OPTIMAL STRUCTURE OF THE ARTERIAL NETWORK OF SKELETAL MUSCLES

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A criterion of optimal structure of the arterial network of a skeletal muscle is suggested, namely minimization of its hydraulic resistance during intensive work. By the use of this criterion the ratio between the mean diameter of the vessels of different orders of branching can be determined. Equations were obtained showing dependence of the hydraulic resistance, volume, and pressure in vessels of different caliber on the order of branching. Rough quantitative estimates of the possible increase in blood flow in an intensively working muscle compared with the same muscle at rest are given.

KEY WORDS: branching systems; maximal vasodilatation; working hyperemia; hydraulic resistance of the arterial network.

While muscles are working, their energy expenditure increases many times over, and because of this the blood flow in the working muscle must be greater than the resting blood flow in order to satisfy the metabolic demands. So that the blood flow in an organ can be increased without any change in its pressure on entry, the regional hydraulic resistance, R_h, of its arterial network must be lowered. When R_h is minimal, the maximal blood flow will be obtained. The most natural and effective method of reducing the regional hydraulic resistance is by increasing the radius of all the vessels of whatever caliber. However, this involves increasing the volume of the arterial system of the organ, which has as its upper limit a certain maximal volume V_Σ. This limiting volume is determined, first, by the functional organization of the muscle (any design in which the vascular system would amount to a considerable part of the volume of the organ would be functionally meaningless) and, second, the strength properties of the vascular wall (the radius of the vessel after dilatation must exceed the radius of the vessel in the resting organ only by that number of times at which the integrity of the vessel wall is not disturbed). Since the maximal blood flow must be attained during intensive work of the muscle, it is naturally in that state that the minimal R_h and maximal volume V_Σ of the arterial network of the organs must be attained. However, it is possible to imagine a set of vascular networks of identical structure, with the same volume V_Σ, but with different values of R_h (because of differences in the ratio between the diameters of vessels of different calibers). Among all these constructions it is necessary to find the one whose hydraulic resistance will be least. The arterial system of a muscle satisfying this condition will be taken to be optimally organized.

The arterial network of a skeletal muscle consists of a branching "pipe" with many branches. To describe such systems whose branching is not by symmetrical dichotomy but contains many monopodia, a convenient method was suggested by Horton [1] and subsequently developed and used by Strahler [2]. Without going into details, let it merely be said that the vessels can be grouped into "branching orders" in accordance with a certain rule; as a result of analysis of a large number of measurements [2-4] it was found that the number of branches in a branching order, and the mean lengths and diameters of vessels of different orders obey the exponential laws:

$$n_i = a^i \quad \frac{l_i}{l_{i+1}} = x \quad \frac{d_i}{d_{i+1}} = y, \tag{1}$$

where n_i is the number of branches in the i-th branching order; l_i and d_i the mean length and diameter of vessels of the i-th order; a the coefficient of branching; and x and y are unknown constants characterizing the length and diameter of the vessels with a change in order number. All these relationships naturally hold

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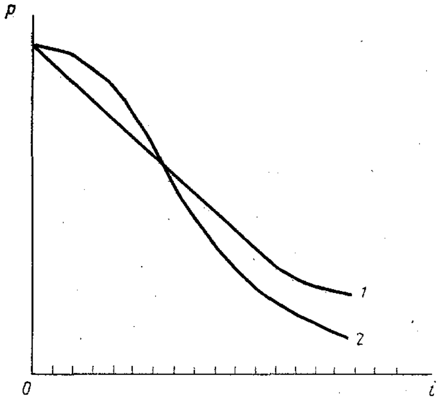

Fig. 1. Arterial pressure as a function of order of branching of vessels for a muscle at rest (2) and during vasodilatation (1).

"on average" and when applied to vascular networks they describe only blood vessels within an organ sufficiently well. Let the large artery supplying the muscle be taken as a vessel of zero order, and the capillaries as order number $z-1$ (the last branching order). The problem is to find values of x and y at which the above-mentioned criterion of optimality is satisfied.

Let us first determine the ratio between the lengths of blood vessels of different orders. It follows from the function of the circulatory system, namely to supply oxygen and nutrients to the tissues and to remove metabolic products from them, that a certain circle centered on any point of an organ (tissue cylinder) must contain a capillary supplying this region. If the characteristic linear dimension of the region is defined as the cube root of its volume, and assuming that the ratio of the length of the vessel to the linear dimension of the region supplied by it is constant and independent of the order number of the vessel, it follows that the ratio of the length of the vessels of successive orders is given by:

$$x=\frac{l_i}{l_{i+1}}=a^{1/3} \tag{2}$$

Let a vessel of the i-th order supply a region whose volume is Ω_i and linear dimension $\omega_i=\Omega_i^{1/3}$, and let a vessel of the (i+1)-th order supply a region of volume Ω_{i+1} with linear dimension $\omega_{i+1}=\Omega_{i+1}^{1/3}$. Since a vessel of the i-th order branches into a vessels of the (i+1)-th order, $\Omega_i/(\Omega_{i+1})\simeq a$ and, consequently, $\omega_i/(\omega_{i+1})\simeq a^{1/3}$, and from the hypothesis $\omega_i/l_i=\text{cosnt}$ we obtain equation (2) (the argument given above is a generalization of the hypothesis of similarity suggested by Chernous'ko [5]).

To determine the ratio between the diameters of the successive orders $y=d_i/(d_{i+1})$, let us minimize the hydraulic resistance of the arterial network of the organ of volume V_Σ. In view of (2), it is easy to obtain an expression for V_Σ:

$$V_\Sigma=\frac{\pi}{4}l_0\sum_{i=0}^{z-1}\left(a^{\frac{2}{3}}\right)^i\cdot d_i^2, \tag{3}$$

where d_i is the diameter of a vessel of the i-th order; l_0 the length of the artery supplying the muscle; z the number of branching orders.

Let us regard blood as a Newtonian fluid. In that case the blood flow q_i in the vessel obeys Poiseuille's rule:

$$q_i=\pi\frac{\Delta p_i r_i^4}{8\eta l_i}, \tag{4}$$

where Δp_i is the pressure drop along the vessel; η the apparent viscosity of blood; r_i the internal radius of the vessel; l_i its length.

The blood flow in one vessel of the i-th order is

$$q_i = \frac{Q}{a^i} \tag{5}$$

where Q is the blood flow through the organ. This equation is not exact, because the considerable asymmetry of the system of the blood flow differs in different vessels of the same order. However, it can be shown that this difference is small and, as a first approximation in this case it can be disregarded. The resistance of the whole system $R_h = \Delta p / Q$, where Δp is the pressure drop along the whole arterial network of the muscle and, according to (4)

$$\Delta p = \frac{8\eta}{\pi} \cdot \sum_{i=0}^{z-1} \cdot \frac{l_i}{r_i^4} \cdot q_i \tag{6}$$

whence

$$R_h = \frac{128\eta}{\pi} \cdot l_0 \sum_{i=0}^{z-1} a^{-\frac{4i}{3}} d_i^{-4}. \tag{7}$$

Minimizing R_h and provided that the volume of the system is equal to V_Σ, we obtain

$$y = \frac{d_i}{d_{i+1}} = a^{1/3}. \tag{8}$$

Thus the arterial network of a muscle in which, in a state of maximal vasodilatation the ratio between the diameters of the vessels of consecutive orders is equal to the cube root of the branching coefficient will be optimally organized in the sense of the criterion now introduced. A similar result, admittedly based on different arguments, was obtained by Murray [6]. Let us compare our estimates for the ratio between the lengths and diameters of the vessels of successive orders with the experimental results obtained by Signal et al. [4]. For the intramural arterial network of the human lungs the following values were obtained experimentally: $a = 3.05$, $x = 1.48$, $y = 1.58$. For this value of the branching coefficient a, equations (2) and (8) give $x = y = 1.45$. Clearly the experimental and theoretical results for the coefficient x are in very close agreement. Comparison of the experimental and theoretical values of the coefficient y is not so demonstrative, for in the present model it is determined for a state of maximal vasodilatation, but this cannot be said for the experimental result.

For vascular networks whose branching is described by equations (1), (2), and (8) it follows that in a state of maximal vasodilatation, first, the total volume of all vessels of the same order is constant and independent of the branching order; in fact $V_{i+1} = V_i \cdot a / xy^2 = V_i$; second, the total area of cross section of all vessels of the same order increases exponentially with an increase in the branching order $S_i = S_0 \cdot a^{i/3}$, where S_0 is the area of cross section of the afferent artery; third, the hydraulic resistance of all vessels of the i-th order is equal to the resistance of all vessels of the (i+1)-th order, since $R_{i+1} = R_i \cdot y^4 / a x = R_i$; fourth, the time during which a certain small volume of blood stays in a vessel of any order τ_i is the same; in fact, $\tau_i = l_i / v_i$, where v_i is the velocity of the blood flow in a vessel of the i-th order, and from the equation of constancy of flow rate $S_i v_i = \text{const}$, it follows that $\tau_i = \text{const}$; fifth, the pressure at the entrance to a vessel of each order is a linear function of the order number (Fig. 1, curve 1). The small decrease in the pressure gradient in vessels of distal orders, reflected in the graph, can be explained, first, by the fact that in vessels with a diameter of under 250-300 μ the non-Newtonian properties of the blood, and in particular the decrease in apparent viscosity [7], begin to have a significant effect, and second, by the fact that as Signal et al [4] showed (admittedly, indirectly), the branching coefficient of vessels of the distal orders is a little higher than the mean branching coefficient. Both these effects, not allowed for in our model, lead to some decrease in the resistance of the vessels of the distal orders compared with that calculated above and, consequently, to a reduction of the pressure gradient.

The argument given above and the results obtained related to the arterial network of an intensively working skeletal muscle. Let us now examine how the parameters of the arterial network change when the muscle switches from a state of maximal activity to a state of rest. Since the length of the vessels is unchanged during transition of the organ from one state into the other, equation (2) remains valid under whatever conditions the muscle is working. This is also natural because equation (2) was obtained from the condition of transportation, whose appearance is the same whatever the state of the organ. It is a different matter with equation (8). We know that the diameters of blood vessels vary depending on the activity of the organ; under these circumstances the diameter of arterioles may be doubled or more when the organ switches from a state of rest to a state of maximal activity [8], whereas the diameter of the large muscular arteries changes only very slightly. Let the diameter of the terminal arterioles of the working muscle be K times greater than in the resting state, and let the diameter of the artery supplying the muscle be unchanged. It follows from the hypothesis that in any steady state the arterial networks of the muscle obeys an exponential law (1) that in a state of rest

$$\frac{d_i}{d_{i+1}} = a^{1/3} \cdot K^{1/z} \cdot \tag{9}$$

This increase in the coefficient y, which is, generally speaking, negligible, leads to a qualitative change in the appearance of the curve of arterial pressure as a function of branching order of the vessels, which for a muscle at rest is S-shaped (Fig. 1, curve 2). The decrease in the pressure gradient in the vessels of distal orders in this case can be explained by the same effects as in hyperemia. The change in resistance of the arterial network of the muscle during its switch from the resting state to a state of maximal activity can be estimated. It follows from equations (1), (2), and (8) that the hydraulic resistance of the arterial network of the working muscle $R_h \approx z \cdot R_0$, where R_0 is the resistance of the afferent artery; z, the number of branching orders. For a muscle at rest, the branching of whose arteries is described by equations (1), (2), and (9), $R_h \approx [(K^4 - 1)/(4 \cdot \text{In} K)] \cdot z \cdot R_0$. Assuming that the diameter of the terminal arterioles of the working muscle is twice their diameter in the resting muscle, the hydraulic resistance of the arterial network of the resting muscle is 5 to 6 times greater than during maximal work. Assuming that the diameter of the arterioles may be increased by more than twice, an even greater change in the resistance of the arterial network of the muscle may be obtained (if K = 3 the resistance of the working muscle will be only about one-twentieth of that at rest). By means of this argument it is possible to assess, admittedly only very roughly, by how much the blood flow in an organ can increase during working hyperemia.

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