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Duality in physiological time: Euclidean and fractal

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*The aim of the present study was to differentiate two modalities of intrinsic time scales : i- the geometric or **Euclidean** modality, which is based on the constant speed of mass transport or of wave transmission in cylindrical structures (arteries, veins, nerves), whose allometric exponent ($T_E=aM^b$) is b = 0.33, where M is body mass (kg) and a the mass coefficient; ii- the **fractal** time scale (T_F), which is characteristic of organs with self-similar branching structures and with volume-specific flows, whose allometric exponent is b = 0.25. The proposed dichotomy could be confirmed by means of the statistical analysis of empirical allometric exponents (b).*

Our findings demonstrate the need to separate the chronology of bulk transport at long distances (inter-organic) which follows an Euclidean geometry (cylinders), from the fractal time scale, which operates at short distances (intra-organic) and is represented by a self-similar branching system which determines both the morphometric and physiometric characteristics within each organ.

Key words: *allometric equations, body mass, Euclidean time, fractal time*

INTRODUCTION

Here we report the first (to our knowledge) attempt to differentiate two time scales for the so-called intrinsic time (T_i) of living beings.

The **extrinsic time** (T_e), measured by means of a clock, deals with chronological phenomena in the physical and chemical sciences. On the contrary, the **intrinsic time** (T_i) belongs only to the realm of the biological sciences and can be associated with body mass (M). Thus, T_i can be expressed by means of Huxley's (1932) allometric equations:

$$T_i = a \cdot M^b$$

where: a = mass coefficient; M = body mass (kg); b = allometric exponent.

For additional information on the subject of dimensional analysis, see Günther (1975), Günther and Morgado (1985) and Günther et al (1992).

EUCLIDEAN OR LINEAR TIME

Lindstedt and Calder (1981) compiled 18 allometric equations for mammals and 9 equations for birds, concerning the intrinsic times (T_i) as related to body mass (M), and obtained for the exponent **b** an average of 0.247 ± 0.049 (mean ± SEM). The 95% confidence limits of the 27 allometric

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Table I

Dimensional analysis of different time functions in physiology and some of its applications

Category	Physical dimensions	Definition	Biological functions
DIRECT (only time)	T	Period	Life span Growth Gestation period
	T^{-1}	Frequency	Heart beat Respiratory cycles
INDIRECT (time dimension associated with length or mass)	LT^{-1}	Velocity	Nerve conduction velocity Pulse wave transmission Air or blood flow velocities
	L^3T^{-1}	Volume-flow	Cardiac output Respiratory air-flow Renal clearances
	MT^{-1}	Mass-flow	Food and water intake Feces excretion

Table II

Allometric characteristics of various velocities of physiological interest

Items	Functions	Units	a	b_E	References	Page
1	Conduction velocity of nerve fibers	$m\ s^{-1}$	120	0.00	Lindstedt & Calder, 1981; Calder, 1984	4 152
2	Pulse wave velocity in thoracic aorta	$cm\ s^{-1}$	540	0.00	McDonald, 1974	418
3	Pulse wave transmission in aorta	$cm\ s^{-1}$	446	0.00	Noordergraaf et al, 1979	486
4	Blood velocity in aorta	$cm\ s^{-1}$	20.7	0.00	Milnor, 1979	R4
5	Mean blood velocity in aorta	$m\ s^{-1}$	0.298	0.07	Günther & León de la B., 1966	32
6	Speed of blood in aorta	$cm\ s^{-1}$	34.6	0.09	Calder, 1984	117
7	Blood velocity in vena cava	$cm\ s^{-1}$	29	-0.01	Calder, 1984	117
8	Air flow velocity (mean) in trachea	$cm\ s^{-1}$	41.9	-0.02	Calder, 1984	96

exponents included b = 0.25. However, the range of the empirical values of those allometric exponents (b) comprises b = 0.13 and b = 0.39.

The above mentioned allometry of chronological processes holds for a wide class of biological phenomena (Table I), in particular, for velocities (LT^{-1}), accelerations (ML^{-2}), mass-flows (MT^{-1}) and volume-flows (L^3T^{-1}), as well as for energy or work (ML^2T^{-2}), and -finally- for power (ML^2T^{-3}).

Among these various physiological time functions, we examined some velocities (LT^{-1}), the mass-flow (MT^{-1}) or bulk flow (L^3T^{-1}) in aorta and trachea, two macroscopic cylindrical structures responsible for the long-distance transport of gases and liquids within the whole organism.

But, what happens to the intrinsic times inside each organ? The answer is related to the **fractal** nature of the arterial, venous, lymphatic and the excretory systems in

different organs, which leads in all instances to area-volume hybrids, described by Sernetz *et al* (1985).

Organ metabolisms (ML^2T^{-3}), measured as oxygen consumption or as ATP and heat productions, are closely related to blood-flows inside each organ (L^3T^{-1}), and also to volume specific flow (L^3T^{-1}/L^3) which finally yields the turnover rate (T^{-1}) or the corresponding frequency.

In Table II, we have summarized eight different velocities, whose empirical allometric exponents (b_E) are all close to zero, indicating: first, that these velocities are independent of body mass (M^0); and second, that our results are in agreement with the second postulate of Lambert and Teissier's (1927) theory of **biological similarity** ($T \propto L$). Finally, we would like to mention another velocity, namely the action potential velocity, which is directly proportional to the diameters of the axons (Withers, 1992). From Heffner and Masterton's (1975) data, we calculated that the diameter of the largest pyramidal tract fibers for 69 mammalian species yielded an allometric exponent of 0.097 ($r^2 = 0.2$), which is practically invariant (Fig 1).
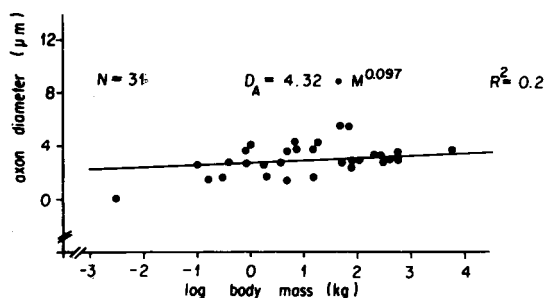

Fig 1. Correlation between axon diameter (µm) of pyramidal tract fibers (ordinate) and the logarithm of body mass (abscissa) of 31 mammalian species. In the equation, DA = axon diameter, M = body mass. Numerical data from Heffner and Masterton (1975); courtesy of Dr F Aboitiz.

In summary, the allometric empirical exponents (b_E) for all **velocity** functions of living beings are very close to zero. Since the great majority of vertebrates follows a geometric similarity (volume = L^3 and $L \propto V^{1/3} \propto M^{1/3}$), the invariance of velocity (Table II) means that the time functions (T) must be proportional to the corresponding length (L). Consequently, the allometric exponent for Euclidean or linear time functions should be **b = 0.33(3)**, with the

Table III

Fractal time functions

Item	Function	Units	a	b_E	b_{VS}	References	Page
1	Cardiac cycle	s	0.25	0.25		Calder, 1984	143
2	Respiratory cycle	s	1.12	0.26		Calder, 1984	143
3	Gut beat duration	s	2.85	0.31		Calder, 1984	143
4	Mean circulatory time	min	0.35	0.21		Calder, 1984	142
5	Glucose turnover rate	mg/min/kg	5.59	-0.25		Schmidt-Nielsen, 1984	146
6	Pulmonary ventilation	ml/min	411.4	0.78	-0.22	Calder, 1984	92
7	Cardiac output	ml/min	188	0.81	-0.19	Calder, 1984	92
8	Basal O_2 consumption	mlO_2/s	0.188	0.75	-0.25	Schmidt-Nielsen, 1984	155
9	Maximal O_2 consumption	mlO_2/s	1.94	0.79	-0.21	Schmidt-Nielsen, 1984	155
10	Water turnover	ml/day	123	0.80	-0.20	Calder, 1984	136
11	Food intake (animal food)	kg food/day	0.234	0.72	-0.28	Calder, 1984	127
12	Renal blood flow	ml/min	43.1	0.77	-0.23	Calder, 1984	133
13	Glomerular filtration rate	ml/min	5.36	0.72	-0.28	Calder, 1984	133
14	Urine production	ml/min	0.042	0.75	-0.25	Calder, 1984	133

only exception of ungulates, which follow McMahon's (1973) **elastic** similarity.

FRACTAL OR CYCLIC TIME

After Mandelbrot (1982) introduced the concept of the fractal geometry of nature, the extrapolation of this new approach to the biological sciences has been very successful (Goldberger & West, 1987; Nelson *et al*, 1990; West & Goldberger, 1987; West, 1990; West & Shlesinger, 1990; Goldberger *et al*, 1990; Yamamoto & Hughson, 1994; Bassingthwaighte *et al*, 1994; among others). However, it is worth mentioning that Weibel and Gomez (1962) anticipated this new geometric approach when they studied the dichotomic branching of pulmonary airways.

In the present paper, we analyze three rhythmic phenomena with endogenous automatisms (Table III, items 1-3); one circulatory time function (Table III, item 4), and finally the turnover rate of glucose (Table III, item 5). Nevertheless, other fractal time functions are associated with bulk transport of gases, liquids and solids. For each of these functions (Table III, items 6-14), we have indicated: first, the original allometric parameters (a and b_E) and, second, the corresponding **volume-specific time exponent** (b_{VS}), *i.e.*, the volume flow ($L^3 T^{-1}$)

when expressed per unit volume (L^3), which always yields the turnover rate of a compartment or the **frequency** of the corresponding function (T^{-1}). The mean value of these 14 empirical allometric exponents (b) is 0.24, which is in agreement with the fractal time exponent (b = 0.25) proposed by Sernetz *et al* (1985).

ORGANISMIC TIME

The main question is to determine which is the time scale for the whole organism, since we must decide between Euclidean (linear) an fractal time scales, as both are simultaneously present in any living being. But if one takes into account that the whole organism is an area-volume hybrid of fractal organization (Sernetz *et al*, 1985), it should be expected that the fractal time scale (b = 0.25) must be prevalent (Tables III and IV).

In consequence, besides the Euclidean and fractal time scales, we should also consider some time functions which affect the whole organism (Table IV). Lindstedt and Calder (1981) found that the mean allometric exponent (b) varies around 0.25 for the **organismic times**, because duration of life, growth processes and gestation period are closely related to the mass-specific basal metabolic rate ($M^{0.75}/M^{1.0} = M^{-0.25}$).

Table IV

Physiological times as functions of the body mass (kg) of eutherian mammals.
(Data from Lindstedt and Calder, 1981)

Item	Organismic Times	Units	a	b
1	Lifespan in captivity	years	11.6	0.20
2	98% Growth time	years	1.21	0.26
3	50% Growth time	years	0.352	0.25
4	Reproductive maturity	years	0.75	0.29
5	Gestation period	days	63.5	0.25
				mean = 0.25

DISCUSSION

It is customary to consider the mean values of the allometric exponent (b) of biological time functions as a single category, despite the fact that at least two different realms can be established. First, the **macroscopic** (Euclidean) bulk-transport systems (circulation, respiration, digestion, among others), and second, the **microscopic** dichotomic branching (fractal) inside each organ. The length scale of the Euclidean transport system goes from meters to millimeters, while the second one (fractal) reaches from millimeters to microns. The driving forces are also different in both cases, being in the Euclidean model a motor organ, as for instance, the heart, the skeletal muscles of respiration (diaphragm and intercostal), and the peristaltic activity in the gastrointestinal tract. On the other hand, in the fractal model, after numerous dichotomic branchings, the driving force is mainly **diffusion** (Fick's laws). Another difference is its morphological characteristic, since in the Euclidean model it is an inter-organic mass-transport system, while the fractal branching occurs inside each organ.

According to Berne and Levy (1983) calculations, the **diffusion** mechanism would employ more than 50 years to transport oxygen at a distance equivalent to the human body length. For this very reason, a rapid mass transport system is needed in multicellular organisms. On the other hand, the fractal geometry is the only solution for the mass transport transition from the macroscopic to the microscopic levels, as well as for the transmission of information in the cellular realm.

The distinction concerning time functions has already been described in relation with **geological time** by Gould (1987), who defined both time concepts as follows:

Time's arrow is an irreversible sequence of unrepeatable events. Each moment occupies its own distinct position in a temporal series, and all moments, considered in the proper sequence, tell a story of linked events moving in a direction.

On the other hand, **time's cycle** is a fundamental state which is immanent in time,

always present and never changing. Apparent motions are part of repeating cycles, and differences of the past will be realities of the future. Time has no direction.

It is worth mentioning that the metaphor of **time's arrow** was introduced in the physical sciences by Eddington (1882-1944) to imply that the direction of time is given by the increase of entropy. Conversely, the **time's cycles** were mainly of empirical origin (astronomy, geology, meteorology and the biological sciences).

The fractal aspects of the time problem were recently summarized by Sernetz et al (1985). These authors established that all organisms are surface-volume hybrids, which function as open, dissipative systems in steady state.

In multicellular organisms we can find the two transport systems in series: one of bulk or mass transport, and the other a self-similar fractal organization, which finally can reach the cellular and the subcellular levels, where numerous heterogeneous catalysis takes place at the immobilized enzyme chains. These intracellular enzyme reactors are supplied with the substrate at a constant rate by means of three macroscopic bulk transport systems: the respiratory, circulatory and digestive apparatuses. Furthermore, any living being is composed of fractal areas, which evolve into the corresponding volumes (organs). Despite the fact that within the vascular system the local flows are of **laminar** nature, inside each organ the flow is of **turbulent** character, this being a consequence of the fractal or self-similar branching, where this turbulent mixing is produced. It should be emphasized that the effect of turbulence is not related with Reynold's number, which in hydraulics defines the existence of laminar or turbulent flows depending on the corresponding diameter of the vessel as well as on its velocity, while the viscosity of the fluid is assumed to be constant.

In Table V, we summarized the main characteristics of both biological time scales. Apparently, the difference among the allometric exponents (b) of biological times is very small ($\Delta b = 0.33-0.25 = 0.083 = 1/12$). Nevertheless, this numerical result should be considered as one of the main causes for the discrepancies among different

Table V

Differences between Euclidean and fractal time scales

Characteristics	Euclidean	Fractal
Allometric exponent	0.33	0.25
Realm	Macroscopic	Microscopic
Geometric form	Cylindrical	Dichotomic branching
Functional relationship	Inter-organic	Intra-organic
Propagation velocity	High	Low
Transport phenomenon	Bulk or waves	Diffusion at cellular level
Specific O_2 consumption	Low in conduction system	High in corresponding organ

Table VI

Quantitative differences (%) between the two biological time scales,
whose allometric exponents are 0.33 and 0.25

Body mass (g)	A (b = 0.33)	B (b = 0.25)	100 · (A-B)/B
1	1.00	1.00	0.0
10	2.15	1.78	21.2
100	4.64	3.16	46.8
1000	10.00	5.62	77.8
10000	21.54	10.00	115.4
100000	46.42	17.78	161.0
1000000	100.00	31.62	216.2

authors concerning the matter of biological time. In this connection, the lifelong controversy between Brody (1945) and Kleiber (1961) concerning the allometric exponent of the basal metabolic rate should be mentioned, despite the fact that in the latter case, the numerical difference of the allometric exponents was even smaller (0.750-0.734 = 0.016). The metabolic rates of all living beings and their relation to body mass (M) was summarized by Hemmingsen (1950), with a mean value of b = 0.751.

The small difference between the biological time exponents (Δb = 0.083) is particularly important in the biological realm. This is due to the fact that the body mass range (McMahon & Bonner, 1983) in the biological world is of 21 orders of magnitude, i.e., between a mycoplasma (10^{-13} g) and a blue whale (> 10^8 g).

Table VI shows the numerical differences between Euclidean and fractal time scales, when both are applied to increasing body masses (M), which in this case are expressed in grams. Despite the fact that this calculation is only restricted to six orders of magnitude of body mass (M), the relative increase of time differences, expressed as percentages, is really impressive, i.e., a mass increase of four orders of magnitude produces a 115.4% increase of the time differences. We may therefore conclude that it is not irrelevant to choose one or the other time exponent to describe chronological events in the biological realm.

Finally, it should be emphasized that the two allometric exponents (b = 0.33 and b = 0.25) are valid for all organisms, because the condition of an open dissipative system in steady state imposes the simultaneous func-

tioning of both, because linear (Euclidean) and fractal entities are connected in series.

ACKNOWLEDGEMENTS

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