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Self-sustained peristaltic waves: Explicit asymptotic solutions

O. A. Dudchenko[1] and G. Th. Guria[1,2,*]

[1]*Moscow Institute of Physics and Technology, 9 Institutskii pereulok, Dolgoprudny, 141700 Moscow Region, Russia*

[2]*National Research Center for Hematology, 4 Novy Zykovskii prospekt, 125167 Moscow, Russia*

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A simple nonlinear model for the coupled problem of fluid flow and contractile wall deformation is proposed to describe peristalsis. In the context of the model the ability of a transporting system to perform autonomous peristaltic pumping is interpreted as the ability to propagate sustained waves of wall deformation. Piecewise-linear approximations of nonlinear functions are used to analytically demonstrate the existence of traveling-wave solutions. Explicit formulas are derived which relate the speed of self-sustained peristaltic waves to the rheological properties of the transporting vessel and the transported fluid. The results may contribute to the development of diagnostic and therapeutic procedures for cases of peristaltic motility disorders.

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Peristaltic pumping is one of the major mechanisms for fluid transport in biological systems. Pumping results from a distinctive pattern of smooth muscle contraction which propagates in a wave down the fluid-containing muscular vessel. It is generally accepted that peristalsis is the primary mechanism behind bolus propulsion through the esophagus [1], the movement of chime in the gastrointestinal tract [2,3], and the functioning of the ureter [4,5]. It has also been suggested that peristaltic contractions play an important role in lymph and blood transport [6–9].

Peristaltic pumping is generally an autonomous process, as many *in vitro* studies on isolated preparations indicate [9–12]. A number of models have been developed which aim to describe peristalsis as an inherent property of the transporting system [13,14]. These models are comprised of large, complicated sets of nonlinear differential equations that require laborious numerical analysis. They do not allow one to easily interpret the pumping indices (i.e., observed wave speed, the volume of transported fluid, etc.) in terms of the parameters which characterize the transporting system.

In this paper we present a much simpler, analytically tractable model of peristaltic pumping. The goal is to derive explicit albeit approximate solutions that would allow one to make qualitative predictions concerning peristaltic motility.

The model relies on a phenomenological description of the interaction between mechanical and electrical activity in the process of peristaltic pumping [15,16]. The electrical activity is represented by a wave of excitation propagating through a set of coupled excitable elements [17]. The mathematical formulation of the problem requires finding self-sustained traveling-wave solutions of the model.

The model equations are as follows:

$$(1+\tilde{\varepsilon})\frac{\partial \tilde{\varepsilon}}{\partial t} = \frac{R_0^2}{16\mu}\frac{\partial}{\partial z}\left[(1+\tilde{\varepsilon})^4\frac{\partial \tilde{p}}{\partial z}\right], \tag{1}$$

$$\tilde{p} + \tilde{\tau}_s\frac{\partial \tilde{p}}{\partial t} = \tilde{E}\left(\tilde{\varepsilon} + \tilde{\tau}_c\frac{\partial \tilde{\varepsilon}}{\partial t}\right) + p_a(\tilde{u}), \tag{2}$$

$$\frac{\partial \tilde{u}}{\partial t} = I(\tilde{\varepsilon}) + f(\tilde{u}) - \tilde{v} + \tilde{D}\frac{\partial^2 \tilde{u}}{\partial z^2}, \tag{3}$$

$$\frac{\partial \tilde{v}}{\partial t} = \tilde{\kappa}(\tilde{u} - \tilde{\delta}\tilde{v}). \tag{4}$$

Equation (1) results from the application of lubrication theory approximations to the equations of motion of an incompressible Newtonian fluid of viscosity μ in a tube undergoing axisymmetric deformation [18–21]. The variables introduced are $\tilde{\varepsilon} = (R - R_0)/R_0$ and $\tilde{p} = p_i - p_e(1 + h_0/R_0)$ (see Fig. 1 caption).

Equation (2) arises from a circumferential stress-strain relationship given by the standard linear solid (SLS) model of the viscoelastic wall material [22,23]. A thin-shell approximation and Laplace's law [20,21] were used to rewrite the stress-strain constitutive equation in terms of $\tilde{p}$ and $\tilde{\varepsilon}$. Parameters $\tilde{\tau}_s$, $\tilde{\tau}_c$ in Eq. (2) define the characteristic time scales of stress relaxation and creep of an unstimulated vessel, respectively. $\tilde{E}$ is the measure of wall stiffness ($\tilde{E} \simeq Yh_0/R_0$ where Y denotes the Young's modulus of the vessel wall material). The SLS model is supplemented with an active force generator represented by the $p_a(\tilde{u})$ term in Eq. (2).

The FitzHugh-Nagumo type phenomenological equations [24,25] with cubic nonlinearity, $f(\tilde{u}) = -\beta\tilde{u}(\tilde{u} - \tilde{u}_{thr})(\tilde{u} - 1)$, $\beta > 0$, $0 < \tilde{u}_{thr} < 1$, are used to model the electrical activity that gives rise to peristalsis [see Eqs. (3) and (4)]. The diffusive term in Eq. (3) stands for synaptic coupling between excitable cells. (Both electrical and chemical synapses are known to contribute to signal transduction [26,27].) The term $I(\tilde{\varepsilon})$ represents mechanosensitive currents arising in response to stretch. (The multiple mechanisms behind mechanosensitivity of peristaltically active systems are discussed, e.g., in [2,11,27,28].) $I(\tilde{\varepsilon})$ is taken to be linear:

$$I(\tilde{\varepsilon}) = \alpha\tilde{\varepsilon}, \quad \alpha = \text{const.} \tag{5}$$

The $\tilde{u}$ variable serves as a quantification of a degree to which the contractile machinery of the wall is activated by the electrical event of excitation. $\tilde{v}$ is the recovery variable: $\tilde{\kappa} > 0$, $0 < \tilde{\delta} < 4/(\beta(1 - \tilde{u}_{thr})^2)$. (The conditions ensure that the system given by Eqs. (3) and (4) has only one stable equilibrium, as characteristic of excitable media [17].) The

*guria@blood.ru

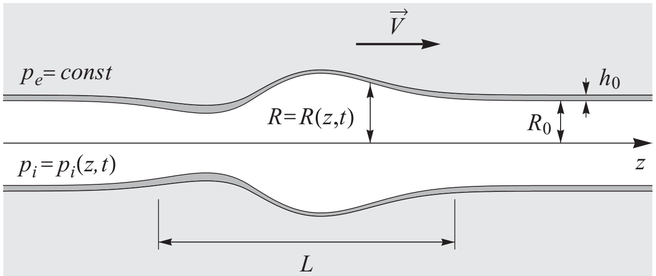

FIG. 1. A schematic representation of a tube undergoing peristalsis. The profile of the lumen is described by $R = R(z,t)$. The internal pressure distribution is given by $p_i = p_i(z,t)$. We assume that before the arrival of the wave the tube is at rest, unstrained and unstimulated, with lumen radius and wall thickness equal to R_0 and h_0, respectively. The external pressure p_e is constant.

capacity to evoke contractions is introduced into the model by the term $p_a(\tilde{u})$:

$$p_a(\tilde{u}) = \Upsilon\tilde{u}, \quad \Upsilon = \text{const}. \tag{6}$$

Numerical analysis of Eqs. (1)–(6) shows that in a certain range of parameter values self-sustained deformation waves can be initiated in the system. In this paper we shall not address the issue of initiation. Instead, we will focus on the problem of existence of self-sustained traveling-wave solutions of the model under consideration. Special attention will be paid to analyzing how the speed of a steadily propagating wave depends on rheological parameters of the transporting vessel and the transported fluid (i.e., parameters $\tilde{E}$, $\tilde{\tau}_s$, $\tilde{\tau}_c$, Υ, μ).

We look for traveling-wave solutions of the form

$$\tilde{p}(z,t) = \tilde{p}(\tilde{\xi}), \quad \tilde{\varepsilon}(z,t) = \tilde{\varepsilon}(\tilde{\xi}), \quad \tilde{u}(z,t) = \tilde{u}(\tilde{\xi}), \\ \tilde{v}(z,t) = \tilde{v}(\tilde{\xi}), \tag{7}$$

where $\tilde{\xi} = z - \tilde{V}t$ and $\tilde{V}$ is the wave speed ($\tilde{V} > 0$ is chosen to search for wave solutions traveling from left to right). The solutions are subject to the following conditions as $\tilde{\xi} \to \pm\infty$:

$$\{\tilde{p}',\tilde{p},\tilde{\varepsilon},\tilde{u},\tilde{v}\} \to \{0,0,0,0,0\}, \tag{8}$$

the prime denoting differentiation with respect to $\tilde{\xi}$.

On integrating Eq. (1) with respect to $\tilde{\xi}$ and inserting Eqs. (5)–(7) into the model, Eqs. (1)–(4) take the form

$$8\mu\tilde{V}[1-(1+\tilde{\varepsilon})^2] = R_0^2(1+\tilde{\varepsilon})^4\tilde{p}', \tag{9}$$
$$\tilde{p} - \tilde{V}\tilde{\tau}_s\tilde{p}' = \tilde{E}(\tilde{\varepsilon} - \tilde{V}\tilde{\tau}_c\tilde{\varepsilon}') + \Upsilon\tilde{u}, \tag{10}$$
$$-\tilde{V}\tilde{u}' = \alpha\tilde{\varepsilon} + f(\tilde{u}) - \tilde{v} + \tilde{D}\tilde{u}'', \tag{11}$$
$$-\tilde{V}\tilde{v}' = \tilde{\kappa}(\tilde{u} - \tilde{\delta}\tilde{v}). \tag{12}$$

Finding a set of functions $\{\tilde{p},\tilde{\varepsilon},\tilde{u},\tilde{v}\}$ satisfying Eqs. (9)–(12) as well as the conditions (8) implies solving a nonlinear eigenvalue problem [29,30] which, in general, requires numerical calculation. To simplify the analysis we will construct an analytically tractable piecewise-linear version of the model. The approach proved to be effective in a number of situations [31–35].

The simplifications we adopt are as follows:

(i) We replace the cubic reaction term $f(\tilde{u})$ with a piecewise-linear approximation

$$f(\tilde{u}) = -\beta[\tilde{u} - H(\tilde{u} - \tilde{u}_{thr})],$$

where $H(\tilde{u} - \tilde{u}_{thr})$ is a Heaviside step function.

(ii) We restrict our analysis to small deformation values so that nonlinear terms in Eq. (9) may be neglected [36]:

$$|\tilde{\varepsilon}| \ll 2/7. \tag{13}$$

Condition (13) has to be checked *a posteriori*, after obtaining the solution, to justify the linearization.

After introducing the following dimensionless quantities,

$$\xi = \tilde{\xi}\Bigg/\left(\frac{R_0}{4\beta}\sqrt{\frac{\alpha\Upsilon}{\mu}}\right), \quad p = \frac{\tilde{p}}{\Upsilon}, \quad \varepsilon = \frac{\alpha\tilde{\varepsilon}}{\beta}, \quad u = \tilde{u},$$
$$v = \beta\tilde{v}, \quad V = \tilde{V}\Bigg/\left(\frac{R_0}{4}\sqrt{\frac{\alpha\Upsilon}{\mu}}\right),$$
$$\tau_s = \beta\tilde{\tau}_s, \quad \tau_c = \beta\tilde{\tau}_c, \quad E = \frac{\beta\tilde{E}}{\alpha\Upsilon}, \quad u_{thr} = \tilde{u}_{thr},$$
$$D = \frac{16\mu\beta\tilde{D}}{\alpha\Upsilon R_0^2}, \quad \kappa = \frac{\tilde{\kappa}}{\beta}, \quad \delta = \beta\tilde{\delta}, \tag{14}$$

the piecewise-linear version of the model takes the following form:

$$-V\varepsilon = p', \tag{15}$$
$$-V\tau_s p' + p = E(\varepsilon - V\tau_c\varepsilon') + u, \tag{16}$$
$$-Vu' = \varepsilon - u + H(u - u_{thr}) - v + Du'', \tag{17}$$
$$-Vv' = \kappa(u - \delta v). \tag{18}$$

For a piecewise-linear set of Eqs. (15)–(18) the problem of finding solutions results in an eigenvalue problem which is analytically tractable for an arbitrary set of governing parameters $\{\tau_s,\tau_c,E,u_{thr},D,\kappa,\delta\}$. The procedure we have followed to construct the solution is given, for example, in [32,37]. An example of the solution obtained is presented in Fig. 2.

A comprehensive discussion of the properties of the solution will be provided elsewhere. In this paper we focus solely on the asymptotic behavior of the solution in two limiting cases that are interesting from a biological standpoint. The cases we deal with are as follows:

(i) $I(\varepsilon) \equiv 0$, i.e., the case of negligible mechanosensitive input into muscle contraction-relaxation control circuits.

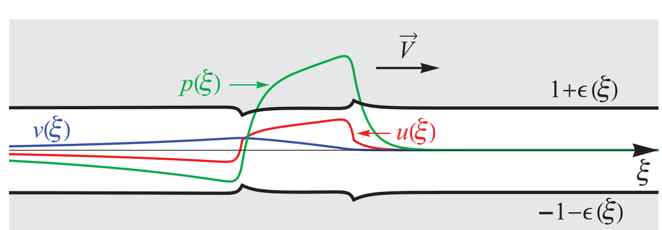

FIG. 2. (Color online) An example of the solution ($\tau_s = 0$, $\tau_c = 0$, $E = 1$, $u_{thr} = 0.3$, $D = 0$, $\kappa = 0.05$, $\delta = 0.1$).

(ii) $D \equiv 0$, i.e., the case of negligible synaptic conductivity between the adjacent tube segments.

Case 1: $I(\varepsilon) \equiv 0$. In this section we discuss the case when currents arising in smooth muscle cells of a given tube segment in response to mechanical deformation are negligible in comparison with those induced by synaptic transmission from the adjacent tissue segment.

One can easily see that when $I(\varepsilon) \equiv 0$ Eqs. (17) and (18) for u and v variables can be solved independently of the equations (15) and (16) that define p and ε. The eigenvalue problem that results from the $\{u,v\}$ equations defines the magnitude of the wave velocity, which is independent of the peculiarities of the mechanical state of the vessel [38]. One can easily derive from Eqs. (17) and (18) that, in the singular limit when the excitable variable u is much faster than the recovery variable v [39], the velocity is given by

$$V_1 = \gamma\sqrt{D}, \tag{19}$$

where

$$\gamma = \frac{1 - 2u_{thr}}{\sqrt{u_{thr} - u_{thr}^2}}. \tag{20}$$

It is worth mentioning that the expression (19) is analogous to the formula for the velocity of uniformly propagating flame front predicted by the Zel'dovich–Frank-Kamenetsky model [41,42]. The solution is unique and exists provided that [43]

$$u_{thr} < 1/2. \tag{21}$$

Case 2: $D \equiv 0$. In this section we consider the case when the mechanosensitive currents are much greater than those induced by synaptic connectivity [44].

The analysis of the system in this special case indicates that even if synaptic connectivity is ceased altogether, self-sustained propagation of peristaltic waves is still possible. The mechanism of propagation is as follows. The transported fluid bolus results in the dilation of the tube segment which, being sufficiently large, causes the vessel segment to contract. (Mechanosensitive currents presented with $I(\varepsilon)$ in the model equations serve as a trigger for contraction.) Contraction pushes the fluid bolus into the adjacent segment where it, in turn, causes dilation. If the dilation reaches a threshold value, active contraction is triggered and the sequence of events repeats itself. Thus, through hydroelastic interactions, a self-sustained wave of deformation propagates along the tube.

We have deduced two asymptotic formulas for the velocity of traveling waves in the $D \equiv 0$ case. Both formulas refer to the singular limit of a slow recovery variable (see Ref. [39]).

The first one is derived under the assumption that the rates at which p, ε, u change during the passage of a peristaltic wave are much smaller than those of stress relaxation and creep within the wall tissue. The reduced set of equations can be obtained from Eqs. (15)–(17) by formally setting the stress and stretch relaxation times equal to zero: $\tau_s = \tau_c \equiv 0$. It was found that the velocity of the traveling front under conditions described above is given by

$$V_{2a} = \sqrt{1 - E + \gamma\sqrt{E}}. \tag{22}$$

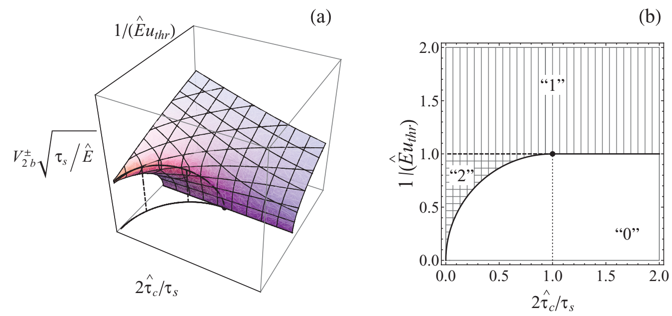

FIG. 3. (Color online) (a) $V_{2b}^{\pm}$ plotted against $2\hat{\tau}_c/\tau_s$ and $1/(\hat{E}u_{thr})$. (b) Bifurcation diagram. The number of traveling-wave solutions in each region is as follows: "0" −0, "1" −1, "2" −2.

A unique traveling front solution corresponding to Eq. (22) exists provided that

$$E < (1 - u_{thr})/u_{thr}. \tag{23}$$

The second asymptotic formula applies to the situation when the excitable variable u reaches quasisteady state on a much shorter time scale than that at which variables p,ε,u change during the passage of the wave. The reduced set of equations is obtained from Eqs. (15)–(17) by resolving Eq. (17) with a steady state approximation, i.e., by setting

$$\varepsilon = u - H(u - u_{thr}).$$

It was shown that the solution of the eigenvalue problem corresponding to this limit is not necessarily unique. The number of the solutions depends on relative values of two parameter combinations (see Fig. 3). The parametric plane is divided into three separate regions with either no solutions (region "0"), one solution (region "1") or two traveling front solutions (region "2"). The critical lines are given by

$$1/(\hat{E}u_{thr}) = 1,$$
$$(2\hat{\tau}_c/\tau_s - 1)^2 + 1/(\hat{E}u_{thr})^2 = 1,$$

where $\hat{E} \equiv E + 1$, $\hat{\tau}_c = \tau_c E/\hat{E}$. The velocities corresponding to the solutions are given by

$$V_{2b}^{\pm} = \sqrt{\hat{E}/\tau_s} \times \sqrt{1 - 2\hat{\tau}_c/\tau_s \pm \sqrt{(1 - 2\hat{\tau}_c/\tau_s)^2 + 1/(\hat{E}u_{thr})^2 - 1}}. \tag{24}$$

The linear stability analysis performed in much the same way as in [32,34,37] indicates that slower fronts [corresponding to the "–" sign in formula (24)] are unstable. The existence condition for stable solution is as follows:

$$\{\hat{E}u_{thr} < 1\} \bigcup \{2\hat{\tau}_c/\tau_s < 1 - \sqrt{1 - 1/(\hat{E}u_{thr})^2}\}. \tag{25}$$

We have introduced a rather simple phenomenological model of biological peristalsis. The model is based on a one-dimensional description of fluid dynamic Eq. (1) coupled to a constitutive equation describing the rheological properties of the contractile vessel wall tissue Eq. (2). The contractile tissue is treated as an active medium in a fashion similar to the one accepted in [46–48] (see Refs. [17,49,50] for additional information on active media research).

It should be noted that Eqs. (1) and (2) and their close analogs have appeared together in previous work to calculate the fluid-wall interaction during peristaltic pumping [20–22]. Similarly, Eqs. (3) and (4) have formerly been used to simulate the electrical activity associated with peristalsis [47]. Combining these equations into a single model, however, has not been suggested previously.

The ability of a transporting system to perform autonomous peristaltic pumping is interpreted as the ability to propagate sustained waves of wall deformation. Hence the mathematical problem of describing self-sustained peristalsis comes to finding traveling-wave solutions of the model and analyzing their dependence on the model parameters.

The solutions obtained in the present paper correspond to single-wave peristaltic pumping such as occurs in the esophagus [1], the gastrointestinal tract (propulsive pumping regimes) [2,3,12,16], and the ureter at low urine formation rates [4,10].

This paper describes the results of the analysis in several biologically relevant limiting cases. In these cases explicit existence conditions for traveling-wave solutions have been established [see (21), (23), (25)]. Explicit formulas have been derived which relate the speed of self-sustained peristaltic waves to mechanical and electrical properties of the transporting system (e.g., the Young's modulus of the vessel, the viscosity of the transported fluid, the sensitization of local reflex responses, etc.) [51]. See Fig. 4 for an example of velocity curves predicted by the model.

It should be noted that asymptotic velocities V_{2a} and V_{2b} (limiting case 2: $D \equiv 0$) correspond to explicit solutions with piecewise-continuous displacement gradients $\varepsilon'(\xi)$ and displacements $\varepsilon(\xi)$, respectively. Rigorously speaking, this means that on approaching the corresponding limiting sets of parameters we overstep (in the vicinity of the matching point) the restrictions imposed by the lubrication-theory–thin-wall approximation. This is a potential weakness of the piecewise-linear modeling. To verify the analytical calculations a series of numerical experiments with a continuous reaction term has been conducted. The comparison of the results reveals that such characteristics of the solution as bounded existence domain and propagation velocity dependence on rheological parameters of the transporting vessel and the transported fluid are robust, independent of the peculiarities of nonlinear function representation. Formulas (22) and (24) provide a good estimate for the velocity of a continuous solution in a wide range of parameters.

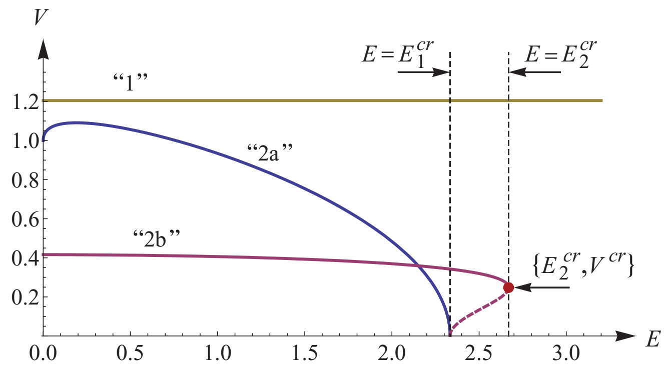

FIG. 4. (Color online) Dependence of traveling front velocity on the Young's modulus of the vessel wall ($u_{thr} = 0.3$, $D = 0.4$, $\tau_s = 25$, $\tau_c = 10$). Curves "1", "2a", "2b" illustrate the dependences $V = V_1$, $V = V_{2a}$, $V = V_{2b}^{\pm}$ given by Eqs. (19), (22), and (24), respectively. Note that hysteresis is expected with variation of parameter E in the limit corresponding to $V = V_{2b}^{\pm}$ (curve "2b"). E_1^{cr}, E_2^{cr}, V^{cr} are given by the following formulas: $E_1^{cr} = (1 - u_{thr})/u_{thr}$, $E_2^{cr} = \frac{\sqrt{\tau_s/(u_{thr}^2 \tau_c)+1-1/u_{thr}^2}-1}{2(1-\tau_c/\tau_s)}$, $V^{cr} = \sqrt{\frac{E_2^{cr}+1}{\tau_s}}\sqrt{1 - 2\frac{\tau_c}{\tau_s}\frac{E_2^{cr}}{E_2^{cr}+1}}$.

We strongly believe that the results, especially the explicit asymptotic formulas (19), (22), and (24) for the velocity of the wave, open up alternative possibilities for the interpretation of a wide range of physiological transport phenomena. In particular they may contribute to diagnostic procedures just as the Moens-Korteweg formula for the velocity of pulse wave propagation contributes to the diagnosis of hypertension [52,53]. The results may also prove useful in the qualitative analysis of the therapeutic effects of various drugs on peristaltic motility.

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[39] If the recovery is slow the velocity of the wave is only weakly dependent on the parameters which characterize the recovery process. The movement of the leading edge of the wave can then be approximated by an advancing traveling front [40]. The eigenvalue problem for the front is formulated by putting $v \equiv v|_{\xi\to+\infty} = 0$ in Eqs. (15)–(18) and searching for $p(\xi)$, $\varepsilon(\xi)$, $u(\xi)$ which satisfy the following conditions: $\{p,\varepsilon,u,u'\} \to \{0,0,0,0\}$ as $\xi \to +\infty$, $\{p,\varepsilon,u,u'\} \to \{1,0,1,0\}$ as $\xi \to -\infty$.

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