Comments on Flow through Collapsible Tubes at Low Reynolds Numbers

In a recent paper by Lyon et al. (Flow through Collapsible Tubes at Low Reynolds Numbers. Circ Res 47: 68-73, 1980), the authors contend that waterfall models adequately predict flow through a Starling resistor only for Reynolds numbers ≤1. Their basic conclusion was that caution should be used when applying waterfall models to the mammalian circulatory system since Reynolds numbers are usually greater than 1 in most blood vessels.

This paper points out what I feel has long been a common misconception: that is, failure to distinguish the basic difference between the waterfall model and the Starling resistor. A Starling resistor is a pressure-regulating system which maintains the pressure proximal to a constriction at a constant value. The maintenance pressure is independent of the flow rate (see panel A of Fig. 1). The only equation describing the Starling resistor model is that $P_s$ equals a constant. This system cannot control flow through the tubing system. When a Starling resistor is connected to a flow source, flow will be determined by the source impedance rather than by the Starling resistor.

The waterfall model differs in that a resistance to flow exists proximal and in series with the Starling resistor (see panel B in the figure). Flow is regulated in a waterfall system since a fixed pressure difference ($P_m-P_s$) exists across a fixed resistance, $R$. In an organ, the Starling resistor becomes the collapsible veins at the distal end of the vascular bed, while the proximal resistance is represented by the capillaries and the arterioles. The graph in the lower panel of the above figure shows the behavior of flow in each of these systems as $P_m$ is varied. In the Starling resistor, $P_m$ is forced to equal $P_s$ at all flows and thus, a horizontal flow line results. Again, note that no functional relationship exists between flow and $P_m$, while on the other hand, flow is a definite function of $P_m$ for the waterfall model.

Because Figures 3 and 4 of the study by Lyon et al. did not correspond to the theoretical curves which describe a waterfall model, the authors concluded that the waterfall model was inappropriate at high Reynolds numbers. I believe, however, that the reason for this nonconformity between theory and empirical data has little to do with the magnitude of the Reynolds number.

First, the curves in Figure 3 and 4 did not demonstrate any slope. This resulted because the author's experimental model did not include a significant series resistance which is the definition of a waterfall model. As the authors reported, the resistance to flow of the patent Penrose tubing was negligible when perfused with water. Only when the viscosity was increased to the point at which the resistance of the segment of tubing upstream of the region of collapse became appreciable (their Fig. 5), did any slope become apparent.

To prove that viscosity and not the Reynolds number was involved, I invite the authors to repeat the experiments taking pressure measurements proximal of $R$, in their Figure 2 rather than distal. If this is done, then the series resistance characteristics of the waterfall model will be met. Then the curves will have parallel slopes, as shown in their Figure 1, with projected intercepts at $P_s-P_e$ for all Reynolds numbers examined.

The authors also failed to observe the sharp zero intercepts which are predicted by the waterfall model at high Reynolds numbers. This non-conformity occurs because Penrose tubing will not completely collapse in response to an external pressure. Rather, it retains small, patent side channels as the authors noted. Veins, which are much more flaccid, do completely collapse. Thus, it is as if there was a patent shunt around the region of collapse in their model which caused the pressure to bleed off as flow was lowered. The dotted lines on my graph show the effect of such a shunt. The lower the

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**Figure 1** Upper panel shows the difference between A, the Starling resistor and B, the waterfall model. The equations describing each of these appear at the right. The solid lines in the lower panel are a plot of flow against perfusion pressure for both models. The broken lines demonstrate the effect of a resistive shunt across the region of collapse for either model.
resistance of the shunt, the greater the effect. When viscosity of the fluid was increased in the study by Lyon et al., the resistance of the shunt was simply increased until it no longer contributed a significant effect. Had the authors used a tubing which had better collapse characteristics in their experimental model, such as a vein, this feature of the curve would not have been observed. Again, viscosity, not Reynolds numbers, was involved.

In actuality, the Lyon et al. study yielded data which were exactly as predicted by theory for all Reynolds numbers studied. In fact, their data further verified the hemodynamic theory of collapsible tubes, since their Figures 3 and 4 demonstrate excellent pressure regulation even at high Reynolds numbers. Their only problems were (1) failure to provide a proximal resistance as required for a waterfall model, and (2) failure to account for shunt flow.

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Reply to the Preceding Letter

Perhaps Dr. Downey misunderstood the aim of our paper. We specifically stated that previously observed discrepancies (Conrad, 1969; Katz et al., 1969; and Moreno et al., 1969) between the pressure-flow relationships of the Starling resistor model and the waterfall model are:

1. The waterfall model predicts total collapse of the blood vessels and absence of blood flow whenever tissue pressure (pressure external to the vessel) is greater than inflow pressure. Total collapse and cessation of flow never was observed in the Starling resistor model by these authors.

2. Self-induced oscillations of the vessel, neither predicted by the waterfall model nor observed in the microcirculation, were prominent in the Starling resistor model.

We did not state that these differences are due to the slope of the curves, as Dr. Downey seems to have inferred.

The flow through small patent side channels, referred to by Dr. Downey as "shunt flow," is well documented for the Starling resistor model, and it is generally agreed that this phenomenon is dependent on compliance of the Penrose tubing (Conrad, 1969; Katz, 1969; Kresch and Noordergraaf, 1972). The self-induced oscillations are also well known. All of the tubing of different materials that we tested exhibited at least one of the above properties (1 and 2) with high Reynolds number flow, but there is the possibility that highly compliant tubing which does not possess these properties may exist. On the other hand, there really is tubing that exhibits properties (1) and (2) and so does not follow the waterfall model. These are the reasons that we state in our paper that the waterfall model cannot be applied indiscriminately to high Reynolds number flow. However, our main point is that when the Reynolds number is low enough to simulate the microcirculation, elastic properties, tube sizes, and method of mounting become insignificant and the waterfall model definitely applies to all collapsible vessels.

Dr. Downey states that the waterfall model requires an upstream resistance in addition to the Starling resistor. We disagree. The waterfall model and the Starling resistor have long been considered synonymous by researchers in this area. The waterfall model was originally presented as a set of mathematical equations by Dr. Solbert Permutt (Permutt et al., 1962) at the Fifth Annual Conference on research in Emphysema. The participants at this conference regarded the two terms, waterfall model and Starling resistor, as the same, and this usage continues (Lopez-Muniz et al., 1968; Green, 1975).

Dr. Downey suggested that if our experiments were repeated while measuring the pressure proximal to an upstream resistance, our results for high Reynolds numbers would conform to the predictions of the waterfall model. This experimental work is not necessary since we can easily calculate the new pressure-flow relationships by the following method:

Let \( P_i \) be the pressure proximal to the upstream constant resistance \( R_i \). Then the formula \( P_i'' - P_i = Q R_i \) applies. Using this equation, Figure 3 (Lyon et al., 1980) can be plotted as \( P_i'' - P_s \) vs. \( Q \), as shown in the diagram (our Fig. 1).

The slopes of the curves of Figure 3 have been increased, but the experimental discrepancies (1) and (2) discussed previously still remain. Thus, adding an upstream resistor does not result in the waterfall model.

Dr. Downey seems to imply that the effects of viscosity are not related to the effects of the Reynolds number. This is not true. Elementary texts of fluid dynamics show that, especially in modeling theory, the Reynolds number is the measure of viscosity (e.g., Shames, 1962). For any fixed flow...
rate and tubing diameter, the Reynolds number is inversely proportional to viscosity. In our experiments, as viscosity was increased. The plateau region of our curves demonstrates these slopes, as expressed by Equations 11 and 12. Dr. Downey states that the equation for flow through a Starling register is \( P = \text{a constant} \). His is an idealized model, while the graphs we show exemplify real experimental results with the Starling resistor.

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References
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