SOME PRINCIPLES IN THE STRUCTURE AND FUNCTION OF THE CAPILLARY BED

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August Krogh [9], the founder of the study of capillaries, suggested that each capillary, because of the presence of contractile elements in its wall, could alter its diameter, there existing in the organism a system of central and local neuro-humoral influences which effected necessary changes in the number of open capillaries.

Later investigators [4, 5] have discovered that the contractile capacity is inherent only in those vessels which contain muscular elements in their walls. However, electron microscopic examination of the capillary wall has led to the discovery in its endothelium of a network resembling myofibrils [6]. Therefore the question of possible contraction by the capillary wall is not yet resolved.

Later, a more complex schema was advanced for the functional structure of the vascular system. According to these investigators [3, 12, 13] the vascular system in all tissues and organs of animals consists of "vascular-functional units" each of which is constructed in the following manner: the direct prolongation of the arteriole is the muscular capillary, called by the authors the central vessel, in which blood always flows ("on duty" capillary of Krogh). At the arterial part of the muscular capillary branches off the "true" capillaries, which form anastomoses with one another as well as with the capillaries of other vascular units. Blood flow in the "true" capillaries depends on the tone of the precapillary sphincters, which are located at the origin of each "true" capillary. Blood from the "true" capillaries is directed toward the venous end of the central vessel. The capillary beds of different organs and tissues differ in the lengths of the central vessel and "true" capillaries and in the number of the latter. The movement of blood along the central vessel depends in the first place on the state of blood flow in the arteriole, which is basically related to central effects. The blood flow in the "true" capillaries depends both on the blood flow in the central vessel (central influences) and on the diameter of the precapillary sphincter (local influences).

The schema was adopted by some physiologists and entered a number of physiology textbooks [7]. The mesentery of warm-blooded animals served as the basic object in studies to elaborate this scheme. But already in the first years after the hypothesis of "structural-functional vascular units" was propounded, doubts began to be expressed that these data could not be transferred to all other organs [2, 8, 10].

However, detailed studies of the microanatomy of the vascular tree in various organs had not been made. This has been the task of the present investigation.

METHODS

Observations and measurements of the capillary bed have been performed mostly vitally using MBS-2 and ML-1 microscopes, "Reichert" stereoscopic magnifier with total magnification to 200. A pneumatic micromanipulator, constructed at the Experimental Factory of the Siberian Department of the USSR Academy of Sciences, was used. Skeletal muscle from the hind legs of frogs, rats and cats and frog lung and skin were used.

RESULTS

A detailed description of the microanatomy of the organs studied has been given in a separate paper [1]. This article will supply a summary analysis of all the material.

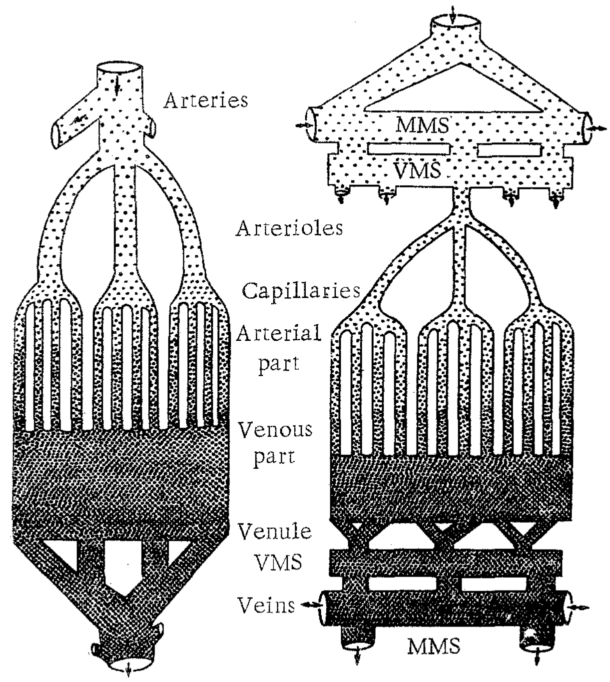

Fig. 1. Diagram of vascular bed of magistral type in skeletal muscle of the frog (left) and warm-blooded animal (right). Arrows indicate direction of blood flow. MMS) Intermuscular network of arteries and veins; VMS intramuscular network of arteries and veins

It must first be noticed that in none of the organs studied, except in separate sections [3, 12, 13], did we observe a capillary bed constructed according to the principle described above.

In frog skeletal muscle a gradual division of arteries and their veins occurs. Anastomoses between different branches of the vascular tree are observed only at the level of the venous sections of the capillaries. This suggests that the blood flow (in larger or smaller parts of the muscle) is determined only by the movement of blood in the vessels leading in an out. Compressing the arterial tree with the micromanipulator at different levels (artery, arteriole, capillary) confirmed this. The anastomoses in the capillary channels provide interchanges only of those parts of the capillary through which the venous outflow runs.

This type of structure in the vascular tree we have called the main line (Fig. 1). The last links (from the effect one the blood flow in the capillaries of such a network) are the arteriole and the precapillary sphincters.*

A concept of the specific importance of each of these links may be obtained by examining the distribution of open capillaries in muscle under resting conditions (Figure 2). A calculation showed that under these conditions at a sufficiently low temperature $1/2$ to $1/3$ of all capillaries located in the frog muscle are functioning. Our attention is directed toward the rather even and sparse distribution of the capillary network. The latter is only possible if the capillary blood flow depends on the tone of its precapillary sphincter. If the directive link in the regulation of capillary blood flow was the arteriole, then a grouped distribution of open capillaries would be seen.

In the skeletal muscle of warm-blooded animals the same principle of capillary bed structure is maintained, but in this case there are anastomoses between large arteries which lead to different muscles (intermuscular network), and between small arteries which run within each muscle (intramuscular network). Similar anastomoses are also found in the venous portion of the vascular tree. This description of the vascular network is not encountered in all muscles, and its purpose is to equate the hemodynamic conditions in the terminal arteries and veins, which are unequally removed from the main line vessels. Other investigators have indicated this previously [11].

From the intramuscular network depart (or are formed as the result of division of large arteries) the terminal arteries of 70-90 microns in diameter, which subsequently branch in a manner similar to that described in the frog. This suggests that the principle of capillary net function in homoiotherm skeletal muscle is similar to that in amphibia.

A different construction of the vascular network is encountered in frog skin (Figure 3). Segmental arteries are connected in a single arterial network for the entire integument located in the hypodermis. A similar net exists for the venous portion of the vascular tree as well. The role of anastomoses in this network is the same as for the vascular bed of homoiothermic skeletal muscle. Compression of separate arteries and veins comprising a network only changes the direction of the blood flow in the corresponding segments.

From the arterial network vessels lead out (designated as arterioles) to capillaries on the surface of the skin. The latter are connected by anastomoses into a single capillary network for the entire integument. The role of separate capillaries in this net is insignificant. Even compression of the arteriole does not stop but only slows the blood flow in the capillaries leading out of it. Compression of 2-3 rows of arterioles leads to the stopping of blood flow in a considerable area of the skin. In special experiments we saw that increase in the skin blood flow is always related to opening of epidermal arterioles and venules.

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* The possibility of the capillaries closing is not excluded.

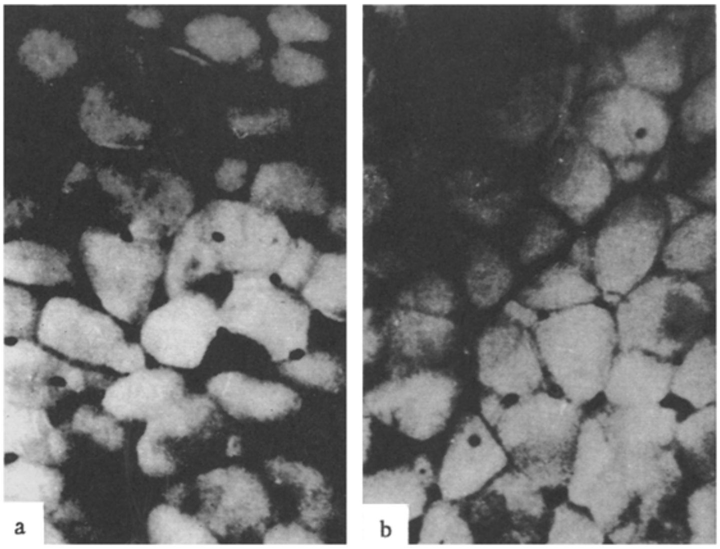

Fig. 2. Transverse section of semimembranosus muscle of frog. Number of open capillaries upon stimulation (left) and without stimulation (right). To produce the resting state the frog was kept to three hours at -6°. Thickness of section 200 microns. Microphotograph. Obj. 10. Oc. 5. Fixation in 10% formalin solution.

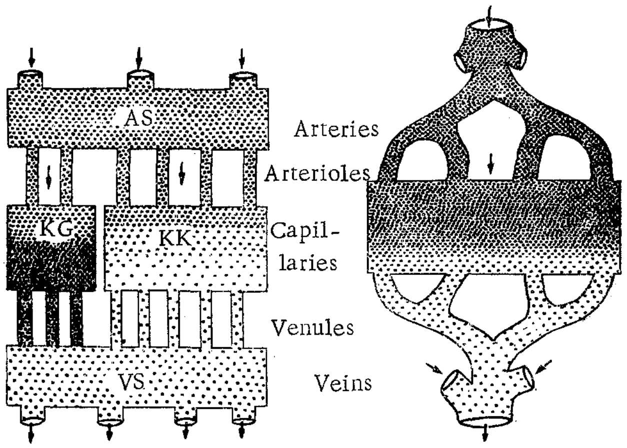

Fig. 3. Diagram of capillary bed of reticular type in frog skin (left) and lung (right). AS) Arterial net in hypodermis; KK and KG) capillary bed on skin surface and in hypodermis; VS) venous network in hypodermis.

The capillary network of the hypodermis is smaller in volume but has similar structure and function.

Upon comparing the two schemata presented for the capillary bed we must notice the basic differences between them. If in the first schema the great role is that of separate capillaries in the regulation of capillary blood flow, then in the concept we have called the network concept, this role is fulfilled by the arterioles. If in muscle fine local changes in blood flow are possible, then in the skin these changes are only focal.

Putting together the information which we presently have on the relative function of certain organs, we are inclined to think that the first description of the capillary bed is related to the nervous system, probably, and the second to parenchymatous organs where there is no functional cellular specialization. Thus, in the frog lung the principle of vascular activity is the reticular system although it appears that its structure sharply differs from the morphology of the dermal vascular system. The pulmonary artery (and vein) in the frog is divided in tree-like fashion, forming gradually smaller and smaller vessels. Only on the upper third of the lungs, i.e. in the areas furthest removed from the heart, do arteriovenous anastomoses appear, connection both arteries and veins.

The arterioles break up into capillaries in such a way that they closely anastomose, even in the arterial portion, among themselves. And only the presence of anastomoses in the arterial section of the capillary network ensures the activity of this system according to the reticular characteristic. In the lungs as well as skin compression on only 2-3 arterioles lead to the cessation of blood flow immediately in the entire group of capillaries.

Evidently the presence of anastomoses in the arterial and venous portions of the vascular tree does not obviate the principle of capillary bed activity. The determining factor is the localization of the anastomoses in the capillary bed; their presence in the venous section guarantees one principle of activity, and in the arterial section—another.

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All abbreviations of periodicals in the above bibliography are letter-by-letter transliterations of the abbreviations as given in the original Russian journal. *Some or all of this periodical literature may well be available in English translation.* A complete list of the cover-to-cover English translations appears at the back of this issue.