Summing up these results we can say that besides the natural stimuli (pressure, temperature, and humoral factors) we must realize that conduction of excitation, effects of propagation and variations in the excitability of associated venous segments also take part in the functional organization of venous peristalsis. The myogenous organization of the pulsation mechanism is the result of the interaction of all of these factors. The venous heart, in contrast to the heart proper, can be tetanized; a definite refractory state does not exist. We conclude that in the smooth venous muscle the contractile elements are neither simultaneously excited nor do they contract at the same time. Additional stimuli are effective at every phase of the pulsation. During the entire systole excitability is not diminished; with the onset of diastole, often even during the beginning of the diastolic pause, excitability disappears completely: this represents an additional constructive-functional difference between the venous heart and the heart proper. A comparison of the autorhythmic mechanism of the actively pulsating veins of the bat wing with the portal vein in bats, mice, rats and lower vertebrates and also with the contractile lymph vessels, will lead to a more soundly based comparative angiology. The self-regulation of the vascular apparatus to be discussed in the following papers may provide an impetus for further fruitful research.

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Overview of circulation in the wing membrane

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In meeting the profound metabolic demands involved in achieving true flight, bats have been successful in specializing their otherwise typical mammalian cardiovascular system rather than having to modify its basic organization. The remarkable efficiency of this system may well be reflected, for example, in the fact that all bats at rest, whether of a hibernating species or not, tend toward what in most other mammals would amount to a functional bradycardia. The problems involved in maintaining adequate circulation and homeostasis in a bat wing in particular must be such as to call upon a maximal number of specializations to maintain a successfully operating system. Unlike birds, bats must maintain nutrient support to living tissue in the outermost boundaries of their flight surfaces. At the same time, they must avoid such complications as excessive capillary pressure and tissue edema in all areas of this extensive wing, whether the animal is at rest or in flight. Moreover, in addition to locomotion, the wing subserves other important needs of the animal such as thermoregulation, during which dramatically sudden engorgement of wing vessels can take place throughout the entire extent of the patagial membranes.

As far as is known, the properties of the capillary beds and tissue spaces themselves are typical of any mammal, despite such extreme demands as those imposed by the centrifugal forces which must of necessity be encountered during flight. It is therefore understandable that augmenting venous (and lymphatic) return by a superbly developed vascular wall pulsation should and does occur, specifically in the flight membranes. But it is by no means the only mechanism utilized. Blood supply to more distal areas of the wing is by way of one prominent artery to each limb (crural to the hindlimb, median to the forelimb). Such terminal branches as radial and ulnar tend to branch off early, in the shoulder region in these cases, and course into the wing and wing membranes as long, relatively slender vessels which offer much higher resistance to flow than the median artery. Such vessels are concerned with supply to the more proximal regions of the patagium. Sudden engorgement of the wing is facilitated by the presence of extremely well-developed arteriovenous anastomoses in terminal phalanges of the digits. Blood flow to the wing appears to remain high even when capillary beds are relatively empty, with much of the blood bypassing the capillary beds by way of the arteriovenous anastomoses and leaving the wing through shunt veins, i.e., the cephalic and uropatagial (which are not rhythmically contractile). Closing off the anastomoses permits a rapid diversion of additional blood into the capillaries without undue dependence upon such factors as increased cardiac output (which might, for example, transiently raise intracranial blood pressures beyond tolerable limits).

The intermediate vessels, which intervene between the major vessels of wing supply and the capillary beds, are arranged in a roughly concentric series of arcades. These arcuate systems are postulated to provide a series of volume reservoirs equidistant from the capillaries they supply, giving capillaries a capacity to operate at very much the same pressure head over an extended range of flow rates. These arcades are associated with 90° angles of branching to make possible maximal arterial pressure drop into tributary vessels (with minimal pressure drop in parent vessels). Arcuate systems are by no means unique to the bat wing, but the additional control provided by prominently-developed junctional sinuses at sites of arterial branching (the 'Indian club' formations of Nicoll and Webb) might give this vascular geometry greater flexibility in bats.

Relative dimensions of the various components of the vascular field do not appear to be the same in the bat wing as in other thin membranes which occur in mammals, a specific case in point being the dog mesentery. In expanding upon calculations of some of the data provided for these structures by Wiedeman and Green (figures 1 and 2) I concluded that total cross-sectional areas do not differ markedly, though it might be significant that lower and higher cross-sectional areas do occur at the respective levels of arterioles and small veins in the bat, these are, respectively, the last and first sites of occurrence of smooth muscle at either end of the complex of non-muscular exchange vessels. However, a relatively

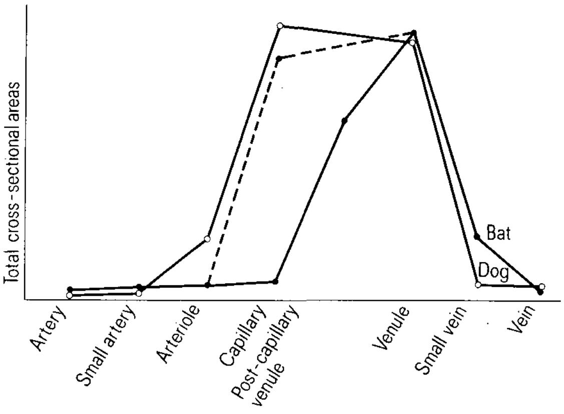

Fig. 1. Total vessel cross-sectional areas as measured in the patagium of living *Myotis lucifugus* (Wiedeman, Circulation Res. *12*, 375, 1963) and calculated from fixed dog mesentery (Green, in: Medical Physics, vol. 1, p. 208. Yearbook Publ., Chicago). Dashed line indicates Kallen's value for the capillary area which would have been found in the bat had it been calculated as for the dog. Figure modified and redrawn from Wiedeman's study. From Kallen, Biology of Bats, vol. III, chapter 3. © Academic Press, New York 1977. Reprinted by permission.

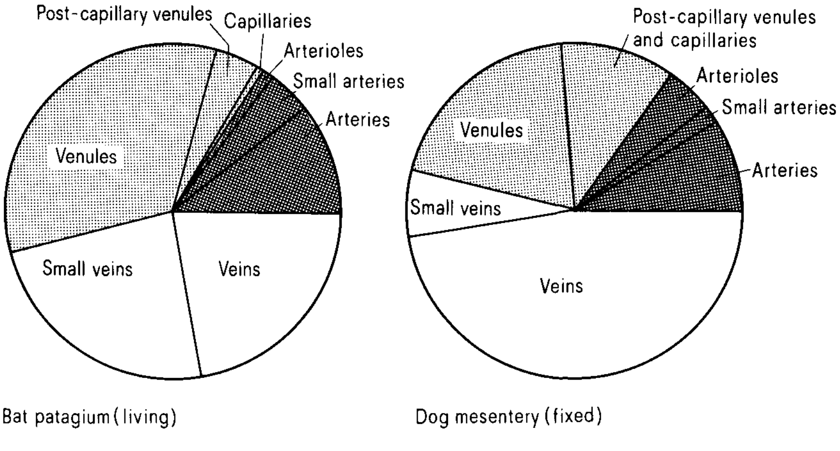

Fig. 2. Percentages of blood volumes contained in various portions of vascular beds in bat wing and dog mesentery. Same source material as figure 1. From Kallen, Biology of Bats, vol. III, chapter 3. © Academic Press, New York 1977. Reprinted by permission.

higher volume is contained in the larger arteries of the bat wing. Less resistance to flow into peripheral areas is thus provided, but it becomes necessary to step down arterial flow and pressure in the relatively smaller vascular compartment here provided by the arterioles. It is perhaps not coincidental therefore that the rhythmical contractility seen in patagial arterioles (with a relatively small total cross-section) becomes extremely prominent, particularly at the level of precapillary sphincters.

The low pressure side of the vascular exchange bed (fig. 2) includes the venules (the so-called 'venous capillaries'). It is therefore far more extensive in bat wing than in dog mesentery. Increased potential area for resorption of interstitial fluids directly into the venous system might thereby be provided in a bat at rest if the downstream action of the contractile veins (with a relatively large total cross-section) tended to empty the venules. In flight however, at least with engorged capillary beds, a similar effect would seem at best to be capable of compensating somewhat for, paradoxically, a relatively greater fluid loss to the interstitium in a situation already favorably disposed toward edema. However, the accompanying lymphatics can likewise act over this expanded region and in themselves exhibit marked morphological specializations at their distal terminations as well as remarkably pronounced active rhythmic vasomotion. One wonders whether the implied high turnover of interstitial fluid in the wing during flight might be of advantage to a bat for such needs as thermoregulation.

A far greater proportion of venous volume of the bat wing is in small veins as opposed to larger ones (figure 2). Such a relationship seems entirely reasonable in terms of the energetic economy of a system in which blood must be returned toward the heart against centrifugal forces generated in flight, and over relatively long distances in any case; a higher intraluminal pressure can be generated by a given wall tension in a smaller vessel.

How important are the rhythmically active veins to the bat, relative to the other factors considered thus far? Like so much of the foregoing discussion, any rational answer to this question must remain a matter of speculation pending further experimental information. There is reason to believe that species differences can be considerable. And we must appreciate that present evidence has been obtained either from the passively outstretched wings of immobilized animals or from isolated vessels in vitro. It is known, for example, that intraluminal pressures in these veins can approach those in the arteries. On the other hand, I know of no attempts to assess actual pressures experienced by bat wing vessels during flight, against which to compare available in vivo and in vitro findings. Such data are sorely needed to better evaluate the overall contribution of active, rhythmic venous vasomotion to the total hemodynamic equilibrium of the wing.

A clearly effective neurogenic control over vascular tone has to date been demonstrated only in the larger arteries of the bat wing membranes. The vasomotion in the rhythmically contractile veins appears essentially myogenic, perhaps to a unique degree. The degree of nervous control over the shunt veins, digital arteriovenous anastomoses and vessels in the limbs proper is to my knowledge unknown. It might well be that a more rigorous comparison of such parameters in the bat might provide us with a far greater insight into factors which favor neurogenic as opposed to myogenic control of certain components of the cardiovascular system, and the ensuing advantages which thereby accrue to the total welfare of a successful organism. (For further discussion and references see Kallen, Biology of Bats, vol. III, chapter 3. Academic Press, New York 1977).

Functional characteristics and physical limitations of the active venous pulse in the bat wing: The effects of pressure and temperature

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Almost a century has past since Luchsinger[1] attempted to examine flow in the bat wing by perfusing it with bovine blood. Since then, the subcutaneous wing vessels of the bat have become a classic model for the investigation of rhythmically active myogenic activity in small blood vessels. In this model, the metarterioles and precapillary sphincters (whose cells are not contiguous) exhibit an asynchronous rhythmic form of vasomotion which stems from the activity of independent pacemaker units, the location of whose focus may, possibly, vary from time to time. On the other hand, the larger veins and venules, which possess continuous muscle coats and are capable of cell to cell propagation, display a more synchronized myogenic pattern of activity which is limited to well-defined independent functional units lying between 2