Blood pressure and flow rate in the giraffe jugular vein

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SUMMARY

Experimental measurements in the jugular veins of upright giraffes have shown that the internal pressure is somewhat above atmospheric and increases with height above the heart. A simple model of steady viscous flow in an inverted U-tube shows that these observations are inconsistent with a model in which the blood vessels in the head and neck are effectively rigid and the system resembles a siphon. Instead, the observations indicate that the veins are collapsed and have a high resistance to flow. However, laboratory experiments with collapsible drain tubing in place of the down arm of the U-tube show internal pressure to be exactly atmospheric and uniform with height. A model of viscous flow in a collapsible tube with non-uniform properties is used to suggest that the observed pressure distribution may be a consequence of the intrinsic cross-sectional area and/or compliance of the veins increasing with distance towards the heart, or the external, tissue pressure falling. Finally, the effect of fluid inertia on steady flow in vertical collapsible tubes with uniform intrinsic properties is analysed, and it is shown that a phenomenon of flow limitation is theoretically possible, in which the supercritical flow in the collapsed vein cannot return to the presumably subcritical flow in the open vena cava, even with the help of an 'elastic jump', if the flow rate is too large. The computed critical flow-rate, of about 80 ml s^{-1}, is about twice the flow-rate estimated to be present in the normal giraffe jugular vein. If there were circumstances in which flow limitation occurred in the jugular veins, it would mean that the cerebral blood flow would be limited by downstream conditions, not directly by local requirements.

1. INTRODUCTION

The cardiovascular system of the giraffe is of interest because of the large range of intravascular pressures caused by the gravitational pressure gradient in an upright animal. The mean central aortic pressure in a 4 m animal is 250 mm Hg (33 kPa) (Goetz & Keen 1957) so the mean arterial pressure in the head is 75 mm Hg, and in the feet it is 400 mm Hg (53 kPa). (Please note that all pressures quotes here are taken relative to atmosphere.) One might ask why the pressure generated by the heart needs to be so high, as a higher pressure P_a at the root of the aorta has at least two disadvantages. There are both a greater tendency to oedema in the feet, which has to be countered by anatomical and physiological adaptations such as tight skin and fascia in the legs (an 'anti-gravity suit'; Hargens *et al.* 1987), and greater energy demands on the left ventricle: if the mean volume flow rate (cardiac output) is Q, the work done by the ventricle per unit time is

$$W = P_a Q. \qquad (1)$$

Hence a greater muscle mass is required: heart mass is 2.3% of body mass in giraffes, compared to about 0.5% in other mammals (Mitchell & Skinner 1993; see also Goetz *et al.* 1960) with a correspondingly greater oxygen requirement.

Burton (1965) pointed out that, in principle, 'it is no harder, in the circulation, for the blood to flow uphill than downhill' and it has consequently been suggested that a siphon mechanism may operate in the head and neck of upright man and, *a fortiori*, in the giraffe (Badeer & Rietz 1979). By permitting flow to be maintained without an exceptionally high left ventricular or aortic pressure, this mechanism could account for the fact that P_a does not change significantly in man with a change in posture (Burton 1965), though there is some change in the giraffe (Goetz *et al.* 1960) (in both cases baroreceptor reflexes also presumably act to moderate changes in P_a). The fact that P_a in the giraffe is so much higher than in man, however, suggests that the siphon mechanism cannot be the whole story, and that the heart has to pump the blood uphill to the head, for some reason. Whether or not the siphon mechanism operates has led to considerable controversy in the literature (Pedley 1987; Seymour & Johansen 1987; Badeer & Synolakis 1989; Hicks & Badeer 1989, 1992; Seymour *et al.* 1993).

One of the arguments against the siphon mechanism is the fact that the giraffe jugular vein is normally partly collapsed, as indicated both by direct observation (Goetz *et al.* 1960) and, especially, by inference from measurements of intravascular pressure which is positive and increasing with height above the heart (Hargens *et al.* 1987), not negative and decreasing as the gravitational gradient and the siphon concept would lead one to expect (Pedley 1987).The measurements of Hargens *et al.* (1987) show the internal pressure to be about 7 mm Hg at 0.3 m above the heart, rising to 16 mm Hg at 1.2 m above the heart. If the vein were an uncollapsed cylinder, of diameter 2.5 cm, the measured pressure distribution would require an absurdly high flow rate of $27\,\mathrm{l\,s^{-1}}$, by Poiseuille's Law; the necessary increase in resistance can be achieved only if the vessel is collapsed. Laboratory studies using highly collapsible tubes (Hicks & Badeer 1989) show internal pressure to be uniformly zero i.e. atmospheric. That this is approximately true for the human jugular vein has also been well-known for many years (Guyton 1962). The purposes of this paper are therefore twofold: (i) to present a firmly based theoretical framework in which the laboratory experiments in physical models (which we have repeated; Seymour *et al.* 1993) can be clearly understood, incidentally showing that the siphon is not a helpful analogy; and (ii) to seek a possible explanation for why the pressure distribution measured in the giraffe jugular vein is not the same as in a highly collapsible tube in the laboratory. It will become clear that a final decision on the full explanation must await further anatomical and physiological measurements on giraffes. There will finally be a discussion of the previously neglected effect of blood inertia which, it is suggested, may lead to the phenomenon of flow limitation, implying that in some circumstances it is conditions in the jugular veins, not in the skull or the heart, that may limit cerebral blood flow.

2. THEORY AND MODEL EXPERIMENTS

Following Hicks & Badeer (1992) we base the discussion on the Poiseuille-like equation linking the flow rate Q through a tube to the gradient in pressure and height along the tube. In a long, straight, uniform tube, the pressure P and height z above a given reference level vary linearly with distance, x, measured

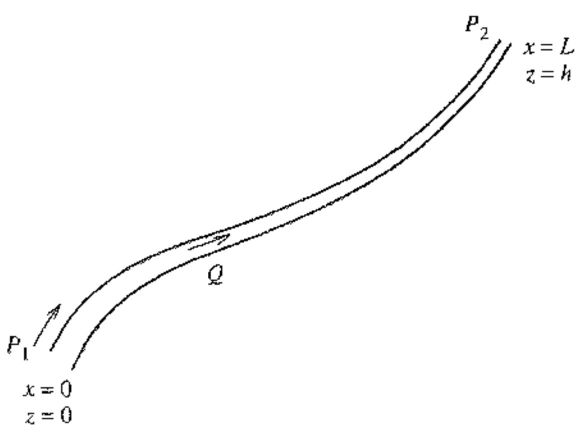

Figure 1. Sketch of a tube of length L with steady flow rate Q through it. The pressures at the two ends are P_1, P_2; x is distance along the tube; z is height above the left hand end.

along the tube in the direction of flow, and their gradients are related to the flow rate by:

$$\mathrm{d}/\mathrm{d}x(P+\rho gz) = -RQ, \tag{2}$$

where ρ is the fluid density (assumed constant), g is the gravitational acceleration, and R is the viscous resistance to the flow per unit length of tube. For a circular tube of uniform cross-sectional area A, the resistance is given by:

$$R = 8\pi\mu/A^2, \tag{3}$$

where μ is the fluid viscosity (Caro *et al.* 1978). If the tube is non-circular, equation (3) cannot be used, but R will still increase as A decreases. Even if the tube is neither straight nor uniform (figure 1), equation (2) can still be used to relate the gradients in P and z to Q as long as the bends and the variations in resistance are sufficiently gradual, or occupy a sufficiently short length of tube, and as long as fluid inertia can be neglected.

When inertia cannot be neglected, a term equal to $1/2\,\rho u^2$ must be added to the expression inside the bracket of equation (2), where $u = Q/A$ is the average velocity of fluid in the tube. In that case equation (2) may be called the Bernoulli-Poiseuille equation (Badeer & Synolakis 1989). We neglect inertia in the subsequent discussion, until at the end of the paper we enquire into its possible effects.

If the tube of figure 1 has uniform cross-section (and hence resistance) the pressure difference between the ends, obtained by integrating equation (2), is given by

$$P_1-(P_2+\rho gh) = LRQ, \tag{4}$$

where L is the length of the tube and h is the height of the downstream end (where $P = P_2$) above the upstream end ($P = P_1$).

We now apply equation (4) to a possible experiment on flow through an inverted U-tube (figure 2*a*). The tube is rigid and of uniform cross-sectional area A and, hence, uniform resistance R. One end, at level $z = 0$, is supplied with fluid by means of a pump which generates pressure P_1 and delivers a flow rate Q; the other end enters a tank that is open to atmosphere, so the pressure there, P_3, is zero, and is also at level $z = 0$. The total length of the tube is taken to be $L+h$; we shall pay particular attention to the pressure, P_2, at a point 2 in the downflow side of the U-tube, at height $z = h$ and distance L (measured along the tube) from the entrance. Applying equation (4) twice, once to the whole tube and once to just the first length L, we obtain

$$P_1-P_3 = (L+h)\,RQ \tag{5}$$

$$P_1-(P_2+\rho gh) = LRQ \tag{6}$$

and we recall that $P_3 = 0$. We deduce from equation (5) that flow can occur whenever P_1 is positive and then, combining equations (5) and (6), we find that

$$P_2 = h(RQ-\rho g) = h[P_1/(L+h)-\rho g]. \tag{7}$$

Thus P_2 will be negative, i.e. subatmospheric, unless P_1 is very large, exceeding $\rho g(L+h)$. Such a system is a siphon, characterized by a positive flow whenever P_1 is positive and by subatmospheric pressure up in the arch of the U-tube.

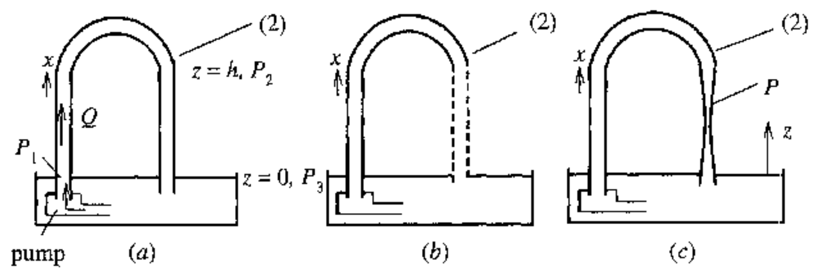

Figure 2. Sketch of possible experiments with an inverted U-tube, supplied with flow rate Q by a pump at $z = 0$ generating pressure P_1. The point (2) is at height $z = h$ and the pressure there is P_2; the pumped fluid is collected in a reservoir at level $z = 0$, where pressure is atmospheric, P_3. (*a*) Complete rigid tube; P_2 is subatmoshperic. (*b*) Tube is cut off at (2); P_2 is atmospheric. (*c*) Tube replaced by collapsible drain tubing below (2); P_2 is atmospheric. (See text for explanation).

Now consider what happens when the length h of tube below the point 2 is cut off, so that the fluid (when flowing) falls freely into the receiving tank below (figure 2*b*). Equation (6) still applies to the remaining length L of the tube, but now P_2 is necessarily atmospheric i.e. zero. It follows immediately that flow is possible only if P_1 is greater than ρgh, and when it is the flow rate is given by equation (6) not equation (5). Thus: (i) the pump has to push the fluid 'uphill' to a height h before flow can occur; and (ii) the flow rate is independent of the depth below point 2 at which the receiving tank is placed. In this sense the system is behaving like a waterfall; it is not a siphon.

Now consider a third experiment, in which the cut-off piece of rigid tube is replaced by a length h of highly collapsible tube such as dialysis tubing (figure 2*c*). Once more, equation (6) determines the relation between $P_1 - P_2$ and Q. The only question is, what is P_2? Here we rely on the results of an earlier laboratory experiment, using this configuration, by Hicks & Badeer (1989), and repeated by Seymour *et al.* (1993). Hicks & Badeer measured the internal pressure at several locations within the vertical collapsible tube, while there was flow through it, and found it to be zero everywhere, to within experimental error (see their figure 3). Thus P_2 is zero, as in the previous example, and it follows immediately that the system does not act as a siphon, that P_1 must exceed ρgh, and that the flow-rate, determined from equation (6), is independent of what is happening downstream of the point 2, including the depth of the receiving tank. In this sense the system again resembles a waterfall; it was just such an analogy that led Permutt *et al.* (1963) to coin the phrase 'vascular waterfall' in the context of the pulmonary circulation.

Of course, the fluid flowing in the collapsible tube below the point 2 is not in free fall, otherwise it would be accelerating, so the system is not identical to a vertical waterfall. In fact the downflow of the fluid is resisted by viscous forces. Hicks & Badeer (1989) observed that the collapsible tube was uniformly collapsed i.e. that the cross-sectional area was (to within observational error) uniform and small; we have made the same observation (Seymour *et al.* 1993). Suppose that the cross-sectional area is A_c, and the corresponding resistance is R_c. What determines these quantities, in the experiment? If we apply equation (4) to the difference between the pressure P at height z and the pressure P_3 at height zero, we obtain:

$$P + \rho gz - P_3 = zR_c Q. \tag{8}$$

The experimental observation is that both P and P_3 are zero. Hence equation (8) gives

$$\rho g = R_c Q. \tag{9}$$

But Q is already known, because equation (6) gives:

$$Q = (P_1 - \rho gh)/LR, \tag{10}$$

so equation (9) tells us that R_c must take the particular value $\rho g/Q$. As P_1 is varied, so Q will vary and R_c must vary too. Because the highly collapsible drain tube cannot support a significant transmural pressure difference, so that P is zero as observed, its cross section must automatically adjust itself so that the viscous resistance exactly balances the driving force of gravity, whatever the flow rate.

Finally we consider a fourth model experiment, also performed by Hicks & Badeer (1989) and repeated by us, in which the collapsible segment of tube was turned to lie horizontally on a flat surface at approximately the level of point 2. According to the above theory, the flow rate Q and the value of P_1 should not be affected by this change, although the details of flow in the collapsible segment will be affected. Hicks & Badeer reported an increase of 12% in P_1 and 15% in the work done, but this is attributable to entry conditions causing a change in the height of the location at which tube collapse began i.e. part of the vertical tube was less collapsed than the rest and therefore had lower resistance. When this change was avoided, in our experiments, the increase in P_1 was abolished.

The above discussion (we believe) clarifies the factors determining the flow rate and pressure distribution in the tubes which make up the simple model experiments. However, a number of questions remain unanswered. The three main ones are: (i) What is the explanation for the observed fact that the internal pressure in the vertical segment of collapsible tube (figure 2*c*) is everywhere zero? (ii) What has any of the above to do with the giraffe jugular vein, and in particular why does the internal pressure increase with height? (iii) Is inertia negligible and what might its effect be if not? Question (ii) is clearly the most important one, but a previous investigation of (i) will help set the scene for a profitable discussion.

3. ELASTIC PROPERTIES OF COLLAPSIBLE TUBES

Figure 3 shows a graph of the experimentally measured transmural pressure difference (internal pressure P minus external pressure P_e) against cross-sectional area A for a uniform piece of latex rubber drain tubing (Shapiro 1977). When the transmural pressure is positive, the tube cross-section is circular and has low compliance (i.e. a large increase in $P-P_e$ is needed for a given increase in A, so the slope of the curve is high) because, for the cross-sectional area to be increased, the circumference of the tube must be stretched. However, below a critical value of $P-P_e$, close to zero, the cross section ceases to be circular and starts to collapse. Now the tube is extremely compliant, because a change in cross-sectional area requires only that the tube wall can change its curvature without an overall circumference change, and drain tubing has such a thin wall that bending is very easy. Only when the tube is highly collapsed does its compliance fall again, because then opposite sides of the tube are in contact everywhere except for two small tunnels at the edges, and it takes a considerable pressure difference to close the tunnels off completely. The central region of high compliance occupies a very narrow band of transmural pressure values (marked ε in figure 3), very close to zero.

In the experiment of figure 2*c*, the external pressure P_e is atmospheric i.e. zero.

1. Let us suppose first that P_2, the pressure at the top of the collapsible segment, is significantly greater than zero. Thus the tube will be circular and its resistance much lower than when the tube is collapsed (see point (i) on figure 3). In this case equation (2) becomes:

$$\mathrm{d}P/\mathrm{d}x = \rho g - RQ, \tag{11}$$

because x, the distance measured along the tube, is directed downwards whereas z is measured upwards.

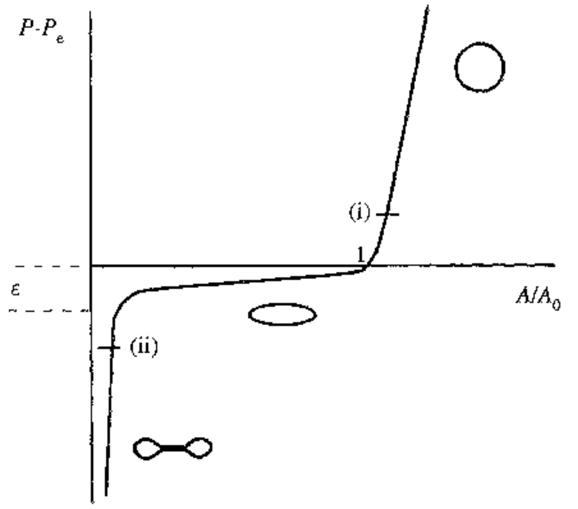

Figure 3. Sketch of relation between transmural pressure $P-P_e$ and cross-sectional area A (the 'tube law') for drain tubing. A_0 is the area at zero transmural pressure. Cross-sectional shapes are shown at different parts of the curve. See text for further explanation.

The low resistance, coupled with the fact that Q is somewhat below the value given by equation (10) because P_2 in equation (6) is greater than zero, means that $\mathrm{d}P/\mathrm{d}x$ will be positive. Thus P, and hence A, will increase with distance down the tube, and this situation is inconsistent with the fact that P must fall to zero at the bottom of the collapsible tube.

2. Similarly, if P_2 is significantly subatmospheric (point (ii) in figure 3), the cross-sectional area will be tiny, the resistance very high and the flow rate greater than the value given by (10). In this case $\mathrm{d}P/\mathrm{d}x$ will be negative, the pressure will fall further, and again this is inconsistent with P rising to zero again at the bottom. It follows that the transmural pressure must lie in the narrow band ε of figure 3, or in other words the internal pressure P, and hence $\mathrm{d}P/\mathrm{d}x$ too, must be everywhere close to zero. The thinner the tube wall, and hence the flatter the middle section of the curve in figure 3, the closer to atmospheric pressure will be the internal pressure. This explains the experimental observations of Hicks & Badeer (1989) and of Seymour *et al.* (1993).

4. RELEVANCE TO THE GIRAFFE JUGULAR VEINS

We must now discuss the relevance of the model experiments with collapsible tubes to the problem of venous return from the head of the giraffe. Various points must be considered.

1. The rigid part of the U-tube is proposed as a model for the carotid arteries and the intracranial vascular system in the head, with the point 2 (figure 2) representing the exit from the skull of all the parallel veins there, feeding into the jugular veins. Although the cross section is not uniform, the vessels are thought to be distended and therefore stiff, as in figure 3: the carotid arteries remain distended because of the high intravascular pressure; even the veins within the skull remain distended because the skull acts as a constant volume chamber filled with incompressible material, so if a vessel starts to collapse, the pressure in the space outside it falls rapidly, preventing further collapse. Thus the resistance of the whole system up to point 2 will remain approximately constant in time, as represented by the quantity RL in the above equations.

2. The anatomy of the venous system is not as simple as the model suggests, for two reasons. First, there may be alternative pathways for venous return from the head, not just the jugulars, such as the vertebral plexus, thought by Falk (1990) to have been an important pathway for venous return in robust australopithecine man, for example. Data on the vertebral plexus, and how much flow it might take, are not available for the giraffe. The model would be affected by the presence of such a parallel system of venous return only if the fraction of the flow occupying the jugulars routinely changed with time in the upright animal, so that the mean flow rate in the jugulars could not be assumed constant, and if the parallel veins were prevented from collapsing. Then this part of the system would behave like a siphon, and very little flow would pass down the (collapsed) jugular veins.

Second, the neck of a giraffe contains a large volume of tissue which is perfused by a vessel system that does not pass through the skull. Smaller veins feed into the jugulars all the way down their length so neither the flow rate nor the (uncollapsed) cross-sectional area, nor the vessel wall thickness and hence its intrinsic compliance, need be regarded as uniform. Some of these features are incorporated in a modified model below.

3. In addition, there is no *a priori* reason to assume that the effective external or perivascular pressure, P_e, around the jugular veins of a giraffe is uniform and equal to atmospheric. Indeed, for the vein to be (partly) collapsed at any level P_e must be equal to or greater than the internal pressure at that level (see figure 4 below). Now, the skin on the neck is around 1.5 cm thick, and this could sustain a substantially raised (or lowered) interstitial fluid pressure, P_t. However, the measurements of P_t by Hargens *et al.* (1987) suggest a value that is approximately uniform, and is normally close to atmospheric (average value = 1 mm Hg; maximum recorded value about 6 mm Hg, minimum slightly negative). There must, in addition, be a structural component of perivascular pressure which is positive. In part this may come from solid elements in the interstitial gel which, if unconfined, would absorb more water and swell. There also may be structural elements which transmit force directly from tight skin, or muscles or tendons, to the blood vessels, though these have not been identified. If so, such elements could well generate a gradient in P_e. Guyton *et al.* (1981) estimate that the total effective perivascular pressure is normally positive, by about 1 mm Hg, in human beings, but it could well be larger in the thick-skinned giraffe.

4. Finally, the relation between transmural pressure and cross-sectional area in blood vessels *in situ*, although still sigmoidal, is significantly different from that for latex tubing. Figure 4 shows the difference schematically for thin-walled latex tubes (Moreno *et al.* 1970; Shapiro 1977), for thin-walled veins (Moreno *et al.* 1970; Morris *et al.* 1974) and for thick-walled latex tubes (Bertram 1987). In each case, the cross-sectional area A is scaled by its value A_0 at zero transmural

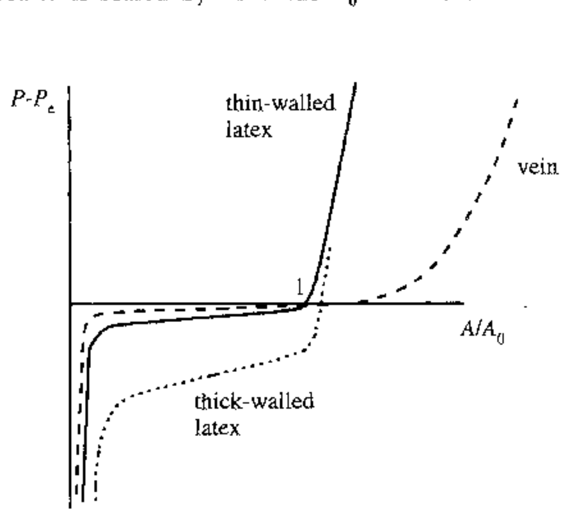

Figure 4. Different types of tube have different tube laws, as indicated schematically here.

pressure. At values of A/A_0 greater than 1, the latex tubes are very much stiffer than veins, reflecting a much larger value of the intrinsic stiffness, K_p, defined in Appendix 1. In their experiments, Moreno *et al.* (1970) used a thin-walled latex tube with $K_p = 143$ Pa and a segment of canine inferior vena cava with $K_p = 0.2$ Pa. As A/A_0 falls to 1, there is a sharp corner in the curve for the thin-walled latex tube and it becomes approximately as compliant, during collapse, as the vein. The venous curve varies much more smoothly and the slope does not become steep until a much larger value of A/A_0 is reached (Moreno *et al.* 1970; Morris *et al.* 1974). Note that the corner for a thick-walled latex tube occurs at a substantially negative transmural pressure difference, reflecting the difficulty of bending the tube wall. The presence of surrounding tissue, for veins, is likely to act like an increase in wall thickness, shifting the pressure-area curve downwards, together with a moderate increase in stiffness, but overall the change in transmural pressure per unit change in cross-sectional area is still expected to be more gradual than for latex tubes, especially for positive values of transmural pressure.

The average pressure gradient down the jugular vein is $dP/dx = -0.1$ mm Hg cm^{-1}, which is -13 Pa cm^{-1} (Hargens *et al.* 1987). To make quantitative estimates we must estimate the average flow rate in one jugular vein (at the top, say); we take it to be $Q = 40$ ml s^{-1}, comparable to that in the carotid artery (Van Citters *et al.* 1968; Mitchell & Skinner 1993). If the jugular vein is uniform, then equation (11) can be used to show that this flow rate with the measured pressure gradient would correspond to a resistance of $R = 2.8$ Pa s cm^{-4}. Because the viscosity of mammalian blood is a factor of 3.9 greater than that of water, equation (3) shows that the cross-sectional area of the vein would, if circular, have to be 0.19 cm^{-2}, corresponding to a diameter of 0.49 cm instead of the 2.5 cm diameter of an undeformed vein (Goetz *et al.* 1960). Thus the vein must indeed be severely collapsed. (Of course, the collapsed vessel would not remain circular, so the formula relating cross-sectional area to resistance would be more complicated than equation (3). A calculation based on the assumption of an elliptic cross section with major axis equal to 2.5 cm leads to an estimate of collapsed cross-sectional area equal to 0.43 cm^2 and minor axis equal to 0.11 cm; see Pedley (1980) for the relevant formulae.) An alternative way of looking at it is to note that, as stated in the introduction, the pressure gradient of 2.8 Pa s cm^{-4}, added to gravity, corresponds to a flow rate of 27 l s^{-1} in a circular tube of diameter 2.5 cm; the resting cardiac output of a giraffe is about 40 l min^{-1} (Goetz *et al.* 1960).

In the light of the above considerations, the previous theoretical model, applicable to the laboratory experiments on uniform thin-walled tubes, should be modified to allow for the variation with distance down the jugular vein of: uncollapsed cross-sectional area, effective vessel wall compliance, external pressure, and flow rate. An appropriate description of the vessel wall is outlined in Appendix 1.

The fluid dynamics of the blood in the vein is again given by equation (11), assuming that the effect of blood inertia is still negligible, so the observation that P is above atmospheric at point 2, and falls uniformly with distance down the vein ($dP/dx < 0$) requires that RQ should exceed ρg and should remain approximately constant. Now Q will, if anything, increase with distance down the vein (see point 2 above) so R will remain constant or decrease with distance. Thus the cross-sectional area must remain constant or increase with distance. As explained above, this is inconsistent with a fall in P if P and A are related by the same curve, as in figure 4, all the way down the vein, because a fall in P would have to be accompanied by a fall in A. However, the variation along the vein of its elastic properties mean that the $P-A$ relation varies with position, with the result that it is possible for the cross-sectional area to remain constant or rise while the internal pressure P is falling. Equation (1.3) from Appendix 1 shows that:

$$\frac{dA}{dx} = \alpha\frac{dA_0}{dx}+\frac{A_0}{K_p F'(\alpha)}\left[\frac{dP}{dx}-\frac{dP_e}{dx}-F(\alpha)\frac{dK_p}{dx}\right], \qquad (12)$$

where A_0 is the undistorted cross-sectional area of the vein, K_p is a measure of its wall stiffness, P_e is the external pressure, α is the ratio of actual area A to A_0:

$$\alpha = A/A_0, \qquad (13)$$

and $F(\alpha)$ is a function describing the shape of the pressure-area relation of the tube, called the 'tube law' (see figure 4). It follows from equation (12) that it is possible for dA/dx to be zero or positive while dP/dx is negative, as long as at least one of the following conditions is satisfied (note that the factor $A_0/K_p F'(\alpha)$ is always positive).

1. $dA_0/dx > 0$: as explained in point 2 above, it seems highly likely that the undistorted cross-sectional area of the vein will increase with distance, to accommodate an increase in flow-rate, but more morphological data are required.

2. $dP_e/dx > 0$:as explained in point 3 above, this is quite likely to be the case but there is no direct supporting evidence, the measured interstitial fluid pressure being uniform.

3. $F(\alpha)dK_p/dx < 0$: the function $F(\alpha)$ is positive when the internal pressure exceeds the external, by definition (see figure 4), so this condition reduces to $dK_p/dx < 0$ i.e. the effective compliance of the vessel wall increases with distance down it. No relevant data are available to indicate how the compliance of the giraffe jugular vein varies along it; such data should be sought.

The above considerations show that a fall in internal pressure with distance down the vein can be consistent with the fluid dynamical requirements represented by equation (11) as long as the intrinsic cross-sectional area and/or compliance of the vessel increase as the heart is approached, or the external pressure falls. Further measurements of the properties of the giraffe jugular vein are, however, required before we can be certain that the above is the explanation for the observed pressure variation in that vessel. Moreover, the hitherto neglected effect of fluid inertia may be important.

5. EFFECT OF INERTIA

The word 'inertia' represents the fact that forces have to be applied to accelerate pieces of matter. Thus if a fluid is accelerated, for example because it is passing from a wide segment of tube to a narrower one, it must experience a favourable pressure gradient or body force (gravity). For steady flow in a gradually varying tube or system of tubes, inertia can be accounted for approximately by adding an additional term to the left hand side of equation (2), as stated above. The equation then becomes:

$$d/dx\,[P+\rho gz+1/2(\rho u^2)] = -RQ, \qquad (14)$$

where $u = Q/A$ is the average fluid velocity. We can thus assess whether inertia is negligible in the giraffe jugular vein by calculating the change in the quantity $1/2(\rho u^2)$ as the flow goes from the uncollapsed segment of vessel to the collapsed portion, and comparing that to the change in gravitational pressure over a comparable length of tube.

It was estimated above that the cross-sectional area of the collapsed giraffe jugular vein is approximately 0.43 cm^2, just less than a tenth of the uncollapsed area. Assuming again that the flow rate is 40 ml s^{-1}, we obtain velocities of 93 cm s^{-1} (collapsed) and 8 cm s^{-1} (uncollapsed). Thus the change in $1/2(\rho u^2)$ in going from the uncollapsed to the collapsed state is about 430 Pa (3.2 mm Hg),the density of blood being close to that of water (10^3 kg m^{-3}). The gravitational pressure gradient, ρg, is 98 Pa per cm, so the inertial effect will be significant if the longitudinal distance over which collapse takes place is around 5 cm or less. If the collapse is very gradual the inertial effect will be insignificant. Laboratory experiments on collapsible tubes show that collapse can occur over a very small distance, even for a thick walled tube (Bertram 1986). It is therefore at least possible that inertia is important.

When inertia is important the behaviour of collapsible tubes can be very dramatic, and the study of collapsible tube flow has generated a large literature (see Shapiro 1977 and references therein; Pedley 1980; Kamm & Pedley 1989). The most dramatic behaviour, involving vigorous self-excited oscillations, is unlikely to occur in a well-tethered vessel such as the jugular vein, but there are significant effects even in steady flow (though 'cervical venous hum' is frequently observed in humans: see Danahy & Ronan (1974) and references therein). Following Shapiro (1977), the basic theory for a tube of uniform intrinsic properties is outlined in Appendix 2.

Here, we briefly investigate the application of that theory to the giraffe jugular vein. In particular we ask whether the collapsibility of the vein can cause flow limitation, as is known to occur in pulmonary airways during forced expiration (Hyatt *et al.* 1958). We take the vein to have uniform properties and to be modelled by the tube law and resistance formulae given in Appendix 3. It is well known that, under normal circumstances, the pressure in the superior vena cava (SVC) is close to atmospheric and, via the tube law, this gives a fixed downstream value, α_d, for the dimensionless cross-sectional area, α. If we take SVC

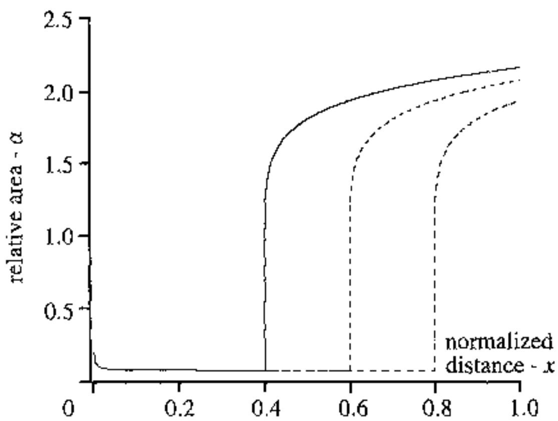

Figure 5. Relative cross-sectional $\alpha = A/A_0$ plotted against fractional distance x along the vein, as computed for three different values of downstream area. The cases considered are those where supercritical flow at small area develops rapidly and an elastic jump is required to achieve the specified downstream condition in each case.

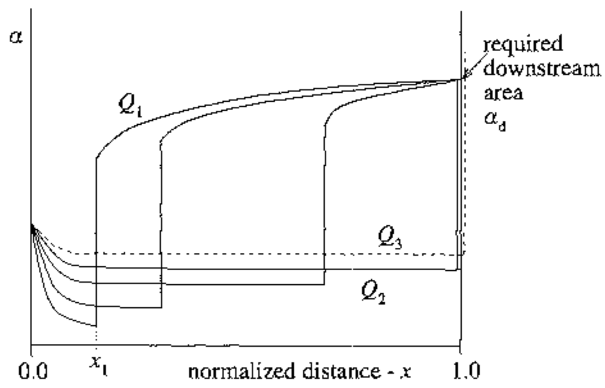

Figure 6. Relative cross-sectional area plotted schematically against fractional distance x along the vein, for various flow-rates Q (all greater than Q^*; see text) and a particular value of downstream area α_d. Here $Q_1 < Q_2 < Q_3$.

pressure to be 1 mm Hg (130 Pa) greater than the external pressure P_e, the (uniform) tube law of equations (1.1) and (3.1) (with $n = 10$) gives $\alpha_d \approx 1.39$. The tube is distended and stiff, and equation (2.2) gives the wave-speed $c(\alpha_d) = 1.16$ m s^{-1}. For each relevant value of the flow-rate Q, which we presume would be determined by the physiological demands of the cerebral circulation, equation (2.5) for α must be solved subject to that downstream boundary condition. We consider a range of values for α at the inlet (α_0).

Appendix 2 reveals the importance of the flow rate Q^* and area α^* at which both viscous resistance balances gravity and the flow is critical (fluid speed = speed at which pressure waves can propagate). For the assumed parameter values, these quantities are 21.4 ml s^{-1} and 0.060, respectively (see figure 9 in Appendix 2). We consider only the case $Q > Q^*$, as our estimate of Q(40 ml s^{-1}) is greater than Q^*; in any case it can be shown that smaller flow rates can be achieved without limitation. From Appendix 2 we know that, for a particular flow rate, the solution of equation (2.5) gives flows which are wholly subcritical or wholly supercritical. The flow at the downstream end is certain to be subcritical, so if the upstream flow is supercritical, then somewhere along the vein there must be a transition, known as an 'elastic jump' (Griffiths 1971; Oates 1975; Shapiro 1977) to return the flow to subcritical velocity. An elastic jump is an abrupt, spontaneous transition between sub- and supercritical flow, analogous to a hydraulic jump (or bore) in shallow-water channels or to a shock wave in gas dynamics. It is accompanied by some loss of mechanical energy and is a way in which rapid, supercritical flows with small cross-sectional area can adjust to higher downstream pressure and area. The location of the jump depends on the precise downstream boundary condition: see figure 5. Thus it is possible to achieve the desired downstream area either with a wholly subcritical flow or with an initially supercritical flow followed by a jump. However, wholly subcritical flows in this case involve a steadily increasing area which does not fit the observation that the jugular vein is collapsed in the upright position. Taking this into account, we focus attention on 'supercritical-jump-subcritical' solutions for this flow regime.

In the supercritical flow α tends to a constant (collapsed) value α_{lim} at which resistance balances gravity. From equation (2.6) we can deduce that α_{lim} is higher for larger values of Q. Figure 6 schematically shows possible solution curves, of α versus distance down the vein, for different values of flow rate Q, all leading to the required downstream area. Starting with a value Q_1 just bigger than Q^*, we see that the area α_{lim} is reached over a small distance from the inlet. In order then to reach the required downstream area a jump is located at a point x_1 along the vein. The size of the jump is determined from conditions just upstream by the 'jump conditions' given by Griffiths (1971), Oates (1975) or Shapiro (1977). If the jump is located before this value x_1 then the area at the outlet would be greater than the required one, whereas a jump located beyond x_1 would give a smaller outlet area, as seen in figure 5. If the flow rate is further increased, the value of α_{lim} increases and the location of the jump moves further downstream. Eventually a flow rate Q_2 is reached for which the jump has to be located exactly at the outlet to achieve the required outlet area. If the flow rate is increased beyond Q_2 to Q_3, then the required downstream area cannot be reached because even if the jump occurs at the outlet, the resulting post-jump area would be larger than required. Hence for a given downstream condition there is a maximum possible flow rate, Q_2 in our example. This 'flow limitation' phenomenon is somewhat different from that thought to be acting in the bronchi during forced expiration, which is a limitation on sub-, not super-, critical flow (Elad & Kamm 1989). Numerical solution of equation (2.5) for a range of values of downstream area α_d gives the results plotted in figure 7. These results are sensitive to the precise value of α_d; for $\alpha_d = 1.39$, as estimated above, we obtain $Q_2 \approx 83$ ml s^{-1}.

The calculated value of the maximum achievable flow rate Q_2 is only about twice the actual estimated value of jugular venous flow. Given the imprecision of

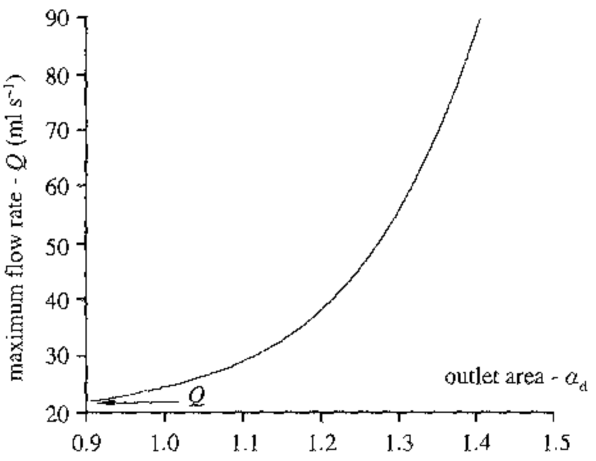

Figure 7. Plot of the computed maximum achievable flow rates against downstream relative area, α_d.

our parameter estimates, this suggests that flow limitation resulting from collapsible tube dynamics could, in some circumstances, govern jugular venous flow in the giraffe, which would then not be controlled by upstream conditions. It would clearly be desirable to obtain more detailed quantitative data on the geometry and elastic properties of the vein, together with measurements of the fluid velocity within it, as well as extending the model to cope with longitudinal variations of P_e or of tube properties such as A_0 and K_p (Shapiro 1977; Elad & Kamm 1989).

Integration of the governing equation (2.5) permits us to estimate the pressure difference between the top and bottom of the giraffe jugular vein. The maximum possible pressure difference, occurring when the flow is supercritical everywhere except for the jump at the downstream end, is predicted to be just under 2 mm Hg (230 Pa). This is considerably lower than the measured difference of about 9 mm Hg (1200 Pa) (Hargens *et al.* 1987). Thus although the answer has the correct sign, the model described in this section and Appendix B does not explain all the observations. As suggested above, it will be important to include longitudinal variations in P_e, A_0 and K_p to hope to achieve quantitative accuracy.

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APPENDIX 1

Description of the pressure area relation of a non-uniform elastic tube

Both theoretical analysis and experiment have shown that the pressure-area relations of elastic tubes of a variety of sizes and wall-thicknesses, but made of the same material, can be described by the following single equation, the 'tube law':

$$P-P_e = K_p F(A/A_0). \tag{1.1}$$

Here P is the internal pressure, P_e is the external pressure, A is the cross-sectional area, A_0 is the undistorted cross-sectional area, at zero transmural pressure ($P-P_e=0$), and K_p is a quantity representing the elastic properties of the material and the wall thickness, and is called the stiffness of the tube (see Shapiro 1977). For a homogeneous elastic material,

$$K_p = [E/12\surd(1-\sigma^2)]\,(h/r)^3, \tag{1.2}$$

where E and σ are the Young's modulus and Poisson's ratio of the material and h/r is the wall thickness-to-radius ratio of the tube when circular and not distended. However, the effect of the surrounding tissue in which a vessel is embedded can also be incorporated into K_p, by increasing the effective value of h/r. Figure 4 shows (schematically) the form of the function $K_p F(\alpha)$, where $\alpha = A/A_0$, for a typical excised vein (Moreno *et al.* 1970; Morris *et al.* 1974) as well as for latex tubes (Bertram 1987; Moreno *et al.* 1970; Shapiro 1977). Note that K_p for a thin walled latex tube is about 30-fold bigger than for a vein of the same wall thickness-to-radius ratio, and that the function $F(\alpha)$ has a significantly different shape for the two types of tube.

To model a tube whose properties vary with distance along it, x, it is necessary merely to allow P_e, A_0 and K_p to be functions of x (it is also possible to let the function F vary independently with x, but we ignore that possibility here). Then, differentiating equation (1.1) with respect to x, we obtain the following equation, from which equation (12) in the text was deduced:

$$\frac{dP}{dx}-\frac{dP_e}{dx} = F(\alpha)\frac{dK_p}{dx}+K_p F'(\alpha)\left[\frac{1}{A_0}\frac{dA}{dx}-\frac{A}{A_0^2}\frac{dA_0}{dX}\right], \tag{1.3}$$

where $F'(\alpha)$ is shorthand for the function $dF/d\alpha$.

APPENDIX 2

Effect of inertia on steady flow in collapsible tubes

Here we revert to a tube of uniform intrinsic properties and external pressure, in which the pressure P, cross-sectional area A and velocity u are taken to vary only with x, the longitudinal coordinate; gravity is taken to act in the direction of flow (see figure 8). The following discussion is based on that of Shapiro (1977). Conservation of mass requires that

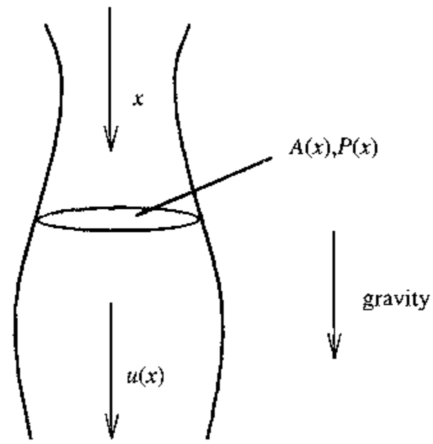


Figure 8. Sketch for the one-dimensional modelling of steady flow in a vertical collapsible tube. Cross-sectional area A, pressure P and fluid velocity u depend on the longitudinal distance x.

$$uA = Q, \tag{2.1}$$

where Q is the flow rate. The dynamics of the fluid is represented by the Bernoulli-Poiseuille equation (14) which gives

$$u\frac{du}{dx}+\frac{1}{\rho}\frac{dP}{dx}-g = \frac{R(A)Q}{\rho}, \tag{2.2}$$

where the resistance R depends on A; in a collapsing tube, R will increase more rapidly, as A decreases, than in a circular tube (see equation 3.3 in Appendix 3). Finally the tube elastic properties are given by equation (1.1) in which P_e, A_0 and K_p are taken to be constants. Combining equations (2.1), (2.2) and (1.1) gives the following expression for dA/dx, significantly different from equation (12):

$$\frac{1}{A}\frac{dA}{dx} = \frac{1}{\rho}\frac{g\rho-R(A)Q}{c^2-u^2}, \tag{2.3}$$

where

$$c^2 = (K_p/\rho)\,\alpha F'(\alpha). \tag{2.4}$$

The quantity c^2 is proportional to the slope of the pressure-area relation and represents a measure of the stiffness of the tube at a given value of relative area α; c itself has the dimensions of a velocity, and is in fact the speed of propagation of small amplitude pressure waves along the vessel (Shapiro 1977; Caro *et al.* 1978). For the purposes of calculation, we shall use the form of $F(\alpha)$, and hence of c^2, given in Appendix 3.

The part of equation (2.3) attributable to inertia is the $-u^2$ term in the denominator. Following Shapiro (1977), we introduce the speed index $S = u/c$, so that, with equation (13), equation (2.4) can be rewritten

$$dx/dx = [\alpha(g\rho-RQ)]/[\rho c^2(1-S^2)]. \tag{2.5}$$

The behaviour of the flow depends crucially on the signs of the numerator and denominator of equation (2.5), in particular on whether S is greater than 1 (supercritical flow), less than 1 (subcritical flow) or equal to 1 (critical flow).

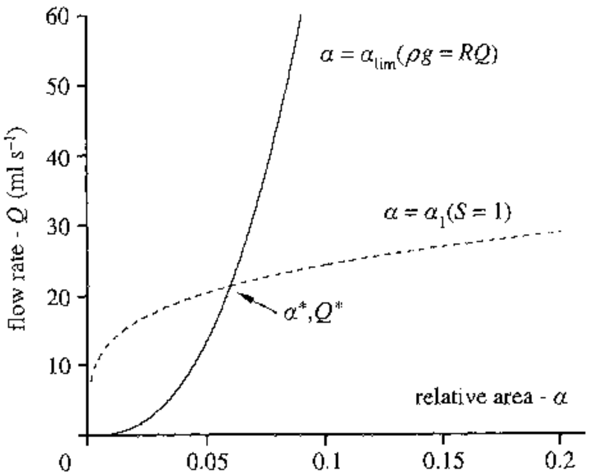


Figure 9. Plots of flow-rate Q versus relative area α for $\alpha = \alpha_{\rm lim}$ (when $\rho g = RQ$), solid curve, and $\alpha = \alpha_1$ (when speed index $S = 1$), broken curve.

The numerator in equation (2.5) is zero when gravitational and resistive forces balance i.e.

$$g\rho = RQ.$$

For a given flow rate Q this specifies a particular value of α which we call $\alpha_{\rm lim}$ (cf. Shapiro 1977); when $R(\alpha)$ is given by equation (3.3) this is

$$\alpha = \alpha_{\rm lim} = [(8\pi\mu Q)/(\rho g A_0^2)]^{2/5}. \tag{2.6}$$

Similarly the denominator in equation (2.5) is zero when $S = 1$, i.e. $\alpha_1 = \alpha$, where

$$A_0 \alpha_1 c(\alpha_1) = Q; \tag{2.7}$$

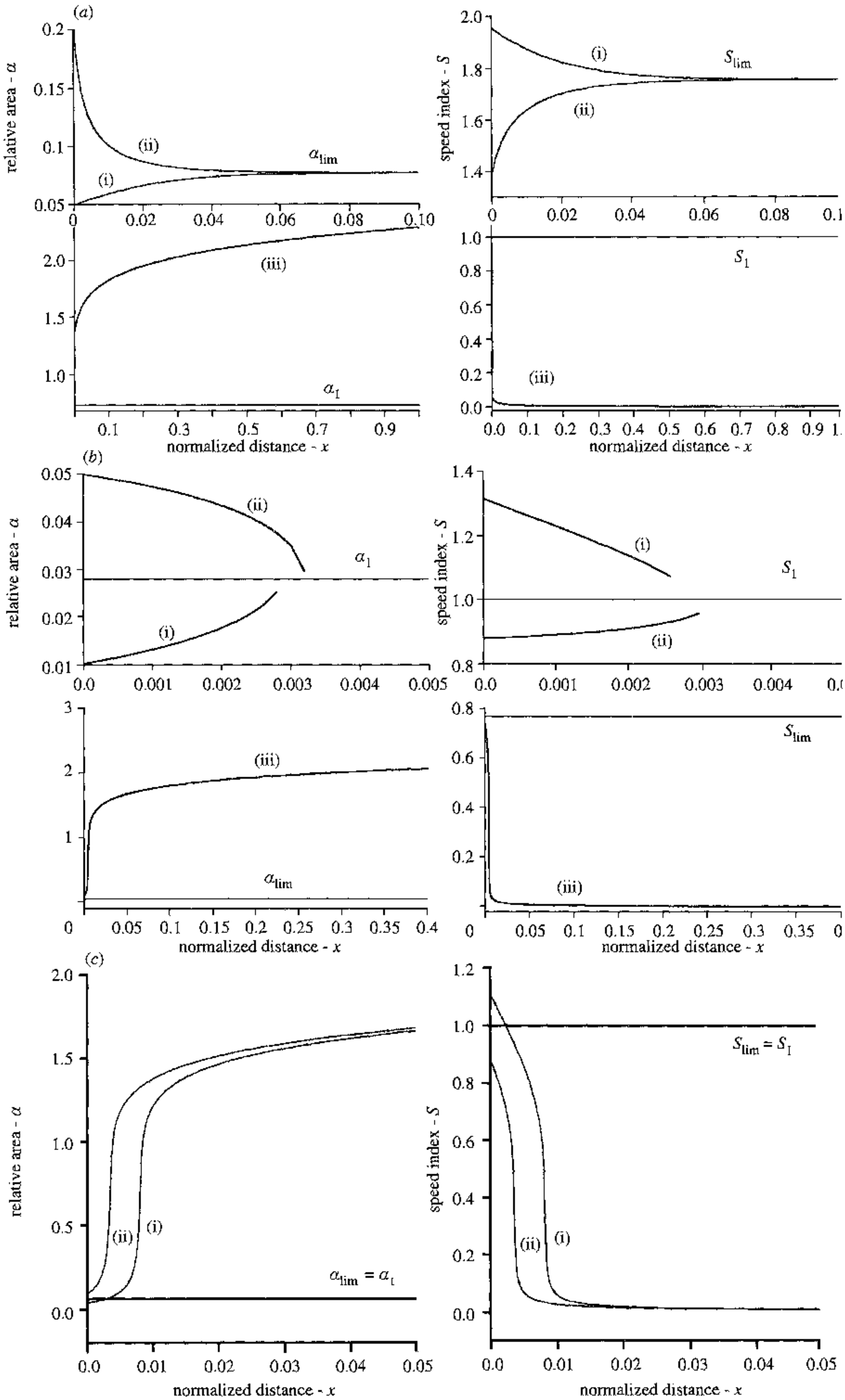
$c(\alpha)$ may be inferred from equation (3.2). The area α^* and flow-rate Q^* at which both (2.6) and (2.7) are satisfied (see figure 9), i.e. $\alpha_{\rm lim} = \alpha_1 = \alpha^*$, play an important role in the theory. Several different cases should be considered, depending on whether Q is greater, less than or equal to Q^*, and on the dimensionless cross-sectional area α_0 at the inlet $x = 0$. The cases are discussed with reference to figure 10 which has been plotted using the functions and constants given in Appendix 3.

1. Suppose $Q > Q^*$ (figure 10*a*), so that $\alpha_{\rm lim} < \alpha_1$. Then there are three possibilities: (i) $\alpha_0 < \alpha_{\rm lim}$ i.e. the tube upstream is sufficiently severely collapsed that RQ exceeds $g\rho$ as well as $S > 1$. Now $d\alpha/dx$ will be positive, so α increases and both u and RQ are predicted to fall. RQ will reach ρg before S reaches 1, so $d\alpha/dx$ will become zero and α will tend to $\alpha_{\rm lim}$ and stay there; S will tend to $S_{\rm lim}$ and the flow will always be supercritical (see curves (i) on figure 10*a*).(ii) $\alpha_{\rm lim} < \alpha_0 < \alpha_1$ i.e. RQ is less than $g\rho$ at the inlet although $S > 1$. Now $d\alpha/dx$ will be negative, so the area will fall, the velocity (and S) will rise, and R will also rise until RQ can balance $g\rho$ again i.e. α will tend to $\alpha_{\rm lim}$ from above (see curves (ii) on figure 10*a* and compare the dialysis-tube experiment described in the text). (iii) $\alpha_0 > \alpha_1$ i.e. the tube is sufficiently distended for both RQ to be less than $g\rho$ and the flow to be subcritical ($S < 1$). Now $d\alpha/dx$ is again positive, so the area will increase with distance down the tube, and the flow will become increasingly subcritical (curves (iii)). In this case the presence of inertia has no qualitative effect on the flow.

2. Now take $Q < Q^*$ (figure 10*b*), so that $\alpha_1 < \alpha_{\rm lim}$. There are again three possibilities, all quite different from those in 1. (i) $\alpha_0 < \alpha_1$, so the tube upstream is again sufficiently collapsed that RQ exceeds $g\rho$ and $S > 1$. Thus $d\alpha/dx$ will be positive. This time, however, S is predicted to reach the value 1 ($u = c$) before gravity and friction come into balance. Hence, from equation (2.5), $d\alpha/dx$ is predicted to be infinite (curves (i) of figure 10*b*). This is clearly impossible: no steady flow with the given flow-rate and upstream area can occur. Moreover, because the fluid speed exceeds the wave speed, it is not possible for a wave to propagate upstream and change conditions at the inlet. What occurs instead is an elastic jump (or shock) (Griffiths 1971; Oates 1975; Shapiro 1977) in which a rapid transition takes place to subcritical flow with a wider cross-section and a lower velocity. (ii) $\alpha_1 < \alpha_0 < \alpha_{\rm lim}$ (curves (ii) of figure 10*b*). Here the tube is sufficiently collapsed at the top end that the resistance overcomes gravity, but not so collapsed that u exceeds c. Thus the numerator of equation (2.5) will be negative and the denominator positive, so $d\alpha/dx$ will be negative. The area will therefore decrease with distance down the tube, so R will increase further, u ($= Q/A$) will increase and c is likely to decrease. Thus the denominator $1 - S$ will become smaller, accelerating the decrease in α. If the tube is long enough, $1 - S$ will be predicted to approach zero and $d\alpha/dx$ to become negatively infinite. That is again not possible and steady flow with the postulated upstream conditions cannot occur; the flow is said to be choked. This time what happens is that a time-dependent wave propagates upstream (possible, because $c > u$) and the incoming flow is adjusted so that choking just does not occur: if there is a point at which $S = 1$, conditions will have adjusted themselves so that $RQ = \rho g$ at the same point. Thus, choking provides a mechanism by which conditions in the collapsible tube determine the flow rate upstream of it. (iii) $\alpha_0 > \alpha_{\rm lim}$ i.e. the flow at the inlet is subcritical ($S < 1$) and the resistance is low. Then $d\alpha/dx$ will be positive, so the area increases, the resistance decreases, and the flow becomes increasingly subcritical. Inertia has no qualitative effect (curves (iii) of figure 10*b*).

3. Finally consider the special case $Q = Q^*$, in which $\alpha_{\rm lim} = \alpha_1 = \alpha^*$. (i) First, let $\alpha_0 < \alpha^*$. Then equation (2.5) gives $d\alpha/dx > 0$, and in fact α is predicted to reach α^* at a finite distance from the inlet. At such a point, both numerator and denominator of (2.5) are

Figure 10. Sketches of the graphs of α (left column) and S (right column) against normalized distance x along the tube, in all possible cases. (i) $Q > Q^*$; (ii) $Q < Q^*$; (iii) $Q = Q^*$. Curves (*a*), (*b*), (*c*) refer to different ranges of values of α at $x = 0$. For full explanation see text.


(a)
relative area - α
speed index - S
(i)
(ii)
(iii)
α_lim
S_lim
α_1
S_1
normalized distance - x
(b)
(c)
α_lim = α_1
S_lim = S_1

zero, which means that a smooth transition can take place from super- to subcritical flow (curve (i) in figure 10*c*), not an abrupt one as at an elastic jump. Once α exceeds α^*, $d\alpha/dx$ remains positive and the flow becomes increasingly subcritical, as also happens if (ii) $\alpha_0 > \alpha^*$.

APPENDIX 3

For the purpose of making specific calculations we choose the following particular forms for the functions relating transmural pressure, wave speed and viscous resistance to dimensionless cross-sectional area α (see equation 13):

$$F(\alpha) = \alpha^n - \alpha^{-3/2}, \tag{3.1}$$

$$c^2 = \frac{K_p}{\rho}\alpha\frac{dF}{d\alpha} = \frac{K_p}{\rho}(n\alpha^n + \tfrac{3}{2}\alpha^{-3/2}), \tag{3.2}$$

$$R = \frac{8\pi\mu A_0^{1/2}}{A^{5/2}} = \frac{8\pi\mu}{A_0^2\alpha^{5/2}}. \tag{3.3}$$

The exponent n in equation (3.1) is taken to have the value 10 for our modelling of veins; the value $n = 20$, as used by Elad *et al.* (1987), is more appropriate for drain tubing (cf. figure 4). The form of $F(\alpha)$ is continuous, yet combines the properties of being very stiff when the tube is distended ($\alpha > 1$), compliant at intermediate α, and stiff again at very small α, where it coincides with the form deduced theoretically by Shapiro (1977). The function $R(\alpha)$ increases more rapidly as α decreases than it would for a circular tube (equation 3).

The values assumed for the various dimensional parameters are:

$A_0 = 5$ cm^2 , as estimated in the body of the paper.

$K_p = 5$ Pa; this is based on equation (1.2), but taking the ratio of wall thickness to radius and the Young's modulus to be somewhat larger than in the dog (Caro *et al.* 1978); the Poisson's ratio, σ, is 0.5 for an incompressible material.

The interstitial pressure has been measured to be 1 mm Hg (133 Pa) at the base and top of the neck, and this is the value assumed for P_e, neglecting any unknown 'solid' pressures.

The length L of the vein is taken to be 2 m.

The properties of blood are taken to be $\rho = 10^3$ kg m^{-3}, $\mu = 0.004$ Pa s^{-1}; $g \approx 10$ m s^{-2}.