

A SUMMARY OF OUR STUDIES CONCERNING THE STRUCTURE AND FUNCTION OF BLOOD CAPILLARIES

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HISTORICAL NOTE

Galen was of the opinion, based upon his macroscopic observations, that the vessels at the end of the arterial tree, have a diameter no greater than that of human hair. Harvey (1628), centuries later, using a hand magnifier, gained the impression that there are “holes through the flesh” which, he assumed, represent channels of communication between the arterial and venous system. Malpighi (1661), who investigated frog’s lung with the microscope, was probably the first to demonstrate the existence of capillary vessels. Later on, Hall (1831) with his anatomical approach was able to show the difference between the arteries and capillaries.

Rouget’s work, toward the end of the last century (1873), called attention to certain contractile elements that he has seen in the capillary walls of the tadpole’s tail. All these observations concerning the nature of blood capillaries were ably summarized and reviewed by Krogh in his book “The Anatomy and Physiology of Capillaries” published in 1930. This paper is a summary of our experiments (References II) which I and my research collaborators made on the Invertebrata, Amphibia and mammals since 1932.

STRUCTURE

The blood capillaries are the microscopic channels which establish connection between the arterial and venous system. The capillary wall is made up of one or two layers.

Nomenclature As a rule, the capillaries are divided into five segments: arterial capillary, distributing capillary, net capillary, collecting capillary and venous capillary. In

addition to these, there are the bifurcations of the arterial capillary and communicating branches.

Lining Cells The lining of the blood capillary wall consists of endothelial cells. The so-called contractile cell may or may not be present. The ratio between endothelial and contractile cells varies considerably in all five segments, and even to a greater extent in different organs. The density of contractile cells is greatest in the arterial capillary wall and it decreases rapidly toward the net capillary and again increases gradually toward the venous capillary. Furthermore, the contractile cells are present in groups at the bifurcation of the arterial capillaries. The number of these contractile cells is greater above the bifurcation than at the lower end.

The width of spaces separating individual endothelial cells varies greatly in the different segments. As one follows the course of the arterial capillary toward the venous capillary, these spaces become gradually greater. And when the capillary lumen dilates the intercellular spaces further enlarge.

Diameter Diameter of the blood capillaries, as a rule, is the smallest in the net capillary and larger toward both the arterial and venous ends. In the sinusoides, the diameter of the net capillary is larger than in either the arterial or venous capillary.

Distribution The distribution of the blood capillaries are found to be varying considerably in different organs. One may classify the distribution of blood capillaries as follows: 1) net type, 2) folded net type, 3) elevated type, 4) basket type, 5) sinusoid type, and 6) sinus type.

Vasomotor Innervation It is reasonable to assume that the vasomotor fibres innervate the blood capillaries.

CONTRACTILITY

The blood capillaries are so constituted as to be able to contract passively and actively.

Passive Contractility The passive type of contractility is a change in the diameter of the capillaries caused by the expansibility of the wall. The arterial capillary has the greatest capacity for passive expansion. The change of the expansibility of the wall is brought about by various chemical substances.

Active Contractility The active contraction of the capillaries is defined as the con-

traction of the capillary wall which can be elicited by physiological means. It appears that the contractile cells are responsible for active contractility. In addition to the vasomotor innervation, the active contractions are governed by hormonal and chemical influences, as well as by the blood pressure changes. It differs greatly in degree in various segments of the capillaries, being the greatest in the arterial capillary and the least or none in the net capillaries. The degree of active contractility of the capillaries is in direct proportion to the number of contractile cells within the wall. A strong active contractility exists at the bifurcation of the arterial capillaries where contractile cells are found in large groups.

Tonus Capillaries have an active and a passive tonus. The former is due to a continuous contraction of the contractile cells, and the latter is produced by the aggregate tension of the wall.

Rhythmical Contractions The blood capillaries, especially arterial capillaries, change their diameter rhythmically through the active contraction of the contractile cells. There is also a passive contraction which is induced by rhythmical blood pressure changes in the arteries.

Vasomotor Action The vaso-constrictors increase the active tonus of the capillaries while the vaso-dilators decrease the active tonus by the release of neuro-effectors from the nerve endings. The constrictor substance is almost identical with adrenalin, the dilator substance with acetylcholine.

Reflexes There are four separate reflex arcs through which the mechanism of the capillaries may be influenced. They link up as follows: 1) within the same capillary system, 2) connecting two or more adjacent capillary systems, 3) heart, artery, vein to capillaries, and 4) organs to capillaries.

Mechanism of Contractions The wall of the capillaries consist of four elements: nerve endings, contractile cells, endothelial cells and intercellular cement substance. The nerve endings release neuro-effectors; the contractile cells produce an active contractility; the aggregate of all four components represents the passive contractile force. Neuro-effector released from vaso-constrictor, adrenalin, pituitrin and certain ions produce contraction by their effect upon the contractile cells. Neuro-effector released from vaso-dilator, histamine, or acetylcholine decrease the active tonus by antagonizing the neuro-effector released from vaso-constrictor or adrenalin. Dilute solution

of adrenalin, pituitrin, lactic acid, etc. increase expansibility by acting on the wall of capillaries.

PERMEABILITY

Site of Penetration The permeability of the blood capillaries is quite different in the various segments. Particles and leukocytes penetrate easily through the net and collecting capillaries, especially near the transitional points.

Path of Penetration The main avenue of penetration through the capillary walls may be through the intercellular cement substance between endothelial cells.

Factors Influencing Penetration Penetration of substances through the capillary wall is influenced by the permeability. The permeability is changed by the contraction or dilatation of the wall in either the active or passive, or by the physico-chemical changes of the wall. On the other hand, the penetration of fluid and particles through the wall is influenced by physical and chemical differences of the fluids in the intra- and extravascular compartments, i.e. hydrostatic pressure, effective osmosis, diffusion tension, partial pressure, electric charge, etc.

Diapedesis of Leukocytes The white blood corpuscles migrate mainly through the walls of net and collecting capillaries. The velocity of migration differs widely in the individual cases.

BLOOD FLOW IN THE CAPILLARIES

In the resting state, when blood volume and pressure decreases, the contraction or dilatation at the bifurcations of the arterial capillaries does control the flow. The direction of the flow in the net capillaries is sometimes changed by the communicating branches. In this way, the blood flow is controlled uniformly throughout the entire capillary bed.

In the active state, in which blood volume and pressure increases, all capillaries dilate uniformly. In this case the blood current is fast and the direction of the flow in the net capillaries remains constant.

When the blood pressure rises, or the venous side is suddenly obstructed the arterial capillary at its bifurcation contracts markedly, thus protecting it from an overload.

When the capillaries are in a state of contraction, the flow remains in the main

capillaries, not in the net capillaries, due to the contraction of the bifurcations of the arterial capillary.

The valves in minute veins, as well as the contractility of the small arteries, control the flow in the capillaries.

The flow in the capillaries is always controlled in the above fashion. The neuro-effectors, chemical substances and blood pressure play an important role in this mechanism.

While blood is perfused through the capillaries, its contents excepting red blood corpuscles, penetrates into, or from the tissue spaces mainly through the intercellular cement substance of the net and collecting capillaries. The penetration of these fluid and particles is influenced by the change of the permeability of the capillaries, namely the dilatation, contraction or physico-chemical change of the wall.

Variations of physical and chemical factors in the intra- and extravascular compartments will also influence the exchange of substances. The water exchange is accounted for by the alteration of hydrostatic pressure and effective osmosis. The penetration of the solute depends on the difference in concentration and electric charge, while the rate of gas exchange is governed by its partial pressure.

Whether fluid and particles penetrate into the tissue spaces or into the capillary lumen depends upon whether the above-mentioned factors act in the same or in opposite directions. The rate and direction are variable in different organs.

DISCUSSION

C.M.B. Rouget (1873) found contractile cells in the blood capillaries on tadpole's tail. An active contractility of the capillaries of frog's nictating membrane was observed by Steinach and Kahn (1903). Hooker (1921) thought that the arteriole has a wall of endothelium and circular smooth muscle only there being no adventitial sheath, but the capillary has no muscle layer. On the other hand, Krogh and Vimtrup described in 1932 that a normal capillary consists of an endothelial tube covered on the outside with branches of smooth muscle cells named after their discoverer Rouget cells, or according to some authors "pericytes." Recently, Zweifach (1949) described the remainder of the capillary wall as a denuded endothelial tube which possess no contractile elements. These are termed none muscular or true capillaries.

In our experiments, contractile cells in net capillary were found in the mesentery, but not in the lungs or liver of frogs and tortoises.

Chambers and Zweifach (1946) divided the nomenclature of the minute blood vessels into six parts from other investigator's reports. The definition of the blood capillary is not yet settled.

Hooker described alterations in the surface tension of the capillary endothelium induced by chemical or nervous influences. Field (1935) found that in the capillary contractions due to electrical stimulation of capillaries of the nictating membrane in the frog, the caliber of the vessel has been altered by folding and also by swelling of the endothelial nuclei. However, we could not observe the active contraction of endothelium of the capillaries.

The principal site of penetration is near the venous side of the capillary bed, according to the work of Landis (1934) performed on frogs, and in Rous, Gilding and Smith's investigation (1930) on rats. The pathway in the capillary wall, Chambers and Zweifach (1940) concluded, leads through the intercellular cement substance that constitutes the inter-endothelial spaces. Starling (1898) emphasized that the water exchange is greatly influenced by the colloid-osmotic pressure. Krogh (1930) called attention to the importance of the state of dilatation or contraction as influencing factors in the capillary permeability. The author's experiments fully substantiate these contentions.

Thoma (1896) and others have endeavoured to establish the pathways through which the diapedesis of the leukocytes is effected, but the mechanism of this migration is still entirely obscure today.

When the capillary bed lost its tonus, by the perfusion of Ringer's solution, the use of adrenalin (Dale and Richards (1919)) or pituitrin (Krogh (1930)) are believed to be effective in reconstituting it. One must bear in mind, however, the fact that either one of these substances acts as a vaso-constrictor only through the stimulation of the contractile cells of the wall, hence, they can augment only the active, and not the passive tonus.

In the regulation of the capillary flow local metabolic processes are believed to be of considerable importance, according to Lewis (1927). The author, however, feels that his experiments suggest that it is the adrenalin that exerts the most important

regulatory influence on the capillary blood flow.

In the resting muscles of frogs, and in warm blooded animals, closed capillaries were frequently observed by Krogh. It was also noted by Richards (1922) that in the frog's kidney, during diminished diuresis, many of the glomeruli are completely shut off from the circulation. They appear either empty or contain some stagnating red cells. This phenomenon may be attributable to the grouped contractile cells found mostly at the bifurcation. Similar observations were recently (1946) made in the bat's wing by Nicoll and Webb.

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IX *General Description*

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〔要 約〕

毛細血管の構造と機能についての研究総括

西 丸 和 義

この論文は毛細血管の構造と機能を無脊椎動物、両棲類、は虫類、哺乳動物と人体について実験追及した、協同研究者との論文 296 編をまとめたものである。

これによって得た毛細血管の概念は、

毛細血管では、その壁の受動的および能動的収縮性に基因して血行調節が行なわれ、またその壁の透過性、およびこれを境とする血液と組織液との間の物理化学的性状の差異に基因して両液間の物質交換が行なわれるものである。