MAINTENANCE OF OPTIMAL LINEAR VELOCITY OF BLOOD FLOW IN THE CAPILLARIES – THE MAIN PURPOSE OF NERVOUS REGULATION OF THE CIRCULATION

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It is usually considered that the object of reflex automatic control of the circulation is to maintain the constancy of the arterial pressure. It is claimed that this is achieved by a closed circuit with a feedback which works in accordance with the principle of deviation of the parameter to be controlled [3, 4]. This principle provides for comparison of the actual and assigned values of the parameter and, consequently, for its preliminary "setting" at a particular stabilized value.

An essential defect of the theory of automatic stabilization of the arterial pressure is that, while claiming that this parameter is the principal magnitude assigned, it does not explain why this particular value and not some absolute value of the pressure is stabilized [1, 7].

When criticizing the conception of stabilization of arterial pressure, L. L. Shik [2] emphasized that it is not constancy of pressure which is essential to the organism, but a definite correlation between the minute volume of the circulation and the total oxygen demand, a correlation which is such that its end result is a tendency toward maintenance of the constancy of pO_2 in mixed venous blood. However, in this conception, stressing that the main purpose of the circulation is to supply the tissues with oxygen, the reason for maintenance of a definite value of the arterial pressure remains unexplained.

In the conception of a multicircuit system of adaptive control of the circulation, developed by one of the authors, the value of arterial pressure, which changes in accordance with the overall activity of the organism, is regarded as an index of the quality of control of the circulation parameters [1]. In this case, however, no explanation is given why this particular value of the arterial pressure should be an index of optimal circulation conditions corresponding to the actual minute volume.

The changing oxygen requirements of the organism are satisfied if certain limitations – consequences of phylogenetic and individual development – are present. The most important of these are the existence of a certain limit to the possible oxygen capacity of the blood, a limit to the blood volume, "assigned" geometrical dimensions of the vascular system and heart, and a limit to the output of the heart.

The supply of oxygen to the tissues also takes place with certain limitations. In particular, one such limitation is a certain length l and perimeter of cross section of the capillary L. The product of these values determines the structural constant of the diffusion surface. This structural limitation is compensated by functional (controllable) variables: the number n – of open capillaries and the blood flow through them, maintaining (in the presence of a certain pO_2 gradient) oxygen supply to the tissues. It may also be recollected that the number of open capillaries is a function of the total resistance of the precapillary vessels of the organ [5, 6]. The latter, in turn, depends on the intensity of its functions. In future, for the sake of simplicity, it will be considered that the permeability of the diffusion surface is unchanged.

We shall show that a certain linear velocity of blood flow exists in a capillary at which the supply of oxygen from it is optimal from the point of view of the steady and adequate nutrition of the tissue along the whole length of the capillary.

The need for a uniform supply of oxygen along the whole course of the capillary emerges from the results of comparison of the distance between neighboring capillaries and their length. In skeletal muscle, for instance, the radius of oxygen diffusion (half the distance between neighboring capillaries) is 20-25 μ, while the length of the capillary is 500-1000 μ [9]. Hence it follows that the oxygen capacity of the

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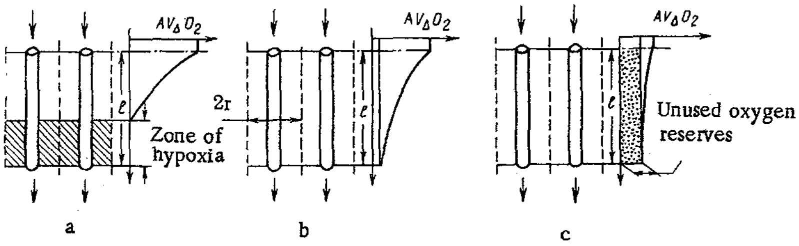

Fig. 1. Scheme of distribution of the oxygen supply to the tissue along the length of a capillary in relation to linear velocity of movement of blood in the capillary. a) Linear velocity below optimal; b) linear velocity optimal; c) linear velocity above optimal; $AV\Delta O_2$—arterio-venous oxygen difference; l —length of capillary; r—radius of diffusion.

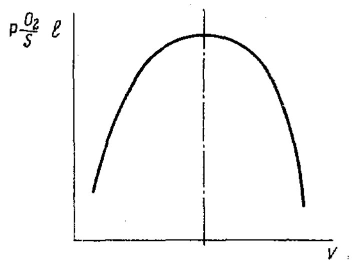

Fig. 2. Character of relationship between oxygen supply to the tissues and velocity of blood flow along capillary. $pO_2/S \times l$ —product of oxygen supplied by a ring of an elementary cylinder of a capillary and its length; V—linear velocity of blood flow in capillary; S—area of ring.

erythrocyte must be expended along a path 25-40 times longer than the radius of diffusion. If the greater part of the oxygen were given up in the initial part of the capillary, the distal part of the tissue would be in conditions of hypoxia or anoxia. Such a state could arise if, in a working organ, i.e., in the presence of a considerable pO_2 gradient, the linear velocity of blood flow along the capillaries were below a certain optimum (Fig. 1, a).

The optimal velocity must be taken as the velocity at which oxygen reaches the tissues uniformly along the whole length and in a quantity determined by the oxygen demand (Fig. 1, b).

If the linear velocity exceeds the optimal value, although the oxygen demand is met, the oxygen capacity of the blood is utilized uneconomically (Fig. 1, c). With an even higher velocity of blood flow, hypoxia may again arise because in these conditions a fall of pO_2 in the tissues may take place as the result of the relatively low rate of dissociation of oxyhemoglobin [8]. This is illustrated in Fig. 2.

By definition, the flow Q through a capillary is the ratio between the fall of pressure P and the resistance R. Dividing both parts of this ratio by the area of cross-section of the capillary, we obtain an expression for the linear velocity of flow:

$$V = \frac{P}{RS}.$$

Substituting for R in this formula its value expressed through a factor of dimensions of the capillary and a factor of blood viscosity, i. e., through $(8/\pi)\,(l/r^4)\,(\eta)$, and expressing the area S by πr^2, we obtain:

$$V = k \cdot P \cdot r^2,$$

where $k = {}^1/_8\, l\eta$. Taking k=1 for a certain "standard" capillary, we obtain:

$$\overline{V} = P \cdot r^2,$$

where P is the fall of pressure along the length of the capillary and r^2 is a measure of the area of its cross section.

The conditions of optimal diffusion in a certain part of the tissue demand that in a system consisting of n "standard" capillaries connected in parallel, the same linear velocity of blood flow is maintained as in a single capillary. The value of this mean linear velocity for a system of capillaries is determined from the formula

$$\overline{V}_h = P_n \cdot r^2 \cdot n,$$

where P is the fall of pressure in the system of capillaries, $r^2 \cdot n$ is their total area, and $\overline{V}_n$ is the mean linear velocity of blood flow in the capillary system, i.e.,

$$\overline{V}_n = \sum_{i=1}^{n} V_i / n,$$

where n represents the number of capillaries.

The only determinant of optimal linear velocity in a system consisting of n capillaries connected in parallel is thus the value of the fall of perfusion pressure P. In turn, this value is set by the mean arterial pressure.

The following hypothesis may be put forward on the basis of the foregoing arguments. The variable flow of blood in the circulatory system must correspond to a perfectly definite value of arterial pressure necessary for maintaining optimal conditions for oxygen diffusion (and for tissue metabolism in a wider sense), by maintaining the required linear velocity of blood flow along the capillaries. The first conclusion to be drawn from this is that the conception of stabilization of arterial pressure is fundamentally unsound. A change in the minute volume of blood, if the arterial pressure is stabilized, would inevitably lead to deviation of the mean linear velocity of blood flow through the capillaries from the optimal value. On the other hand, in the conception of regulation of the overall blood flow by the central nervous system [3], rightly emphasizing the relationship between this value and the oxygen demand, the arterial pressure is represented purely as the force moving the flow of blood, and the significance of the pressure receptor zones is disregarded. The contradiction is resolved if allowance is made for the informative value of the arterial pressure as a magnitude which, through the pressure receptor zones, reflects the mean linear velocity of blood flow in the capillary, and thereby the adequacy of the conditions of tissue metabolism.

The relationship between oxygen supply along the course of the capillary as a function of linear velocity has a maximum (Fig. 2). Consequently, the arterial pressure, as a reflection of the mean linear velocity of blood flow in the capillaries, must also have a certain value corresponding to conditions of adequate and uniform gas exchange along the length of the capillary, i. e., to the condition of optimal tissue metabolism. In this sense, this magnitude of arterial pressure is an informative index of the optimal relationship between tissue metabolism and minute volume of the circulation. Consequently, the main purpose of nervous regulation of the circulation is to establish a level of arterial pressure which, during variations in minute volume, will ensure stabilization of the fundamental parameter of the tissue circulation – the mean linear velocity of blood flow in the capillaries.

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