Long-wavelength peristaltic pumping at low Reynolds number

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(Received 11 April 1974)

An asymptotic expansion is found for the low Reynolds number flow induced in an axisymmetric tube by long peristaltic waves of arbitrary shape. Expressions are determined for the relationship between the mean pressure gradient and the volume flux, for the mean rate of working by the wall of the tube and for the shear stress at the wall. A necessary and sufficient condition for the occurrence of trapping (that is, regions of separated flow near the axis of the tube in a reference frame moving at the wave speed) is obtained. It is shown that reflux (that is, a mean flux in the negative axial direction in a layer of fluid adjacent to the wall when the net mean flux is positive) occurs whenever there is an adverse mean pressure gradient, independently of the shape of the wave. An estimate of the amount of reflux is derived.

1. Introduction

The fluid mechanics of peristaltic pumping have been studied for some years and a review of much of the literature is presented by Jaffrin & Shapiro (1971). A major application of the work on this problem is to the understanding of the ureter (for example, Boyarsky *et al.* 1971). The Reynolds number of the flow in the ureter is not large and the ratio e of the tube radius to the wavelength of the peristaltic wave is invariably small. Hence the analysis commonly is carried out under the assumption of zero Reynolds number and with the neglect of axial velocity gradients in the momentum equation; that is, classical lubrication theory is used. Analyses until about 1970 were restricted to sinusoidally varying tubes. However, Lykoudis & Roos (1970) point out that the shape of the ureter during peristalsis is far from sinusoidal, and so they consider the flow through a tube of arbitrary wave shape. On the other hand, they are interested primarily in determining the maximum pressure in a tube with a wall profile which varies algebraically in the axial direction.

In the present work, the fluid mechanics of a peristaltic pump of arbitrary wave shape are studied in order to obtain some general properties of peristalsis. The analysis of Lykoudis & Roos is extended by accounting, to first order in e^2 , for the inertial and viscous effects which they neglect. ('Inertial effects' are due to the nonlinear advection terms in the equations of motion, while 'viscous effects' are caused by those viscous diffusion terms previously neglected.) The asymptotic solution is obtained formally by the method used by Manton (1971) in the study of flow through slowly varying tubes at low Reynolds number. Owing to the unsteady nature of the present problem, the boundary conditions at the tube wall are different from those associated with steady flow through a tube of fixed shape.

2. Formulation of problem

We consider the motion of a viscous incompressible fluid in the domain $-\infty < x^* < \infty$, $0 < r^* < a(x^* - ct)$, $0 \le \theta < 2\pi$, where t is time and (x^*, r^*, θ) are cylindrical polar co-ordinates such that $r^* = 0$ is the axis of symmetry of the tube and the wall of the tube is $r^* = a$. The wall profile is represented by an axisymmetric wave of constant shape propagating at speed c. For axisymmetric motion, the equations for the conservation of momentum and volume are

$$\begin{array}{c} u_t + uu_{x^{\bullet}} + vu_{r^{\bullet}} + p_{x^{*}} / \rho = v\{u_{x^{\bullet}x^{\bullet}} + (r^*u_{r^{\bullet}})_{r^{\bullet}} / r^*\}, \\ v_t + uv_{x^{\bullet}} + vv_{r^{\bullet}} + p_{r^{\bullet}} / \rho = v\{v_{x^{\bullet}x^{\bullet}} + (r^*v_{r^{\bullet}})_{r^{\bullet}} / r^* - v / r^{*2}\}, \\ u_{x^{*}} + (r^*v)_{r^{\bullet}} / r^* = 0, \end{array}$$

$$(2.1)$$

where (u, v) are the fluid velocity components in the (x^*, r^*) directions, respectively, p is the pressure, v is the constant fluid viscosity, ρ is the constant fluid density and the subscripts (x^*, r^*, t) denote partial differentiation with respect to (x^*, r^*, t) , respectively.

The boundary conditions on the velocity components are taken to be

$$v = da/dt \quad \text{on} \quad r^* = a, \tag{2.2a}$$

$$u = 0 \quad \text{on} \quad r^* = a,$$
 (2.2b)

$$v = 0 = u_{r^*}$$
 on $r^* = 0.$ (2.2c)

Condition (2.2a) is simply the kinematic constraint that the radial motion of fluid particles at the wall corresponds to that of the wall. The no-slip condition (2.2b) implies that there is no axial movement of the wall, and so the wall material is necessarily extensible. Conditions (2.2c) ensure that the solution is regular at the axis.

For a periodic wall profile, the axial length scale is represented by the wavelength λ . (For a solitary wave, λ is simply the axial extent of the disturbance.) Thus the function *a* is assumed to be of the form

$$a(x^* - ct; a_0, \lambda) = a_0 s(x), \qquad (2.3)$$

where $x = (x^* - ct)/\lambda$ and a_0 is the root-mean-square radius of the tube; that is

$$\int_{0}^{1} s^{2}(x) \, dx = 1. \tag{2.4}$$

Following Manton (1971), we seek a quasi-steady solution of the system (2.1) with (2.2) for the case when the radius of the tube varies slowly in time and in the axial direction. In particular, we introduce a normalized vorticity component $\omega(x,r;\epsilon)$ and stream function $\phi(x,r;\epsilon)$ such that

$$\begin{aligned} \omega &= (a_0/c) \,\Omega \quad \text{with} \quad \Omega = u_{r^{\bullet}} - v_{x^{\bullet}}, \\ \phi_r/r &= u/c - 1, \quad \epsilon \phi_x/r = -v/c, \end{aligned}$$
 (2.5)

where $r = r^*/a_0$ and $\epsilon = a_0/\lambda$ ($0 < \epsilon \leq 1$). Clearly, r is the normalized radial co-ordinate and x is a slowly varying normalized axial co-ordinate in a frame of reference moving at the wave speed.

By putting (2.3) and (2.5) into (2.1) and (2.2), the normalized equations of motion become

$$\omega = (\phi_r/r)_r + \epsilon^2 \phi_{xx}/r, \qquad (2.6a)$$

$$\operatorname{Ree}\{\phi_r(\omega/r)_x - \phi_x(\omega/r)_r\} = ((r\omega)_r/r)_r + e^2\omega_{xx}, \qquad (2.6\,b)$$

subject to the conditions

$$\phi = -\frac{1}{2}\beta, \quad \phi_r = -s \quad \text{on} \quad r = s(x),$$
 (2.7)

$$\phi, \phi_x/r, (\phi_r/r)_r \to 0 \quad \text{as} \quad r \to 0,$$
(2.8)

where $Re = a_0 c/\nu$ is a characteristic Reynolds number of the flow. We note that Re is an appropriate Reynolds number because the maximum volume flux through the peristaltic pump is $\pi a_0^2 c$, as shown in §4 below. If $\pi a_0^2 c\alpha$ is the mean volume flux through the tube in a stationary reference frame then we find from (2.3)–(2.5) and (2.7 α) that the stream-function parameter β is related to the normalized mean flux by

$$\alpha = 1 - \beta. \tag{2.9}$$

Condition (2.7a) and (2.9) suggest the mechanics of peristalsis. In the frame moving with the wave, there is a flux of normalized magnitude β in the negative axial direction owing to the adverse (or zero) pressure gradient. However, by accounting for the Galilean transformation, there is a net positive flux in the stationary frame of reference. The energy for the transport process comes from the working of the tube wall against the radial force exerted by the fluid on the wall.

We consider the solution of (2.6)–(2.8) when the Reynolds number is formally $O(\epsilon)$; in particular, we set

$$Re = R\epsilon,$$
 (2.10)

where $R = \lambda c/\nu$ is O(1). Thus the analysis is less general than that of Manton (1971), where Re is of order unity. On the other hand, it does allow the first-order effects of both the inertial and viscous terms to be included conveniently in an expansion correct to $O(\epsilon^2)$. Moreover, it is seen from (2.6*b*) that the expansion to $O(\epsilon^2)$ is valid for any Re that is o(1).

3. Flow field

The flow field is described by the stream function and vorticity, and so we seek asymptotic expansions of the form

$$\phi = \sum_{n=0}^{\infty} e^{2n} \phi^{(n)}(x,r;R), \quad \omega = \sum_{n=0}^{\infty} e^{2n} \omega^{(n)}(x,r;R).$$
(3.1)

The sequences $\{\phi^{(n)}\}\$ and $\{\omega^{(n)}\}\$ are determined by substituting (2.10) and (3.1) into the system (2.6)–(2.8) and solving successively the sequence of equations obtained by equating the coefficients of like powers of ϵ^2 . Because the method and

M. J. Manton

the physical interpretation of the terms included are discussed by Manton (1971), we state the result alone:

$$\begin{split} \phi &= \frac{1}{2} (\beta - s^2) \left(r/s \right)^4 - (\beta - \frac{1}{2} s^2) \left(r/s \right)^2 \\ &- Re \, \epsilon (s^{-1} \, ds/dx) \left(\beta - \frac{1}{2} s^2 \right) \left\{ \frac{1}{36} (\beta - s^2) \left(r/s \right)^8 - \frac{1}{6} (\beta - \frac{1}{2} s^2) \left(r/s \right)^6 \right. \\ &+ \frac{1}{4} (\beta - \frac{1}{3} s^2) \left(r/s \right)^4 - \frac{1}{9} (\beta - \frac{1}{4} s^2) \left(r/s \right)^2 \right\} \\ &- \frac{1}{24} \epsilon^2 s^6 \{ (\beta - s^2)/s^4 \}_{xx} \left\{ (r/s)^6 - 2(r/s)^4 + (r/s)^2 \right\} + O(\epsilon^4), \end{split}$$
(3.2)
$$\omega &= \frac{4}{s^3} \left(\beta - s^2 \right) \left(r/s \right) - \frac{4 \, Re \, \epsilon}{s^4} \frac{ds}{dx} \left(\beta - \frac{1}{2} s^2 \right) \left\{ \frac{1}{3} (\beta - s^2) \left(r/s \right)^5 \right. \\ &- \left(\beta - \frac{1}{2} s^2 \right) \left(r/s \right)^3 + \frac{1}{2} (\beta - \frac{1}{3} s^2) \left(r/s \right) \right\} \\ &- \epsilon^2 s^3 \{ (\beta - s^2)/s^4 \}_{xx} \left\{ \frac{1}{2} (r/s)^3 - \frac{2}{3} (r/s) \right\} - \epsilon^2 \beta s(s^{-2})_{xx} (r/s) + O(\epsilon^4). \end{aligned}$$
(3.3)

It is seen that the inertial correction is proportional to the local slope of the wall, whilst the viscous correction involves the curvature and the square of the slope of the wall.

4. Pressure distribution

Lykoudis & Roos (1970) assert that any model of peristaltic pumping which is to be compared with the behaviour of the ureter ought to predict the instantaneous pressure distribution along the tube. This is because the instantaneous pressure is measurable and has a distinct signature, and because the mean pressure gradient is generally zero in a healthy ureter (Kiil 1957, p. 59). To calculate the pressure, we let $p = (8\lambda\rho\nu c/a_0^2)q$, (4.1)

where
$$q = \sum_{n=0}^{\infty} \epsilon^{2n} P^{(n)}(x,r;R)$$

put (2.5), (2.10), (3.2), (3.3) and (4.1) into (2.1), and equate the coefficients of like powers of ϵ^2 . This yields systems of equations for the set $\{P^{(n)}\}$ which can be solved successively (Manton 1971). It is found finally that

$$q(x,r) = \int^{x} \frac{dx}{s^{4}} (\beta - s^{2}) - \frac{Re \epsilon}{8s^{4}} (\beta^{2} - \frac{1}{3}\beta s^{2} + \frac{2}{3}s^{4} \ln s) + \frac{\epsilon^{2}}{s^{3}} \frac{ds}{dx} \{ (\beta - \frac{1}{2}s) \left[(r/s)^{2} - \frac{2}{3} \right] + \frac{1}{2}\beta \} + \frac{4}{3}\epsilon^{2} \int^{x} \frac{dx}{s^{4}} (\beta - \frac{1}{2}s^{2}) \left(\frac{ds}{dx} \right)^{2} + O(\epsilon^{4}).$$
(4.2)

The leading term in (4.2) implies that the maximum and minimum pressures occur at positions where $s^2 = 1 - \alpha + O(\epsilon^2)$; i.e. in the contracted region of the tube.

We now introduce the normalized mean pressure gradient

$$\gamma = q(1,r) - q(0,r), \tag{4.3}$$

which equals the ratio of the pressure rise in the tube over a wavelength to the pressure drop over a length λ in a tube of fixed radius a_0 with a mean fluid velocity c. Because s is periodic (4.2) and (4.3) give

$$\gamma = \int_0^1 \frac{dx}{s^4} \left(\beta - s^2\right) + \frac{4}{3} \epsilon^2 \int_0^1 \frac{dx}{s^4} \left(\beta - \frac{1}{2} s^2\right) \left(\frac{ds}{dx}\right)^2 + O(\epsilon^4).$$
(4.4)

 $\mathbf{470}$

(For a solitary wave, (4.4) follows from the assumption that s(0) = s(1) and that the derivatives of s are negligible at x = 0 and x = 1.) For a given wave shape, (4.4) yields the linear relationship between the imposed pressure gradient and the resultant flow rate. Comparison of (4.2) and (4.4) shows that, although there is no first-order inertial correction to the mean pressure gradient, inertial effects do produce a first-order correction to the local pressure distribution in the tube. There is also a local radial pressure gradient of order e^2 which does not affect the mean axial pressure gradient. For the algebraic wave shape used by Lykoudis & Roos (1970) to model the ureter, these first-order effects produce corrections which are less than 1 % of the peak pressure in the tube.

For a peristaltic pump we must have $\alpha \ge 0$ and $\gamma \ge 0$; hence (2.4), (2.9) and (4.4) imply that, correct to $O(e^2)$ at least,

$$s_{\min}^2 < \beta \leq 1$$
 or $0 \leq \alpha < 1 - s_{\min}^2 < 1$, $(4.5a, b)$

where the subscript 'min' denotes the minimum value of a function. Thus the mean flux through a peristaltic pump is less than $\pi a_0^2 c$, and the upper limit on the flux is determined by the degree of contraction of the tube. Equation (4.4) can be used to obtain an upper bound on the mean flux in terms of the imposed pressure gradient, namely

$$\alpha < 1 - s_{\min}^4 \gamma - s_{\min}^4 / s_{\max}^2 + O(e^4), \tag{4.6}$$

where the subscript 'max' denotes the maximum value of a function. However, (4.6) is more restrictive than (4.5b) only at large adverse pressure gradients. An upper limit on the adverse pressure gradient against which the pump can work is given from (4.4) and (4.5a) by

$$\gamma < 1/s_{\min}^4 - 1/s_{\max}^2 + O(\epsilon^4).$$
 (4.7)

The inequalities (4.5)-(4.7) suggest that the general dilation of the tube wall or its inability to contract fully ought to decrease greatly its pumping efficacy.

5. Rate of working of wall of tube

The energy required to pump fluid through the tube by peristals comes from the working of the tube wall against the radial force exerted by the fluid on the wall. Because there is assumed to be no axial velocity at the wall, the axial force exerted by the fluid on the wall does no work. By considering the motion in a frame moving at the wave speed, we find that the radial force per unit area acting on the fluid at the wall $r^* = a$ is

$$F = \left(\sigma_{rr} - \sigma_{xr} \epsilon \frac{ds}{dx}\right) / \left\{1 + \epsilon^2 \left(\frac{ds}{dx}\right)^2\right\}^{\frac{1}{2}},\tag{5.1}$$

where the stress tensor is given by

$$\sigma_{ij} = -p\delta_{ij} + 2\rho\nu e_{ij} \tag{5.2}$$

and the rate-of-strain components are

$$e_{xx} = \frac{\partial u}{\partial x^*}, \quad e_{rr} = \frac{\partial v}{\partial r^*}, \quad e_{xr} = \frac{1}{2} \left(\frac{\partial v}{\partial x^*} + \frac{\partial u}{\partial r^*} \right).$$
 (5.3)

M. J. Manton

From (2.5), (2.6a), (2.7) and (5.1)–(5.3) it can be shown that

$$F = \left\{ -p + \epsilon \rho \nu (\Omega + 2c/a) \frac{ds}{dx} \right\} / \left\{ 1 + \epsilon^2 \left(\frac{ds}{dx} \right)^2 \right\}^{\frac{1}{2}}.$$
(5.4)

The net rate of working of the wall over a wavelength is

$$W_0 = \int_0^\lambda 2\pi a F v \, dx^*. \tag{5.5}$$

Thus, introducing the normalized rate of working

$$\delta = W_0 / 8\pi \rho \nu c^2 \lambda, \tag{5.6}$$

which is the ratio of W_0 to the rate of energy dissipation by the fluid over a length λ of a tube of constant radius a_0 with a mean flow velocity of c, we find from (2.2*a*), (2.3), (3.3), (4.4) and (5.4)–(5.6) that

$$\delta = 1 + \gamma - \beta \int_0^1 \frac{dx}{s^2} - \frac{2}{3} \epsilon^2 \left\{ \int_0^1 \frac{dx}{s^2} (\beta - \frac{5}{4} s^2) \left(\frac{ds}{dx} \right)^2 + \frac{3}{16} \int_0^1 dx \, s \left(\frac{ds}{dx} \right)^3 \int_0^x \frac{dx'}{s^4} (\beta - s^2) \right\} + O(\epsilon^4).$$
(5.7)

In deriving (5.7) we assume without loss of generality that s(0) = 1 = s(1). Equations (4.4) and (5.7) show that the net rate of working δ of the wall is a linearly increasing function of the mean pressure gradient γ and mean flux α . As for γ , the first-order inertial correction to the local rate of working of the wall does not contribute to the net rate of working over a full wavelength.

The inequalities (4.5 a) may be used in (5.7) to obtain upper and lower bounds on δ ; in particular, correct to $O(\epsilon^2)$,

$$\gamma + 1 - 1/s_{\max}^2 \leq \delta < \gamma + 1 - (s_{\min}/s_{\max})^2.$$

This suggests that the power supplied to the system is minimized for a given pressure gradient γ by taking s_{\max} as close to unity as possible. On the other hand, conditions (2.4) and (4.5) imply that the mean flux approaches zero as s_{\max} approaches unity.

6. Shear stress at wall of tube

The shear stress at the wall $r^* = a$ is

$$T = \left\{ \left(\sigma_{rr} - \sigma_{xx}\right) e \frac{ds}{dx} + \sigma_{xr} \left[1 - e^2 \left(\frac{ds}{dx}\right)^2 \right] \right\} / \left\{ 1 + e^2 \left(\frac{ds}{dx}\right)^2 \right\}.$$
(6.1)

It is found from (2.5), (2.6a), (2.7), (5.2), (5.3) and (6.1) that the shear stress is a linear function of the vorticity at the wall; in particular,

$$T = \rho \nu \Omega + 2(\rho \nu c/a) \epsilon^2 \left(\frac{ds}{dx}\right)^2 \left\{ 1 - \epsilon^2 \frac{d}{dx} \left(s \frac{ds}{dx}\right) \right\} / \left\{ 1 + \epsilon^2 \left(\frac{ds}{dx}\right)^2 \right\}.$$
 (6.2)

The second term in (6.2) arises from the finite radial velocity at the wall; the shear stress at the wall of a fixed tube is given by the first term alone. Normalizing T with respect to the shear stress at the wall of a tube of constant radius a_0 with a mean flow velocity c, we set

$$\tau = (a_0/4c\rho\nu)T. \tag{6.3}$$

472

Hence it is seen from (3.3), (6.2) and (6.3) that the shear stress may be written as

$$\tau = \frac{1}{s^3} \left\{ (\beta - s^2) + \frac{1}{6} Re \, \epsilon \beta (\beta - \frac{1}{2} s^2) \frac{1}{s} \frac{ds}{dx} + \frac{2}{3} \epsilon^2 \left[\frac{1}{2} (\beta + \frac{1}{4} s^2) s \frac{d^2s}{dx^2} - (\beta - \frac{3}{8} s^2) \left(\frac{ds}{dx} \right)^2 \right] + O(\epsilon^4) \right\}.$$
(6.4)

Condition (4.5 a) and (6.4) imply that the shear stress must change sign during peristalsis. Although there is no flow separation at the wall in the wave frame of reference, the axial velocity in the stationary frame does change sign at points where $s^2 = \beta$ to zeroth order in ϵ^2 . Unlike the flow through a fixed tube (Manton 1971), this flow reversal is not associated with local separation at the wall: it occurs over the whole tube and is due to the oscillatory nature of the flow. On the other hand, local regions of separated flow can occur near the axis of the tube, and this is discussed in § 7 below.

The maximum shear stress τ_{\max} occurs, to zeroth order in ϵ^2 , at the point of maximum contraction. For a given wall shape, τ_{\max} decreases with increasing mean flow volume flux. Equation (6.4) shows that as the Reynolds number increases the point of maximum shear stress moves onto the region of positive wall slope where the radial velocity is negative.

An upper bound on the shear stress is found from (4.5 a) and (6.4) to be given by

$$\tau_{\max} < 1/s_{\min}^3 + O(e^2),$$
 (6.5)

and so is determined by the degree of contraction of the tube. On the other hand, the function τ has a minimum when $s^2 = 3\beta + O(\epsilon^2)$. Thus the minimum shear stress which occurs during dilation must satisfy, to O(1),

$$\tau_{\min} \ge -(2/3^{\frac{3}{2}})\beta^{-\frac{1}{2}} > (2/3^{\frac{3}{2}})s_{\min}^{-1}.$$

This lower bound on the magnitude of τ_{\min} occurs because the radial velocity gradients decrease with increasing dilation.

Lykoudis & Roos (1970) show that the pressure distribution in the ureter is modelled well by the wave shape

$$s(x) = \begin{cases} B + Ax^n & \text{for } 0 < x < X, \\ B + AX^n & \text{for } X < x < 1, \end{cases}$$
(6.6)

where typical values are A = 6.9, B = 0.014, X = 0.69 and n = 4, corresponding to a wavelength λ of 36 cm and a root-mean-square tube radius a_0 of 0.15 cm. The behaviour of the wall shear stress for this profile is shown in figure 1, where the mean pressure gradient is taken to be zero (i.e. $\gamma = 0$). Taking $c = 3 \text{ cm s}^{-1}$, $\rho = 1 \text{ g cm}^{-3}$ and $\nu = 0.007 \text{ cm}^2 \text{ s}^{-1}$, we find that the maximum stress of 10.4dyne cm⁻² occurs at the maximum contraction while the minimum stress of $-14.5 \text{ dyne cm}^{-2} \text{ occurs at } x = 0.21$. The inertial and viscous terms in (6.4) yield corrections of less than 0.1 % to the zeroth-order term in the contracted region of the ureter. It is noted that some uncertainty is associated with such estimates of the properties of the ureter. This arises particularly because, unlike the present model, the contracted ureter is convoluted and not precisely round.



FIGURE 1. Distribution of wall shear stress $\tau(x)$ calculated from (6.4) for the wave shape s(x) given by (6.6) with A = 6.9, B = 0.014, X = 0.69 and n = 4; $\beta = 2.3 \times 10^{-4}$, corresponding to zero mean pressure gradient.

7. Trapping

In a reference frame moving with the wave speed, the motion is steady and so streamlines correspond to particle lines. It is seen from (3.2) that, provided that s^2 is less than about 2β , the stream function ϕ decreases monotonically from zero to $-\frac{1}{2}\beta$ as r/s increases from zero to one. Thus, in this frame of reference, all the flow is in the negative axial direction. If s becomes large, however, ϕ is positive near the axis and becomes negative only near the wall. There is then a bolus of fluid around the axis which is separated from the free-stream flow near the wall in the dilated regions of the tube. This corresponds to the phenomenon of trapping which is described by Shapiro, Jaffrin & Weinberg (1969) for a sinusoidal wall profile.

Trapping in the flow is identified by the existence of stagnation points on the axis r = 0. It can be shown from (3.2) that the axial velocity ϕ_r/r is zero on r = 0when $\beta = \frac{1}{2}s^2\{1 - \frac{1}{3}\epsilon^2(ds/dx)^2 + O(\epsilon^4)\}.$ (7.1)

Using (2.9) and (7.1), we see that there is no trapping when

$$\alpha < 1 - \frac{1}{2}s_{\max}^2 + O(\epsilon^4);$$

that is, a necessary condition for no trapping is that α is less than $\frac{1}{2}$. This suggests that peristals is most efficacious when trapping does occur. Moreover, it was

found in §6 that the shear stress on the wall of the tube is reduced by increasing the mean flux α . We note that for $\alpha > 1 - \frac{1}{2}s_{\min}^2$ the region of trapped fluid extends along the whole axis, and there is a continuous stream of fluid moving in the positive axial direction near the axis. However, condition (4.5*a*) implies that this cannot occur in a peristaltic pump because it requires a favourable pressure gradient.

8. Reflux

A single definition of reflux is not universally accepted (see Boyarsky *et al.* 1971, pp. 248–250). Physiologists associate reflux with a net mean flux in the negative axial direction, while Shapiro *et al.* (1969) refer to the more subtle phenomenon of a mean flux in the negative axial direction in a layer of fluid near the tube wall although the net mean flux over the whole cross-section is positive. The former definition corresponds simply to α being negative; that is $\beta > 1$. We see from (4.4) that, to O(1),

$$\beta = (\gamma + I_1)/I_2$$
, where $I_n = \int_0^1 dx/s^{2n}$. (8.1)

Thus large-scale reflux occurs when the normalized adverse pressure gradient γ exceeds $I_2 - I_1$. For a given γ (> 0) and wave shape, this condition will be satisfied as the wave amplitude decreases.

On the other hand, Shapiro *et al.* find that local reflux takes place in a sinusoidally varying tube whenever there is an adverse pressure gradient (i.e. when $\gamma > 0$). We now show that such reflux is induced by an adverse pressure gradient independently of the wave profile. Because streamlines correspond to particle path lines in the wave frame of reference, the mean volume flux corresponding to a given value of ϕ is, from (2.5*b*),

$$L(\phi) = \int_{0}^{1} dx \int_{0}^{r(\phi)} 2r(\phi_{r}/r+1) dr;$$

$$L(\phi) = 2\phi + \int_{0}^{1} r^{2}(\phi) dx.$$
(8.2)

that is,

Inverting (3.2) we find that near the wall of the tube

$$(r/s)^{2} = \{(\beta - \frac{1}{2}s^{2}) - [(\beta - \frac{1}{2}s^{2})^{2} + 2\phi(\beta - s^{2})]^{\frac{1}{2}}\}/(\beta - s^{2}) + O(\epsilon^{2}).$$
(8.3)

By putting (8.3) into (8.2), the mean flux L is given formally as a function of the stream function ϕ .

At the wall r = s we have $L(-\frac{1}{2}\beta) = \alpha$, as required. Thus reflux occurs if the mean flux a short distance from the wall is greater than α ; that is, if for some $\Delta > 0$ $L(-\frac{1}{2}\beta + \Delta) > \alpha$. (8.4)

The left-hand side of (8.4) can be calculated by expanding $L(\phi)$ in a Taylor series about the point $\phi = -\frac{1}{2}\beta$. Thus, neglecting terms $O(\epsilon^2)$, we find from (4.4), (8.2) and (8.3) that

$$L(-\frac{1}{2}\beta + \Delta) = \alpha + 4\gamma\Delta^2 - 16\Delta^3 \int_0^1 \frac{dx}{s^8} (\beta - s^2)^2 + O(\Delta^4).$$
(8.5)

M. J. Manton

Therefore, condition (8.4) is satisfied if and only if there is an adverse pressure gradient (i.e. $\gamma > 0$). The maximum value of $L(\phi)$ is seen from (8.5) to occur when $\Delta = \Delta_m$, where

$$\Delta_m = \gamma \bigg/ 6 \int_0^1 \frac{dx}{s^8} (\beta - s^2)^2 + O(\Delta_m^2).$$
(8.6)

Hence (8.5) and (8.6) show that the mean reflux is

$$L_{re} = L(-\frac{1}{2}\beta + \Delta_m) - \alpha = \frac{1}{27}\gamma^3 / \left\{ \int_0^1 \frac{dx}{s^8} (\beta - s^2)^2 \right\} + O(\Delta_m^4).$$
(8.7)

It is seen from (8.1) and (8.7) that L_{re} is proportional to γ^3 for small adverse pressure gradients. As $\gamma \to \infty$, L_{re} decreases as γ^{-1} ; however, condition (4.6) is violated for large γ and so there is large-scale reflux in this asymptotic state. The limiting adverse pressure gradient against which the pump can work occurs when there is no mean flux ($\alpha = 0$). Thus the local reflux L_{rm} just before largescale reflux occurs is given from (2.9), (8.1) and (8.7) by

$$L_{rm} = \frac{1}{27} (I_2 - I_1)^3 / (I_4 - 2I_3 + I_2)^2.$$

At this point, when $\gamma = I_2 - I_1$, the magnitude of the reflux near the wall equals that of the forward flux near the axis of the tube.

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 $\mathbf{476}$