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The tree of convective heat streams: its thermal insulation function and the predicted 3/4-power relation between body heat loss and body size

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Abstract

Two parallel fluid streams in counterflow and in close thermal contact convect an energy current longitudinally, in the direction of the warmer stream. This paper describes the flow of convective heat currents through two identical tree networks superimposed, and oriented in counterflow. The convective currents form a single tree. The fluid flow is laminar through straight tubes. The ratios of successive tube diameters and tube lengths are deduced from the minimization of flow resistance subject to two constraints, total volume and total tube volume. It is shown that the total heat current convected by the double tree is proportional to the total volume raised to power 3/4. The conclusion is that the resistance to the loss of body heat governs the relation between metabolic rate and body size in all animals. \oslash 2001 Elsevier Science Ltd. All rights reserved.

1. The old heat transfer theory of body heat loss

Allometric laws are widely recognized power-law relations between geometric and functional (flow) parameters of living bodies. They are accurate over wide ranges of body size $[1-6]$. Predicting these relations from a purely theoretical standpoint has been a real challenge. This paper is about one of the most challenging of all allometric laws, the proportionality between metabolic rate and body mass M (or volume V) raised to the power 3/4.

The pre-1984 history of the theoretical attempts to predict this relation was recounted by Schmidt-Nielsen [2]. From this history, most relevant to the present work is the earliest theory; the metabolic rate must be

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proportional to the heat loss from the body to the ambient. Since the convective heat loss is proportional to the body surface, the metabolic rate must be proportional to the length scale $(V^{1/3})$ squared, i.e. body mass or volume raised to power 2/3. I refer to this earliest explanation (principle) as the heat transfer theory. It is outlined in detail in [6].

The heat transfer theory was effectively discredited in the second half of this century by mounting observations of birds and mammals, indicating an exponent much closer to 3/4 than 2/3. The heat transfer theory was pushed aside completely by the flow network models of West et al. [7] and Banavar et al. [8], which drew attention to a class of interesting relations between geometric and flow parameters in an optimized tree network for fluid flow. To discuss these models is not the objective of my paper, which instead presents a theory, not a model. It is sufficient to note that, as in earlier optimizations of fluid tree networks

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in physiology and river morphology $[9-12]$, West et al.'s [7] optimization was based on invoking the minimization of pumping power, this among several other important assumptions.

My objective is to propose a much more direct and familiar explanation for the 3/4-power exponent. I submit this as a purely engineering alternative to the more recent and more complicated explanations that have been proposed. My explanation is based on the discarded heat transfer theory.

2. Constructal tree-shaped flows

Why should anyone question the current models by resurrecting an abandoned theory? I have two reasons. First, the invocation of the minimization of pumping power makes sense, because reduced power consumption makes sense to the animal (the animal would need less food to survive). Less food means a lower metabolic rate, i.e. a lower rate of heat loss to the ambient. That is why in my view the minimization of pumping power goes hand in hand with the old heat-loss doctrine, not against it. Minimum pumping power consumption and minimum loss of body heat are parts of the same *constructal* principle, how to be the fittest, how to perform best, under constraints [1].

The second reason is that by minimizing pumping power alone, the analysis [7] of the fluid tree leads to the 3/4-power law that correlates mammals and birds. The 3/4 exponent does not correlate cold-blooded vertebrates [2], even though the bodies of reptiles, amphibians and fish are also dominated by flow structures shaped as trees.

Heat transfer is the new element introduced by the following analysis. Unlike in the heat loss theory of the 19th century, heat transfer is not considered to be in isolation. It is combined with the more recent progress made, based on pumping power minimization in fluid tree networks $[6-12]$.

The starting point of this inquiry is not West et al.'s [7] tree model but my own constructal designs, which I published from 1996 [13-16]. Constructal trees are purely engineering designs for flow with minimum resistance between one point (source, sink) and an infinity of points (volume, area). The optimization is subjected to two constraints, fixed total volume and fixed channel volume. It begins with the smallest subvolume (called elemental volume), the size of which is assumed to be fixed. The optimization continues in a sequence of steps of assembly or construction, from small to large, in order to cover the total given volume. In the end, every feature of the point-volume flow is known as the result of the optimization principle. Even the integor 2 for dichotomy (bifurcation, pairing) is deduced from the optimization principle. The resulting flow path is a dichotomous tree $-$ a purely theoretical structure, designed for an engineering purpose.

There is no room and no need to reproduce here the geometric features of the theoretical fluid tree, which are explained in [6,16]. I found that the main features of that structure can be illustrated briefly by optimizing a plane construct consisting of a Tshaped junction (Fig. 1A). For simplicity, assume right angles and Hagen-Poiseuille flow with constant properties. Extensive numerical optimization work on constructal trees for conduction heat transfer [15] has shown that the optimization of the angle of confluence plays only a minor role in the overall resistance of the construct.

The stream \dot{m}_i encounters the flow resistance of two L_{i+1} tubes in parallel, which are connected in series with one L_i tube. When the resistance is minimized by fixing the total tube volume, we find the optimal diameter ratio $D_{i+1}/D_i = 2^{-1/3}$. This old result is known as Murray's law [9,10]. It is an extremely robust result, because it is independent of the lengths (L_i, L_{i+1}) and

Fig. 1. The construction of the tree of convective heat currents, (A) the constrained optimization of the geometry of a T-shaped construct; (B) the stretched tree of optimized constructs; (C) the superposition of two identical trees oriented in counterflow; (D) the convective heat flow along a pair of tubes in counterflow; and (E) the three resistances for heat flow from the animal body to the ambient.

the relative position of the three tubes. It is independent of geometry.

New is the optimization of the lengths when the space allocated to the construct is fixed. In Fig. 1A, the space constraint is $2L_{i+1}L_i$ =constant. This second minimization of the flow resistance yields the optimal length ratio $L_{i+1}/L_i = f = 2^{-1/3}$, which happens to match the optimal diameter ratio. The optimized diameter and length ratios are drawn to scale in Fig. 1A.

In the tree that was optimized step by step into three-dimensional parallelepipedic constructs [6,16], the tube lengths increase by factors in the cyclical sequence 2, 1, 1, 2, 1, 1, \ldots The average of this factor for one step is $2^{1/3}$; therefore, the optimization of the plane construct of Fig. 1A is a condensed summary of the optimized three-dimensional construct averaged over each three-step cycle. The averaged tree is laid out (stretched) in Fig. 1B, so that we can see all the tubes and levels (i) of construction. The number of tubes at level *i* is $N_i = 2^i$ and the total number of levels is *n*.

This concludes the introductory analysis of the theoretical tree. It is not necessary to accept the constructal method as the origin of this structure. The following heat transfer analysis may also be started right from here, by accepting the tree network heuristically, i.e. as an assumption, or model.

3. Tree of convective heat currents

We now turn our attention to the flow of heat between the root and the canopy of the tree. This proposal is new. Interesting is the heat lost by a warmblooded animal through the volume situated under its skin. The trees of blood vessels are one geometric feature under the skin, but not the only one. The other is the superposition of the arterial and venous trees, so closely and regularly that tube i of one tree is in counterflow with tube i of the other (Fig. 1C). The existence of counterflows of blood and other fluids is widely recognized in physiology [2,3]. It is also recognized in bioengineering where it serves as basis for a successful model of heat transfer through living tissues [17,18].

The counterflow formed by two tubes of level i is shown in the detailed drawing of Fig. 1D. The arterial stream is warmer than the venous stream: heat flows transversally, from stream-to-stream. Consider now the adiabatic control surface drawn with dashed line around the counterflow. Since the enthalpy of the warmer stream is greater than that of the colder stream, the counterflow convects longitudinally the energy current $q_i = m_i c_p \Delta T_{t,i}$, where, c_p is the blood specific heat, and $\Delta T_{t,i}$ is the stream-to-stream temperature difference at level *i*. It is known in bioheat transfer [17,18] and even earlier in cryogenic engineering [19,20] that such a counterflow sustains a longitudinal temperature gradient, $\Delta T_i/L_i$, and that the convective energy current is proportional to this gradient,

$$
q_i = \frac{(\dot{m}_i c_p)^2}{h_i p_i} \frac{\Delta T_i}{L_i} \tag{1}
$$

In this expression h_i and p_i are the overall stream-tostream heat transfer coefficient and the perimeter of contact between the two streams. In the case of blood counterflow, the stream-to-stream thermal resistance h_i^{-1} is the sum of two resistances; the resistance through the fluid in the duct $(\sim D_i/k_f$, where, k_f is the fluid thermal conductivity), plus the resistance through the solid tissue that separates two tubes ($\sim t_i/k$, where k is the tissue thermal conductivity). Even when the tubes touch, t_i is of the same order as D_i . In addition, since $k_f \sim k$, we conclude that $h_i \sim k/D_i$, and Eq. (1) becomes

$$
\Delta T_i \sim \frac{q_i L_i k}{\dot{m}_i^2 c_p^2}
$$
 (2)

The double tree structure of fluid streams is a single tree of convective heat streams with zero net mass flow. The convective tree stretches from the core temperature of the animal (at $i = 0$) to the skin temperature. The latter is registered in many of the elemental volumes $(i=n)$ that happen to be near the skin. The many counterflows of the double tree sustain the overall temperature difference ΔT (constant),

$$
\Delta T = \sum_{i=0}^{n} \Delta T_i \sim \frac{q_0 k}{\dot{m}_0^2 c_p^2} \sum_{i=0}^{n} N_i L_i
$$
 (3)

In going from Eq. (2) to Eq. (3) we used the continuity relations for fluid flow $(N_i m_i = m_0,$ constant) and heat flow ($N_iq_i=q_0$, constant). Recalling that $L_{i+1}/L_i=f$, we substitute $L_i = L_0 f^i$, $L_n = L_0 f^n$ and $N_i = 2^i$ into Eq. (3), and after rearranging we obtain

$$
q_0 \sim \left(\frac{q_0}{\dot{m}_0}\right)^2 \frac{k L_n f^{-n} [(2f)^{n+1} - 1]}{c_\rho^2 \Delta T (2f - 1)}
$$
(4)

Separated on the right hand side are the quantities that are constant, and the quantities that depend on n (the number of construction steps). Note that the ratio q_0/m_0 is independent of body size (n) because both q_0 and \dot{m}_0 are proportional to the metabolic rate.

The volume scale is estimated by regarding the stretched tree as a cone in Fig. 1B. The base of the cone (at $i=n$) has an area of size $N_n L_n^2 \sim 2^n L_n^2$. The height of the cone is of the same order as the sum of all the tube lengths, $L_0 + L_1 + ... + L_n = L_0(1 - f^{n + 1})/$ $(1-f)$. In conclusion, the volume scale is

$$
V \sim L_n^3 \left(\frac{2}{f}\right)^n \frac{1 - f^{n+1}}{1 - f} \tag{5}
$$

4. Heat loss versus body size

The relation between metabolic rate and total volume is obtained by eliminating *n* between Eq. (4) and Eq. (5). The result is visible in closed form if we assume that *n* is sufficiently large so that $(2f)^{n+1} \ge 1$ in Eq. (4) and $f^{n+1} \ll 1$ in Eq. (5). In this limit, q_0 is proportional to 2^n , and V is proportional to $(2/f)^n$. From this follows the nakedly simple result

$$
\frac{\log q_0}{\log V} = \frac{3}{4} \tag{6}
$$

which means that q_0 must be proportional to $V^{3/4}$. The proportionality between metabolic rate and body size raised to the power 3/4 has been predicted from pure theory. It can be verified numerically that Eq. (6) is accurate even for small n .

The 3/4 exponent that has been so puzzling over the years is a reflection of the optimized ratio of successive tube lengths, inside a *fixed space*, $L_{i + 1}/L_{i} = f = 2^{-1/3}$. Geometry is the key. Specifically, if we use $f = 2^{-a}$ in the derivation of Eq. (6), instead of 3/4, we obtain $(1+a)^{-1}$, where, $a = 1/3$. The 3/4 exponent is intimately tied to the optimization that generated the tube length ratio subject to the total volume constraint, after the ratio of tube diameters had been optimized subject to the tube volume constraint. This double geometric optimization, the two constraints, and the pairing of tubes into constructs larger than the fixed elemental volume, is the essence of the constructal method [1,6,13-16].

5. Discussion

In summary, what had been missing was the combination of (i) the tree architecture optimized for minimum pumping power and (ii) the convective heat transfer (or, better, thermal insulation) characteristics of two identical fluid trees superimposed in counterflow. Putting (i) and (ii) together into a body heat-loss theory of animal design is the contribution of constructal theory.

The convective thermal resistance posed by the trees in counterflow $(R_1$ in Fig. 1E) resides inside the animal. This runs in parallel with a second internal resistance (R_2) associated with the conductive heat leak through the solid tissue $(R_2$ was neglected in the preceding analysis). On the outside of the animal, the heat current flows through the convective resistance associated with the body surface exposed to the ambient (air, water).

In cold blooded vertebrates the temperature drop across the internal resistance (R_1, R_2) is minimal, and, when environmental temperature changes occur, the dominant resistance is R_3 . Consequently, the heat loss and metabolic rate should follow closely $V^{2/3}$.

In warm blooded animals, a significant thermal resistance is located on the body side of the skin, $(R_1^{-1} + R_2^{-1})^{-1}$. In larger animals R_1 is less than R_2 , the heat current is carried convectively by the double tree (R_1) , and the metabolic rate follows the observed $V^{3/4}$ trend.

The conductive resistance R_2 is proportional to the body thickness scale $V^{1/3}$ divided by the body surface $V^{2/3}$, hence $R_2 \sim V^{-1/3}$. The tree resistance R_1 is proportional to $V^{-3/4}$. The ratio $R_2/R_1 \sim V^{5/12}$ shows that R_2 becomes progressively weaker (i.e. the preferred path) as the body size decreases. In that limit the exponent in the power law between heat loss and body size becomes 1/3. In other words, from heat transfer theory alone we should expect a gradual decrease in the power-law exponent as the body size decreases. At the other end, 3/4 is the asymptotic value of the exponent for large body sizes.

The lung is also a tree of convective currents, which results from the superposition of two air-flow trees, the inhaling flow and the exhaling flow. The convective tree is made up of currents of heat, and constitutes a heat-loss path of the same type as the tree analyzed above. Cold air warms up gradually along the air passages during inhaling. Warm air is cooled down gradually along the same passages during exhaling. The air passage (its wall tissue) acts as a regenerative heat exchanger in the proper engineering sense [6,20]. In addition to the convective tree for heat, and based on the same in and out mechanism, the lung works as a tree-shaped path for the loss of water.

Another way to summarize the theoretical progress that we just made is to recognize that the body surface of warm blooded animals does not serve the same heat transfer function as the surface of cold blooded animals. In mammals and birds the surface (or, better, the vascularized tissue under the surface) serves a thermal insulation function. That is why it has also been possible to predict, from the geometric minimization of heat transfer, the well-correlated proportionality between hair strand diameter and body size length scale raised to the power 1/2 [21].

In lizards and salamanders the surface has the opposite mission, it must facilitate the transfer of heat between body and ambient and vice versa. For the past three decades in thermal engineering, Bergles [22] argued that the dorsal protuberances of large lizards (the stegosaurus was Bergles' favorite) are fins in the proper engineering sense, extended surfaces optimized

for augmenting thermal contact. The present analysis supports this view, and goes one step further to suggest that the entire cold blooded body is elongated (fin like), because it must permanently maximize its contact with the ambient.

Acknowledgements

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