho_m L_m^{-1}}$ (Table 1) for wing muscles contracting in the stationary regime $\lambda = 0$. Hill's pioneering observation of the fundamental frequency-length scaling law, determining dynamic similarity in the efficient flyers solely via the universal (speed-, period-, and mass-independent) *slow-muscle* elastic modulus $E_{m0}^{(max)}$ (Table 1) can be compared with seminal Kepler's law $T_{planet}^{(exp)-1} \propto L_{planet}^{(exp)-3/2}$ (see Eq. (2) taken at $\lambda = -1$), determining the mechanical similarity between trajectories of planets driven solely by gravitation. Later, the hovering flight motors were also recognized in birds by observation of the wing frequencies $T_{hover}^{(exp)-1} \propto M^{-1/3}$ (Ellington, 1991), that is also equivalent to observation of the universal Strouhal numbers $S_{hover} \propto M^0$ (Table 1).

When an animal travels or cruises slowly for long distances, maintaining constant the optimal speed $V_{cruis}^{(max)} \sim \sqrt{E_0^{(max)} / \rho_b}$ invariable with bodyweight and frequency (Table 1), or moves throughout the terrestrial, air, or water environment resisting drag forces, the limbs, wings, and fins are expected to be tuned via elastic muscle modulus to maintain universal muscular pressure (Table 1). In turn, this effect gives rise to the constant limb-muscle *safety factor* (ratio of muscle strength to peak functional stress), foreseeing by Hill (1950). Moreover, the peak body force output $F_{body}^{(exp)} \propto M^{2/3}$, exerted on the environment during running, flying, and swimming by animals ranged over nine orders of body mass, was documented by Alexander (1985). The theoretical suggestion that the stationary-state mechanics, equilibrating all drag forces, is due to slow locomotory muscles, is corroborated by the statistically regressed data on the force output $F_{m-slow}^{(max)} \propto M_m^{2/3}$ remarkably established in both biological and human-made *slow motors* by Marden & Allen (2002).

The optimum-speed regime $\lambda = 1$ has been recognized through the equilibration of the air drag by wings of *flapping birds*, manifesting the basic scaling rule for wing frequencies $T_{flap}^{(exp)-1} \propto M^{-1/6}$ (Ellington, 1991), also corresponding to the observation of $S_{flap} \propto M^0$ (Table 2). Earlier, the non-stationary flight regime has been foreseen by Hill's notion that larger birds flap their wings more slowly than smaller ones (Hill, 1950).

As explicitly shown in Eq. (16), the stabilization of the uniformity in Strouhal numbers in both dynamic regimes $\lambda = 0$ and $\lambda = 1$ explains empirically puzzled animal flight and

swim (Whitfield, 2003). Indeed, Taylor et al. (2003) experimentally established such a kind of the universal similarity through the almost constant Strouhal numbers (laying between 0.2 and 0.4) in cruising with a high power efficiency dolphins, flapping birds, and bats. This observation suggests two patterns of *efficient flyers* distinguished by hovering ($\lambda = 0$) and flapping ($\lambda = 1$) modes of slow and fast flight gaits. The corresponding examples of slow-swimming and fast-swimming motors are the gaits to swim established through different swimming techniques for the same fish, using their pectoral fins to swim slowly, but undulating the whole body to swim fast (Alexander, 1989). Unifying flying and swimming animals in *fast gaits*, the data by Taylor et al. (2003) suggest the dynamic similarity pattern of *efficient flapping flyers* and *undulating swimmers*. These and other introduced patterns of dynamic similarity are studied in Kokshenev (2011).

3.2.5 Mechanically efficient fast animals

In experimental biology, it is well known that forces required for fast gaits in animals are proportional to body weight, but since the force generation is more expensive of metabolic energy in faster muscles, small animals show apparently low efficiencies in running (Alexander, 1989). Efficient fast biological motors in running, flying, and swimming animals were established by Marden & Allen (2002) through the scaling equation $F_{opt}^{(max)} = \mu_{fast}^{(max)} M$ (Table 2), where the relative force amplitude $\mu_{fast}^{(max)} = 2g$ was re-estimated by Bejan & Marden (2006a, Fig. 2C). Given that the muscular field in running, flying, and swimming animals is twice as many as the gravitational field, adopted above for the lower threshold of a slow run in the walk-to-run transition, the statistical data $\mu_{fast}^{(max)} = 2g$ may be conventionally adopted as a universal threshold of fast modes in fast gaits. This threshold associated with the slow-run-to-fast run transient state $\lambda = 1$ may in turn determine the pattern of efficient fast animals, including fast running mammals, reptiles, insects; flapping birds, bats, and insects; undulating fish and crayfish, according to Marden & Allen (2002) and Bejan & Marden (2006a). The pioneering observations of the transient-state speeds $V_{trans}^{(exp)}$ and frequencies $T_{trans}^{(exp)-1}$ at the trot-to-gallop continuous transition in quadrupeds ($V_{trot-gall}^{(exp)} \propto M^{0.22 \pm 0.05}$ and $T_{trot-gall}^{(exp)-1} \propto M^{-0.15 \pm 0.03}$; Heglund et al., 1974; Heglund & Taylor, 1988), make evidence for, within the experimental error, the predicted stabilization of the uniform (body mass independent) muscular field, i.e., $\mu_{run}^{(exp)} \propto M^{-0.07 \pm 0.08}$, when tested by the scaling relation $\mu_{trans}^{(pred)} \sim V_{trans} T_{trans}^{-1}$ prescribed by dynamic regime $\lambda = 1$ (Table 2). Likewise, the same generic dynamic regime explains stabilization of the uniformity in the muscular field activated in 13 running animals (from a mice to horses) observed indirectly by Heglund & Taylor (1988) at experimental conditions of the *preferred* trotting speeds and the *preferred* galloping speeds, providing respectively the determinants of similarity $\mu_{trot}^{(exp)} \propto M^{0.09 \pm 0.07}$ and $\mu_{gall}^{(exp)} \propto M^{0.02 \pm 0.07}$. The revealed large experimental error is most likely caused by small quadrupedal species (one laboratory mice, two chipmunks, three squirrels, and three white rats of bodyweight not exceeding one kg), which should be excluded from the dynamic similarity pattern, as potentially having low mechanical efficiency (Alexander, 1989).

Bipeds, showing the resonant frequency $T_{trans}^{(exp)-1} \propto M^{-0.178}$ near the slow-walk-to-fast-run transition (Gatesy & Biewener, 1991), indicate the dynamic similarity pattern of *efficient fast walkers*. The scaling rule $V_{opt}^{(exp)} \propto M^{0.17}$ empirically established by Garland (1983) for maximal speeds in running terrestrial mammals ranging in five orders in body mass

(from smallest bipedal rodents to largest quadrupedal elephants) indicates observation of the pattern of *efficient runners in mammals*.

The dynamically similar continuous resonant states were clearly revealed by Farley et al. (1993) in a trotting rat, dog, goat, horse and a hopping tammar wallaby and red kangaroo. The realistic modeling on the basis of leg-spring model of animals of leg length $L_{leg}^{(exp)} (\sim L_b^{(exp)})$ provided the following scaling equations for the stride frequency $T_{run}^{(exp)-1}$, peak force output $F_{run}^{(exp)}$, maximum body stiffness $K_{run}^{(exp)}$, swept angle $\Theta_{run}^{(exp)}$, and dynamic length change $\Delta L_{run}^{(exp)}$, namely

$$\begin{aligned} T_{run}^{-1} \sim \Delta T_{run}^{-1} \propto M^{-0.19 \pm 0.06}, F_{run}^{(exp)} = 30.1 M^{0.97 \pm 0.14}, K_{run}^{(exp)} \propto M^{0.67 \pm 0.15}, \\ \Theta_{run}^{(exp)} \propto M^{-0.03 \pm 0.1}, \text{ and } \Delta L_{run}^{(exp)} \sim L_b^{(exp)} \propto M^{0.30 \pm 0.15}. \end{aligned} \quad (17)$$

One can see that all the observed scaling exponents are consistent (within the experimental error) with those predicted by the dynamic similarity regime $\lambda = 1$ described in Table 2. These data introduce the dynamic similarity pattern of *efficient trotters and hoppers*.

4. Concluding remarks

Following the concept of mechanical similarity, underlaid by the key principle of minimum action in analytical mechanics, the theory of dynamic similarity in animal locomotion is proposed. Exploring the intrinsic property of locomotory muscles to be tuned, via the variable muscle elasticity, to the natural cyclic frequency characteristic of high level efficiency of locomotion, the scaling rules driving the dynamic similarity in inanimate mechanical elastic systems are suggested for the special case of active-force animate elastic systems. The linear-displacement dynamic approach to contracting locomotory muscles, whose resonant frequencies are required by the principle of minimum mechanical action, establishes two different universal patterns of the dynamic regimes of similarity in different-sized animals distinguished by the dynamic scaling exponent λ . The determinants of the stationary locomotion of animals moving at optimal constant speeds (the case $\lambda = 0$) and the non-stationary locomotion at gradually changing speeds ($\lambda = 1$), including the transient-mode speed transitions, are self-consistently inferred and described in Tables 1 and 2, respectively. Exemplified by the non-stationary dynamic regime $\lambda = 1$, the two principal sets of determinants of the dynamic similarity are suggested by the universal exponents for the speed and frequency scaled with body mass, which may be equivalently presented by the corresponding Froude and Strouhal numbers or by other universal dimensionless numbers determining the states of dynamic similarity in different-sized animals.

The primary determinant, playing the role of the unique criterion of the linear dynamic similarity, is shown (in Eq. (16)) to be the Strouhal number, whose universality in animals across body mass indicates establishing of the linearity between the stride or stroke length and the body length in each animal, falling into one or other dynamically similar regime. In the special case of non-stationary dynamic similarity controlled by fast locomotory muscles, the Froude number may be equivalently chosen as a unique criterion of similarity, as hypothesized by Alexander (Alexander, 1976; Alexander & Jayes, 1983; Alexander, 1989). Since the scaling theory of similarity deals only with scaling relations, but not with scaling equations, Alexander's strict requirement that dynamic similarity between running animals should equal Froude numbers is not generally required by the theory. Instead, the theory of dynamic similarity stands only that changing with speed Froude numbers should be

invariable with body mass in animals considered in a certain dynamic state or domain of dynamically equivalent states. A generalization of the proposed theory of the discrete-state dynamic similarity to continuous-state similarity in animals, determining, respectively, by discrete equal and different variable magnitudes of the Froude numbers, will be discussed in the next part of this study (Kokshenev, 2011).

The two kinds of dynamic similarity regimes in animals, well distinguished by the scaling rules established for a number of mechanical characteristics, may explain seemingly controversial experimental observations as well as illuminate some theoretical principles conceptually inconsistent with the mechanical similarity principle of analytical mechanics.

Hill's pioneering observation of bodyweight independence of optimal speeds in a hover flight mode of sparrows and humming birds (Hill, 1950), showing a sharp inconsistency (McMahon, 1975; Jones & Lindstedt, 1993) with the scaling rules for speeds in quadrupeds established at the trot-to-gallop transition (Heglund et al., 1974) can readily be understood by the observations of two distinct dynamic similarity regimes $\lambda = 0$ and $\lambda = 1$. Likewise, a more recent claim on that the similarity between humans running at *fixed* speeds, accurately simulated under the requirement of equal Froude numbers, was surprisingly found (Delattre et al., 2009) to be in sharp disagreement with the scaling rules of dynamic similarity in fast running animals reliably established by Farley et al. (1993). A new kind of similarity discovered in running humans arrived the authors to a puzzle conclusion that neither of Froude and Strouhal numbers is appropriate as determinant of dynamic similarity. In this special case, the proposed theory tells us that the dynamic similarity between humans running at the stationary-speed conditions (Table 1) cannot be constrained by constant Froude numbers, as erroneously was adopted in the study by Delattre et al. (2009).

Another Hill's surmise on the constant limb muscle stress, resulted in the universality of the limb safety factor in animals efficiently moving in slow gaits, has been generalized without grounds to all fast gaits by a number of researches. For example, in attempting to introduce "equivalent speed" states $\lambda = 1$ during trot-to-gallop transition McMahon postulated a constant stress in homologous muscles (McMahon, 1975, Table 4), when suggested the uniform muscle stress $\sigma_{m-slow} \propto M^0$, corresponding to the case of $\lambda = 0$. The postulated stress evidently contrasted with the already existing data on peak isometric stress, linearly varying with sarcomere length (Huxley & Neidergerke, 1954), i.e., $\sigma_{m-fast} \propto L_m$ (Table 2), and the data on muscle stress later revealed the linearity to fiber length in running and jumping animals (Alexander & Bennet-Clark, 1976). Likewise, when the axial-displacement dynamic similarity (i.e., $\Delta L_{m-fast} \propto L_m$) discussed for fast locomotory muscles is generalized to non-axial-displacement elastic similarity in long limb mammalian bones ($\Delta L_{bone}^{(bend)} \propto D_{bone}$, where D_{bone} is bone's diameter; Kokshenev, 2007, Eq. (15)) new puzzled consequences of biomechanical scaling may be revealed. One impressive example is the axial compressive stress $\sigma_{bone}^{(axial)} \propto L_{bone}$, estimated as the peak limb bone stress $\sigma_{bone}^{(exp)} \propto M^{0.28}$ for the avian taxa, matching well the spring-leg data $\sigma_{leg}^{(exp)} \propto M^{0.30}$ from running quadrupeds following from Eq. (17), has been shown to provide the anecdotal small largest terrestrial giant weight, no much greater than 20 kg (Biewener, 2005). This puzzle was understood by that instead of axial stress, which is in fact non-critical, the bending stress $\sigma_{bone}^{(bend)} \propto D_{bone} / L_{bone}$, having small but non-zero positive exponent, i.e., $\sigma_{bone}^{(bend)} \propto M^{0.08}$, likely establishes the critical mass of terrestrial giants (Kokshenev & Christiansen, 2011).

One more "least-action principle" in biomechanics was recently declared for walk gaits in humans (Fan et al., 2009). The standard variational procedure was worked out to establish a symmetric point ($T/2$) in the middle of the two-step stride cycle in human gaits, at which all

important mechanical characteristics expose the extreme (minimum or maximum) behavior. This misleading principle of the existence of the symmetrical point, even though consistent with the well-known symmetrical nature of a walk and a run, due to which each equivalent leg moves half a stride cycle out of other leg (e.g., Alexander & Jayes, 1983, p.142) was in fact incorporated, likely unconsciously, into the studied model through symmetric mechanics of the supposedly equivalent human legs.

The constructal theory of dynamic similarity by Bejan & Marden (2006a, b) treats the potential energy of the body falling in the gravitational field g as a useful energy of terrestrial locomotion. Considering only the aerial phase in a stride cycle, the theory excludes the ground contact and thereby all muscular forces providing the body propulsion force $\mu_{fast}^{(exp)} M$. It is surprisingly that the same theoretical framework excluding muscle forces has resulted in the muscular field $\mu_{fast}^{(exp)} = 2g$, since the suggested scaling factors in the basic scaling relations, shown in Eq. (8), are weighted solely by the gravitational field. Hence, it has been demonstrated by the authors that consistency between the principle of destruction of minimum useful energy in the gravitational field (the case $\lambda = 1$ in Eq. (2)) may exist under the additional condition postulated in Eq. (7), in fact borrowed from another, more general mechanical principle.

Following the requirement of equality of Froude numbers, experimental biologists mostly study the discrete-state dynamic similarity in animals. For example, Bullimore & Burn (2006) have remarkably established (see their Table 4) the universal criterion of dynamic similarity $St_{trot}^{(exp)}$ ($= 0.70, 0.67$, and 0.60) from 21 horses trotting at arbitrary chosen fixed Froude numbers $Fr_{trot}^{(exp)}$ ($= 0.5, 0.75$, and 1). This finding corroborates McMahon's suggestion (acknowledged by Alexander, 1989) on that besides the Froude number the Strouhal number should be simultaneously constant, as followed from the universality of the Groucho number (McMahon et al., 1987). In contrast, the study by Bullimore & Donelan (2008) of the criteria of dynamic similarity in spring-mass modeled animals suggested four independent determinants, at least. Given that the authors have clearly convinced the reader of that the equality of only two dimensionless numbers is not sufficient for establishing of the dynamic similarity between in-plane modeled animals (Bullimore & Donelan, 2008, Fig. 4), a question arises about what kind of dynamic similarity was reported by Bullimore & Burn (2006) established in real trotting horses through the only one determinant Fr ?

Bullimore & Donelan (2008, Table 2) have analyzed the well known solutions of the planar spring-mass model through Buckingham's Π -theorem of the dimensional method (e.g., Barenblatt, 2002) and claimed that minimum four independent dimensionless numbers following from the set of mechanical quantities (V, K, V_z, Θ_0) are required for the observation of dynamic similarity in bouncing modes of animals. First, one can see that the landing angle Θ_0 should be excluded from the proposed set of physically independent quantities, since the horizontal landing speed V and the vertical landing speed V_z definitively determine the angle $\Theta_0 = \arctg(V/V_z)$, as can be inferred from Fig. 1 by Bullimore & Donelan (2008). Then, the requirement to control vertical speed via the model-independent relation $V_z \sim \mu\beta T$ allows one to reduce the proposed set to the equivalent set (T^{-1}, V, μ, β) , where the body stiffness is substituted by muscular field via the body stiffness $K \sim \rho_b A \mu$. The resulted set of four quantities (St, Fr, μ, β) is dynamically equivalent to the originally suggested set (V, K, V_z, Θ_0), but among three determinants (St, Fr, μ) the only one is physically independent. Two other dimensionless numbers play the role of auxiliary determinants in the dynamic similarity, whereas the duty factor may indicate transient-mode and crossover-gait universal states of the same dynamic regime $\lambda = 1$. Hence, it has been repeatedly demonstrated that the

application of Buckingham's theorem only provides a way of generating sets of dimensionless parameters, but does not indicate or even substitute most physically meaningful relations. This well known statement is also illustrated by the provided above study of two scaling equations Eq. (2) and (5), suggesting the same set of three possible determinants of dynamic similarity, respectively provided by the physical concept and the dimensional method.

When comparing the frameworks of dynamic similarity and elastic similarity, respectively elaborated to scale the patterns of fast locomotion gaits and the patterns of primary functions (motor, brake, strut, or spring) of locomotory muscles (Kokshenev, 2008, Table 1), belonging to the same body's elastic system, one can see that in both cases the muscle contractions fall into the same dynamic similarity regime $\lambda = 1$ generally governed by the same uniform muscular field. However, the two distinct (gait and function) muscle patterns should not provide the same scaling rules for dynamic muscle characteristics, including the dynamic length noted by Alexander (1989, p.1212), since the dynamic conditions of muscle cycling are distinct. Indeed, the dynamic cycling in similar locomotion is synchronized with the collective muscle dynamics, corresponding to the condition of maximum overall-body mechanical efficiency, whereas the elastic similarity between individual muscles specialized to a certain mechanical function is likely governed by the requirement of maximum power, generally not matching the condition of minimal oxygen consumption. The observation by Hill (1950, Fig. 1) that the muscle power and efficiency maxima are rather blunt and close in space makes it possible to work at maximum power with nearly maximum efficiency. Further analysis of non-linear dynamic similarity in muscle functions and animal locomotion, including powering intermittent gaits (Alexander, 1989, p.1200), will be discussed elsewhere.

5. Acknowledgments

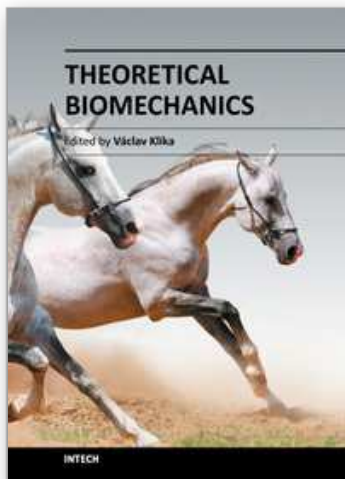
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During last couple of years there has been an increasing recognition that problems arising in biology or related to medicine really need a multidisciplinary approach. For this reason some special branches of both applied theoretical physics and mathematics have recently emerged such as biomechanics, mechanobiology, mathematical biology, biothermodynamics. This first section of the book, General notes on biomechanics and mechanobiology, comprises from theoretical contributions to Biomechanics often providing hypothesis or rationale for a given phenomenon that experiment or clinical study cannot provide. It deals with mechanical properties of living cells and tissues, mechanobiology of fracture healing or evolution of locomotor trends in extinct terrestrial giants. The second section, Biomechanical modelling, is devoted to the rapidly growing field of biomechanical models and modelling approaches to improve our understanding about processes in human body. The last section called Locomotion and joint biomechanics is a collection of works on description and analysis of human locomotion, joint stability and acting forces.

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Phone: +86-21-62489820
Fax: +86-21-62489821

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