## MATCHED ASYMPTOTIC EXPANSIONS OF THE GREEN'S FUNCTION FOR THE ELECTRIC POTENTIAL IN AN INFINITE CYLINDRICAL CELL\*

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Abstract. The potential is studied for a microelectrode current source inside a nerve fiber. The problem is represented by a point source in an infinitely long cylindrical conductor surrounded by a thin, low conductivity membrane bathed in a perfectly conducting medium. The potential satisfies Laplace's equation with a mixed boundary condition containing a small parameter  $\varepsilon$ . As  $\varepsilon \to 0$  it approaches a homogeneous Neumann condition and the problem becomes singular. Asymptotic expansions are obtained in terms of  $\varepsilon$  by matching an inner expansion (valid at the source) to an outer expansion (valid away from the source). The inner expansion contains algebraic switchback terms whose orders are half-odd-integer powers of  $\varepsilon$ , as well as terms whose orders are integer powers of  $\varepsilon$  which can be expressed as algebraic terms plus Fourier series with Fourier integral coefficients. The outer expansion is made uniform by introducing a strained axial coordinate, which appears in an exponential factor multiplying an asymptotic series depending on radial position and radial location of the source. The asymptotic expansions are identical to results obtained directly from the eigenfunction expansion of the exact solution for arbitrary  $\varepsilon$ .

1. Introduction. It has become apparent recently that a number of problems in biology require the solution of Laplace's equation with a boundary condition which describes the properties of the membrane surrounding a biological cell, separating the interior from the exterior, and buffering the internal environment from external disturbance [6], [1]. The membrane serves as an electrical buffer because its resistivity is much greater than the resistivity of the cell interior. The membrane boundary condition, therefore, contains a small parameter  $\varepsilon$ , the ratio of the internal resistance to the membrane resistance in appropriate units. The presence of the small parameter suggests the use of perturbation expansions in the solution of the problem and such expansions are particularly appropriate to biological problems [6] since they display the dependence of the solutions on the parameters of the problem and thereby provide physical insight. Both of these qualities are frequently of more importance in biology than the precise dependence of the potential on spatial coordinates.

Here we consider a problem which arises when the electrical properties of cylindrical cells are investigated by the application of current to the interior of the cell from a microelectrode, a glass micropipette filled with conducting salt solution. The potential in the interior of the cell obeys Laplace's equation. The boundary condition is that the normal derivative of the potential at the inside surface of the membrane (proportional to the normal component of current) is proportional to the potential difference across the membrane. If the microelectrode is considered a point source of current, the solution to the problem is

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the Green's function for the electric potential in a cylinder with a membrane boundary condition.

The analysis of the problem can be done by exact methods [3], [5], for arbitrary v, or it can be done by asymptotic methods. Regular perturbation expansions are not possible since in the limit  $\varepsilon \to 0$ , the boundary condition approaches a homogeneous Neumann condition in which no current flows across the membrane. Since current is being injected into the interior of the cell, a homogeneous Neumann condition on all boundaries is clearly impossible. and the problem is singular. Asymptotic expansions have been obtained by direct expansion of the exact solution [3], [5], and by the method of multiple scales [1]; the latter result has difficulties we discuss below. The present analysis uses the method of matched asymptotic expansions which allows the interpretation of each term in the expansion as the solution to a physical problem. This property is important if one wishes to generalize the results to account for the effects of nonlinearities, which are usually present in biological applications. In addition, the singular perturbation solutions are easily generalized to irregular geometries: e.g., the leading term in the asymptotic expansions is valid for a cylinder of arbitrary cross section.

2. The mathematical problem and its singular nature. The problem for determining the potential may be written, in cylindrical coordinates,

$$\frac{1}{r}\frac{\partial}{\partial r}\left(r\frac{\partial V}{\partial r}\right) + \frac{1}{r^2}\frac{\partial^2 V}{\partial \theta^2} + \frac{\partial^2 V}{\partial x^2} = -\frac{1}{r}\delta(x)\delta(r - R)\delta(\theta),$$
(1)
$$\frac{\partial V}{\partial r}(x, 1, \theta) + \varepsilon V(x, 1, \theta) = 0,$$

$$V(\pm \infty, r, \theta) = 0,$$

where the coordinate along the cylinder axis is denoted by x (to conform to the notation in the biological literature on one-dimensional cable theory) and r and  $\theta$  are the usual radial coordinate and polar angle in the plane perpendicular to the x-axis.

The problem posed by (1) can be solved exactly, for any  $\varepsilon$ , in the form of a double infinite sum or a single infinite sum of infinite integrals of Bessel functions [5]. The behavior of these exact solutions for small  $\varepsilon$  can then be obtained by taking appropriate limits of the solutions, letting  $\varepsilon \to 0$  in a region including the source and in a region some distance from the source.

Since we are only interested in the small- $\varepsilon$  behavior of the solution, we can alternatively by-pass the exact solution entirely and apply the techniques of singular perturbation theory to (1). The procedure is to generate a sequence of problems from (1). Each problem in the sequence is simpler than the original problem; its solution corresponds to one term in the expansion of the exact solution in powers of  $\varepsilon$ . We find one sequence of problems, and its corresponding expansion of the potential, which is valid near the source, another which is valid far from the source, and use the technique of matching [2] to join the two together in the intermediate region where they are both valid. This mathematical approach

is justified by the physical insight gained since each individual term in the expansions is the solution of a relatively simple problem. It is also reassuring that in a number of similar problems, the asymptotic representation determined this way corresponds to a direct  $\varepsilon$ -expansion of the exact solution.

Let us consider first the basis for the singular nature of the problem. When  $\varepsilon$  is small, the boundary condition at r=1 in (1) implies that the current flow will be predominantly in the axial direction, i.e., only a small fraction of the local current  $O(\varepsilon)$ , crosses the membrane in an axial distance of O(1). We are tempted to try to find an expansion in the small parameter  $\varepsilon$ , in which the leading term is the potential for  $\varepsilon=0$ . Denoting this term by  $V_1(x,r,\theta)$ , we see from (1) that  $V_1$  satisfies

(2) 
$$\frac{1}{r}\frac{\partial}{\partial r}\left(r\frac{\partial V_1}{\partial r}\right) + \frac{1}{r^2}\frac{\partial^2 V_1}{\partial \theta^2} + \frac{\partial^2 V_1}{\partial x^2} = -\frac{1}{r}\delta(x)\delta(r-R)\delta(\theta),$$

$$\frac{\partial V_1}{\partial r}(x, 1, \theta) = 0.$$

The boundary condition at r=1 in (2) implies that no current crosses the membrane; all the current is confined to the interior of the cell. Consequently,  $V_1$  must contain a part which is linearly decreasing with increasing |x|. This would lead to a potential of  $V_1 \to -\infty$  as  $|x| \to \infty$ , making it impossible to satisfy the boundary condition at  $|x| = \infty$  in (1), namely that V = 0 at  $|x| = \infty$ . To avoid this divergence, any expansion which contains  $V_1$  can be valid only over a limited range of x, designated the near field, which contains the source point. At large distances from the source, we must look for another, far-field, expansion.

We expect that as  $\varepsilon \to 0$ , the region of validity of any near-field expansion of which  $V_1$  is a part, becomes larger. If there is a linearly decaying potential over a large distance, and the potential approaches zero as  $|x| \to \infty$ , then the potential at x = 0 must be very large, i.e.,  $V(0, r, \theta) \to \infty$  as  $\varepsilon \to 0$ . Clearly,  $V_1$  must be O(1), and cannot be the leading term in the expansion. The leading term can be found by matching to the far-field solution, and therefore we first solve the far-field problem.

3. Far-field potential. In the far field, a long distance from the source, current flow is predominantly in the axial direction. Since only a small fraction of the current within the cell, at any value of x, leaks out of the cylinder in an axial distance of O(1), the variation in the x direction will be slow. We therefore, for convenience in ordering the far-field expansion, write the far-field potential in terms of a new slow variable  $x^*$ . Denoting the potential in the far field by W, we write the following expansion:

(3) 
$$W(x^*, r, \theta; \varepsilon) = \zeta_0(\varepsilon)W_0(x^*, r, \theta) + \zeta_1(\varepsilon)W_1(x^*, r, \theta) + \cdots,$$

where the slow variable is defined by

$$(4) x^* = x\eta(\varepsilon),$$

 $W_n$  is of O(1),  $\zeta_n/\zeta_{n-1} \to 0$  as  $\varepsilon \to 0$ , and in accordance with the physical argument given above, it is expected that  $\eta \to 0$  as  $\varepsilon \to 0$ .

Substituting (3) and (4) in (1), and noting that the source is outside the present domain, we have

(5) 
$$\nabla^2 W = 0 = \zeta_0 \eta^2 \frac{\partial^2 W_0}{\partial x^{*2}} + \zeta_1 \eta^2 \frac{\partial^2 W_1}{\partial x^{*2}} + \dots + \zeta_0 \nabla_t^2 W_0 + \zeta_1 \nabla_t^2 W_1 + \dots,$$

where  $\nabla_t^2 = (1/r)(\hat{c}/\partial r)(r\,\hat{c}/\partial r) + (1/r^2)(\hat{c}^2/\partial \theta^2)$  is the transverse Laplacian, and on the boundary, r = 1, we have

(6) 
$$\frac{\partial W}{\partial r} + \varepsilon W = 0 = \zeta_0 \frac{\partial W_0}{\partial r} + \zeta_1 \frac{\partial W_1}{\partial r} + \cdots + \varepsilon \zeta_0 W_0 + \varepsilon \zeta_1 W_1.$$

Requiring that (5) and (6) be satisfied to each order of  $\varepsilon$ , the lowest-order  $\varepsilon$  problem is

(7) 
$$\nabla_{t}^{2}W_{0} = 0,$$

$$\frac{\partial W_{0}}{\partial r}(x^{*}, 1, \theta) = 0,$$

$$W_{0}(\pm \infty, r, \theta) = 0.$$

The second problem is

(8) 
$$\nabla_{t}^{2}W_{1} = -\frac{\partial^{2}W_{0}}{\partial x^{*2}},$$

$$\frac{\partial W_{1}}{\partial r}(x^{*}, 1, \theta) = -W_{0}(x^{*}, 1, \theta),$$

$$W_{1}(\pm \infty, r, \theta) = 0,$$

where we have set

$$\varepsilon \zeta_0 = \zeta_1$$

to obtain the r = 1 boundary condition in (8).

Writing an expansion for  $\eta(\varepsilon)$  in the form

(10) 
$$\eta(\varepsilon) = \eta_0(\varepsilon) + \eta_1(\varepsilon) + \eta_2(\varepsilon) + \cdots,$$

where the  $\eta_i(\varepsilon)$  are an ordered sequence, we further set

$$\zeta_0 \eta_0^2 = \zeta_1$$

to obtain the equation in (8). Thus

(11) 
$$\eta_0 = \sqrt{\varepsilon}.$$

We could take  $\eta = \eta_0$ , with  $\eta_1 = \eta_2 = \cdots = 0$ , and still obtain a sequence of problems of increasing order in  $\varepsilon$ . It will be seen below, however, that we would not be able to maintain uniform validity of the asymptotic expansion for W at large  $x^*$ . Assuming  $\eta(\varepsilon)$  to have the more general form (10) makes it possible to obtain a uniform expansion.

The third problem is found by collecting terms of the next higher order in  $\varepsilon$  in (5) and (6) and is

(12) 
$$\nabla_t^2 W_2 = -\frac{\hat{c}^2}{\hat{c}x^{*2}} (W_1 + 2\alpha_1 W_0),$$

$$\frac{\partial W_2}{\partial r} (x^*, 1, \theta) = -W_1(x^*, 1, \theta),$$

$$W_2(\pm x, r, \theta) = 0,$$

where we set

$$\varepsilon \zeta_1 = \zeta_2$$

to obtain the r = 1 boundary condition in (12), and

$$\eta_1 = \alpha_1 \varepsilon \eta_0$$

to obtain the equation in (12). Continuing this process of collecting terms of equal order in  $\varepsilon$  in (5) and (6), we obtain, for the fourth problem,

$$\nabla_{r}^{2}W_{3} = -\frac{\partial^{2}}{\partial x^{*2}}(W_{2} + 2\alpha_{1}\dot{W}_{1} + (\alpha_{1}^{2} + 2\alpha_{2})W_{0}),$$

$$\frac{\partial W_{3}}{\partial r}(x^{*}, 1, \theta) = -W_{2}(x^{*}, 1, \theta),$$

$$W_{3}(\pm \infty, r, \theta) = 0.$$

Combining (3), (9)–(11), (13), (14) and the additional requirements on  $\zeta_3$  and  $\eta_2$  needed to obtain (15), we have, for the far-field expansion of the potential,

$$(16) W(x^*, r, \theta; \varepsilon) = \zeta_0(\varepsilon)[W_0(x^*, r, \theta) + \varepsilon W_1(x^*, r, \theta) + \varepsilon^2 W_2(x^*, r, \theta) + \cdots],$$

where the axial coordinate variable is

(17) 
$$x^* = \sqrt{\varepsilon} x(1 + \alpha_1 \varepsilon + \alpha_2 \varepsilon^2 + \cdots).$$

So far  $\zeta_0(\varepsilon)$ , the order of the leading term in the W expansion, is unknown. It will be determined by matching to the near field. The constants  $\alpha_1, \alpha_2 \cdots$  in the expansion of  $x^*$ , which couple different orders of W in the sequence of problems, will be determined by requiring uniform validity of the W expansion (16) for all values of  $x^*$ .

We now return to (7) and begin to solve the sequence of problems. The solution to the first problem (7) is independent of r and  $\theta$ . Thus we have

(18) 
$$W_0(x^*, r, \theta) = F(x^*),$$

where  $F(x^*)$  is an as yet arbitrary function of  $x^*$ . We must go to the second problem, (8), to determine its functional form.

From (8) and (18) we obtain

(19) 
$$\frac{1}{r} \frac{\partial}{\partial r} \left( r \frac{\partial W_1}{\partial r} \right) + \frac{1}{r^2} \frac{\partial^2 W_1}{\partial \theta^2} = -F''(x^*).$$

$$\frac{\partial W_1}{\partial r} (x^*, 1, \theta) = -F(x^*).$$

$$W_1(\pm \infty, r, \theta) = 0.$$

where prime denotes differentiation with respect to  $x^*$ .

Since the inhomogeneous term in the equation, and the boundary condition at r = 1, are both independent of  $\theta$ , clearly, W is independent of  $\theta$ . Examining (12) and (15) the same reasoning then implies that  $W_2, W_3, \cdots$  are all independent of  $\theta$ 

Integrating the equation in (19) twice (noting that  $\partial^2 W_1/\partial\theta^2$  is zero), we obtain, for the solution which is bounded at r=0,

(20) 
$$W_1(x^*, r) = -\frac{r^2}{4}F''(x^*) + G(x^*),$$

where  $G(x^*)$  is an, as yet, arbitrary function of  $x^*$  which cannot be determined until we go to the next problem, (12), for  $W_2$ .

Substituting the result (20) in the r = 1 boundary condition of (19) yields

(21) 
$$F'' - 2F = 0,$$

and hence

(22) 
$$W_0(x^*) = F(x^*) = A e^{-\sqrt{2}|x^*|},$$

where A is a constant to be determined by matching to the near field.

Substituting  $W_0$  and  $W_1$ , from (18) and (20) in (12) and using (21) to eliminate derivatives of F, and deleting the  $\theta$ -dependence in accordance with our findings, we obtain

(23) 
$$\frac{1}{r}\frac{\partial}{\partial r}\left(r\frac{\partial W_2}{\partial r}\right) = (r^2 - 4\alpha_1)F - G'',$$

$$\frac{\partial W_2}{\partial r}(x^*, 1) = \frac{1}{2}F - G,$$

$$W_2(\pm \infty, r) = 0$$

for the next problem.

Integrating the equation in (23) twice and requiring the result to be finite at r = 0, we obtain

(24) 
$$W_2(x^*, r) = \frac{r^4}{16}F - r^2\left(\alpha_1F + \frac{1}{4}G''\right) + H(x^*),$$

where  $H(x^*)$  is an arbitrary function of  $x^*$ .

Substituting the expression (24) for  $W_2$  and (22) for F in the r=1 boundary condition in (23) yields

(25) 
$$G'' - 2G = -4A(\alpha_1 + \frac{1}{8}) e^{-\sqrt{2}|x^*|}.$$

The right-hand side of (25) is a homogeneous solution of the equation. Therefore the particular solution contains a term proportional to  $x^*$  times  $\exp{(-\sqrt{2}|x^*|)}$ . If such a term appears in G, then for sufficiently large  $|x^*|$  (i.e.,  $|x^*| \gtrsim \varepsilon^{-1}$ ) the equality

$$\lim_{\varepsilon \to 0} \frac{\varepsilon W_1}{W_0} = 0$$

will not be satisfied and hence the expansion (16) will not be valid uniformly in  $x^*$ . To avoid this we require the right-hand side of (25) to vanish, which occurs if

$$\chi_1 = -\frac{1}{8}$$

It is now clear why we could not assume the simple relation  $x^* = \sqrt{\varepsilon} x$  but required the more general form (17). The freedom to choose  $\alpha_1, \alpha_2, \cdots$  allows us to force all of the  $x^*$ -dependence of W into  $\exp(-\sqrt{2}x^*)$ , eliminating non-uniformities in the expansion.

With the choice (26) of  $\alpha_1$ , the solution to (25) is

(27) 
$$G(x^*) = B e^{-\sqrt{2}x^*},$$

where

(28) 
$$x^* = \sqrt{\varepsilon} \left( 1 - \frac{\varepsilon}{8} + \cdots \right),$$

and B will be determined by matching to the near field.

Substituting (22) and (27) for F and G in (20) we obtain for the second term in the far-field expansion

(29) 
$$W_1(x^*, r) = (-\frac{1}{2}Ar^2 + B)e^{-\sqrt{2}x^*}.$$

We shall now continue the same procedure in the next problem (15), to obtain an expression for  $W_2$ , and to find  $x^*$  to one more order in  $\varepsilon$ .

Substituting (18), (20) and (24) in (15) and using (21), (25) and (26) we obtain, for the next problem

$$\frac{1}{r}\frac{\partial}{\partial r}\left(r\frac{\partial W_3}{\partial r}\right) = -\left(\frac{r^4}{8} + \frac{r^2}{2} + \frac{1}{32} + 4\alpha_2\right)F + \left(r^2 + \frac{1}{2}\right)G - H'',$$

$$\frac{\partial W_3}{\partial r}(x^*, 1) = -\frac{3}{16}F + \frac{1}{2}G - H,$$

$$W_3(\pm \infty, r) = 0.$$

Integrating the equation in (30) once, setting r = 1 in the result, and substituting this in the r = 1 boundary condition yields the equation

(31) 
$$H'' - 2H = (\frac{5}{96} - 4\alpha_2)F.$$

Repeating our earlier arguments, we require the right-hand side of (31) to be zero in order to maintain uniformity of the expansion in  $x^*$ . This yields

$$\alpha_2 = \frac{5}{384},$$

and

$$(33) H(x^*) = C e^{-\sqrt{2}x^*},$$

where C is to be determined by matching, and we now have  $x^*$  to one more order:

(34) 
$$x^* = x\sqrt{\varepsilon} \left( 1 - \frac{\varepsilon}{8} + \frac{5}{384} \varepsilon^2 - \cdots \right).$$

Substituting (22), (27) and (33) for F, G and H and (26) for  $\alpha_1$ , in (24) we obtain

(35) 
$$W_2(x^*, r) = \left\lceil \frac{Ar^2}{8} \left( 1 + \frac{r^2}{2} \right) - \frac{Br^2}{2} + C \right\rceil e^{-\sqrt{2}|x^*|}.$$

Substituting (22), (29) and (35) in (16) we obtain, for the far-field expansion

(36) 
$$W(x^*, r; \varepsilon) = \zeta_0(\varepsilon) e^{-\sqrt{2}|x^*|} \left[ A + \varepsilon \left( -\frac{Ar^2}{2} + B \right) + \varepsilon^2 \left( \frac{Ar^2}{8} \left( 1 + \frac{r^2}{2} \right) - \frac{Br^2}{2} + C \right) + O(\varepsilon^3) \right],$$

where  $x^*$  is given to  $O(\varepsilon^2)$  by (34). The three constants A, B and C, and the function  $\zeta_0(\varepsilon)$  are to be determined by matching the  $x^* \to 0$  limit of  $W(x^*, r; \varepsilon)$  to the  $|x| \to \infty$  limit of the near-field expansion,  $V(x, r, \theta; \varepsilon)$ . We accomplish this by writing both W and V in terms of x and requiring that the  $x \to \infty$  limit of the near-field expansion be identical to the far-field expansion. This procedure is discussed in detail, with many examples, elsewhere [2].

Substituting the expression (34) for  $x^*$  in (36), expanding the exponential to  $O(\varepsilon^{5/2})$ , multiplying by the expression in square brackets, and arranging terms in ascending powers of  $\varepsilon$ , we obtain

$$W\left(x\sqrt{\varepsilon}\left(1-\frac{\varepsilon}{8}+\frac{5\varepsilon^{2}}{384}-\cdots\right),r;\varepsilon\right)$$

$$=\zeta_{0}(\varepsilon)\left[A-\varepsilon^{1/2}A\sqrt{2}|x|+\varepsilon\left[A\left(x^{2}-\frac{r^{2}}{2}\right)+B\right]\right]$$

$$+\varepsilon^{3/2}\sqrt{2}|x|\left[A\left(\frac{1}{8}-\frac{x^{2}}{3}+\frac{r^{2}}{2}\right)-B\right]$$

$$+\varepsilon^{2}\left[A\left(-\frac{x^{2}}{4}+\frac{x^{4}}{6}-\frac{r^{2}x^{2}}{2}+\frac{r^{2}}{8}+\frac{r^{4}}{16}\right)+B\left(x^{2}-\frac{r^{2}}{2}\right)+C\right]$$

$$+\varepsilon^{5/2}\sqrt{2}|x|\left[A\left(-\frac{5}{384}+\frac{x^{2}}{8}+\frac{x^{2}r^{2}}{6}-\frac{3r^{2}}{16}-\frac{r^{4}}{16}-\frac{x^{4}}{30}\right)+B\left(\frac{1}{8}-\frac{x^{2}}{3}+\frac{r^{2}}{2}\right)-C\right]+O(\varepsilon^{3})\right].$$

The expansion (37) of W in near-field coordinates contains integral powers of  $\sqrt{\epsilon}$ , whereas the expansion (36) in far-field coordinates contains only integral powers of  $\varepsilon$ . The powers of  $\sqrt{\epsilon}$  arise from expanding the exponential in (36). It should be noted that an individual term of  $O(\epsilon^n)$  in (36) contributes to all orders equal to or greater than  $\epsilon^n$  in (37). Consequently, although each term in (36) is the solution to a particular problem in the far-field, each term in (37) is not related in any simple way to a physical problem in the far-field.

4. Near-field potential. In the vicinity of the point source the potential is a rather complex function of position, and there is no simple mathematical representation in terms of elementary functions, as there is in the far field. The potential has a singularity at the source point; the current diverges from this point, half going toward  $x = +\infty$ , and half toward  $x = -\infty$ . Close to the source, the lines of current flow are diverging outward, equally in all directions. Those lines which are directed toward the membrane must curve to avoid the membrane as, again, only a small fraction of the local current leaves the cylinder. As the current flows down the cylinder, the lines become predominantly in the axial direction, and the potential joins smoothly onto the far-field potential calculated in § 3.

In terms of the asymptotic expansions representing the near and far fields, this behavior requires that the near-field expansion increase in powers of  $\sqrt{\varepsilon}$  so it can join to the expansion (37) of the far field. Furthermore, in accordance with the arguments following (2), which concluded that the O(1) term in the near field has a linear dependence on |x| as  $|x| \to \infty$ , we see that the second term in (37) must be O(1) in order to match the near field. Consequently,

(38) 
$$\zeta_0(\varepsilon) = \frac{1}{\sqrt{\varepsilon}},$$

and the near-field expansion must be of the form

(39) 
$$V(x, r, \theta; \varepsilon) = \varepsilon^{-1/2} V_0(x, r, \theta) + V_1(x, r, \theta) + \varepsilon^{1/2} V_2(x, r, \theta) + \varepsilon V_2(x, r, \theta) + \cdots$$

Substituting (39) in (1), and requiring the large-x behavior in each order to conform to (37), we obtain the following sequence of near-field problems:

(40) 
$$\nabla^{2} V_{0} = 0,$$

$$\frac{\partial V_{0}}{\partial r}(x, 1, \theta) = 0,$$

$$V_{0}(x, r, \theta) \to A \quad \text{as } |x| \to \infty,$$

$$\nabla^{2} V_{1} = -\frac{1}{r} \delta(x) \delta(r - R) \delta(\theta),$$

$$\frac{\partial V_{1}}{\partial r}(x, 1, \theta) = 0.$$

$$V_{1}(x, r, \theta) \to -A\sqrt{2} |x| \quad \text{as } |x| \to \infty,$$

$$\nabla^{2}V_{2} = 0,$$

$$\frac{\partial V_{2}}{\partial r}(x, 1, \theta) = -V_{0}(x, 1, \theta),$$

$$V_{2}(x, r, \theta) \to A\left(x^{2} - \frac{r^{2}}{2}\right) + B \quad \text{as } |x| \to \infty,$$

$$\nabla^{2}V_{3} = 0$$

$$\frac{\partial V_{3}}{\partial r}(x, 1, \theta) = -V_{1}(x, 1, \theta),$$

$$V_{3}(x, r, \theta) \to \sqrt{2}|x| \left[ A\left(\frac{1}{8} - \frac{x^{2}}{3} + \frac{r^{2}}{2}\right) - B \right] \quad \text{as } |x| \to \infty,$$

$$\nabla^{2}V_{4} = 0,$$

$$\frac{\partial V_{4}}{\partial r}(x, 1, \theta) = -V_{2}(x, 1, \theta),$$

$$V_{4}(x, r, \theta) \to A\left(-\frac{x^{2}}{4} + \frac{x^{4}}{6} - \frac{r^{2}x^{2}}{2} + \frac{r^{2}}{8} + \frac{r^{4}}{16}\right) + B\left(x^{2} - \frac{r^{2}}{2}\right) + C$$

$$\Delta^{2}V_{5} = 0,$$

$$\frac{\partial V_{5}}{\partial r}(x, 1, \theta) = -V_{3}(x, 1, \theta),$$

$$V_{5}(x, r, \theta) \to \sqrt{2}|x| \left[ A\left(-\frac{5}{384} + \frac{x^{2}}{8} + \frac{x^{2}r^{2}}{6} - \frac{3r^{2}}{16} - \frac{r^{4}}{16} - \frac{x^{4}}{30}\right) + B\left(\frac{1}{8} - \frac{x^{2}}{3} + \frac{r^{2}}{2}\right) - C \right]$$

$$\Delta^{2}V_{5}(x, r, \theta) \to \sqrt{2}|x| \left[ A\left(-\frac{5}{384} + \frac{x^{2}}{8} + \frac{x^{2}r^{2}}{6} - \frac{3r^{2}}{16} - \frac{r^{4}}{16} - \frac{x^{4}}{30}\right) + B\left(\frac{1}{8} - \frac{x^{2}}{3} + \frac{r^{2}}{2}\right) - C \right]$$

$$\Delta^{2}V_{5}(x, r, \theta) \to \sqrt{2}|x| \left[ A\left(-\frac{5}{384} + \frac{x^{2}}{8} + \frac{x^{2}r^{2}}{6} - \frac{3r^{2}}{16} - \frac{r^{4}}{16} - \frac{x^{4}}{30}\right) + B\left(\frac{1}{8} - \frac{x^{2}}{3} + \frac{r^{2}}{2}\right) - C \right]$$

The delta function source appears in the  $V_1$  problem, consistent with the linear decrease with x as  $|x| \to \infty$ . All other orders of the potential are source free.

Each even(odd) order problem (except for the first two) is coupled to the preceding even(odd) order problem via the boundary condition on the r=1 surface. The physical interpretation of this coupling is that the current crossing the membrane in the *n*th problem is proportional to the membrane potential in the (n-2)nd problem. The even order problems are coupled to the odd order problems by their asymptotic behavior as  $|x| \to \infty$ , i.e., the constants  $A, B, C, \cdots$ , appear in both even and odd order problems.

It should be noted that the  $V_1, V_3, \cdots$  terms alone are sufficient to satisfy (1) at small x. It is only from considerations of the large-|x| behavior required of the near-field potential in order to match the small- $x^*$  behavior of the far-field potential, that we conclude that  $V_0, V_2, \cdots$  terms are even necessary. These terms are thus known as "switchback" terms.

By direct substitution of the  $|x| \to \infty$  asymptotic forms of  $V_0$ ,  $V_2$  and  $V_4$  in the respective equations and boundary conditions (40), (42) and (44), it is seen

that the  $|x| \to \infty$  forms are the solutions valid for all x. Thus

$$(46) V_0 = A,$$

(47) 
$$V_2 = A\left(x^2 - \frac{r^2}{2}\right) + B,$$

(48) 
$$V_4 = A\left(-\frac{x^2}{4} + \frac{x^4}{6} - \frac{r^2x^2}{2} + \frac{r^2}{8} + \frac{r^4}{16}\right) + B\left(x^2 - \frac{r^2}{2}\right) + C.$$

Now we evaluate the constant A. Integrating (41) over the large volume of the cylinder between -x and x,  $|x| \to \infty$ , and using the divergence theorem, we obtain

(49) 
$$-1 = \lim_{|x| \to \infty} \int_0^{2\pi} d\theta \int_0^1 r \, dr \int_{-x}^x dx \, \nabla^2 V_1$$
$$= \lim_{|x| \to x} \int_0^{2\pi} d\theta \int_0^1 r \, dr \left[ \frac{\partial V_1}{\partial x}(x, r, \theta) - \frac{\partial V_1}{\partial x}(-x, r, \theta) \right]$$
$$= -2\pi A \sqrt{2},$$

where in accordance with the r=1 boundary condition in (41), the integral over the surface of the cylinder is zero, leaving only the integral over the discs at  $\pm x$ . The last equality follows from substitution of the asymptotic behavior of  $V_1$ , as  $|x| \to \infty$ , obtained from (41). Solving for A, we obtain

$$A = \sqrt{2}/(4\pi),$$

Substituting in (41), we obtain the large-|x| behavior of  $V_1$ ,

(51) 
$$\lim_{|x| \to \infty} V_1(x, r, \theta) = -\frac{|x|}{2\pi},$$

which completes the specification of the problem for  $V_1$ . In order to solve the problem, it is convenient to decompose the near-field potential  $V_1$  into two terms,

(52) 
$$V_1(x, r, \theta) = \Phi_1(x, r, \theta) - \frac{|x|}{2\pi}.$$

Substituting (52) in (41), we obtain the problem for  $\Phi_1$ ,

(53) 
$$\nabla^{2}\Phi_{1} = -\delta(x) \left[ \frac{1}{r} \delta(r - R) \, \delta(\theta) - \frac{1}{\pi} \right],$$

$$\frac{\partial \Phi_{1}}{\partial r}(x, 1, \theta) = 0,$$

$$\Phi_{1}(\pm \infty, r, \theta) = 0.$$

The source term in (53) is the unit point source at (0, R, 0) plus the uniform disc sink in the x = 0 plane. The net current source for  $\Phi_1$  is zero, i.e., all the current which enters the cylinder at the point (0, R, 0) is removed uniformly in the cross section  $(0, r, \theta)$ . Unlike the problem for  $V_1$ , which contains unit current flowing

outward as  $|x| \to \infty$ , the problem for  $\Phi_1$  contains no current flow as  $|x| \to \infty$ . The boundary value problem (53) may be solved by Fourier transformation in the  $\theta$ - and x-coordinates. Defining the double Fourier transform of  $\Phi_1$ , by

(54) 
$$\psi_1^{(n)}(k,r) = \int_0^{2\pi} d\theta \, e^{-in\theta} \int_{-\infty}^{\infty} dx \cos(kx) \Phi_1(x,r,\theta)$$
$$\Phi_1(x,r,\theta) = \frac{1}{2\pi^2} \int_0^{\infty} dk \cos(kx) \sum_{n=-\infty}^{\infty} e^{in\theta} \psi_1^{(n)}(k,r)$$

noting that  $\Phi$  is even in x and  $\theta$ , we see that the problem (53) becomes, in Fourier transform space,

(55) 
$$\frac{\frac{1}{r}\frac{\partial}{\partial r}\left(r\frac{\partial\psi_{1}^{(n)}}{\partial r}\right) - \left(k^{2} + \frac{n^{2}}{r^{2}}\right)\psi_{1}^{(n)} = -\frac{1}{r}\delta(r-R) + 2\delta_{0n}.$$

$$\frac{\partial\psi_{1}^{(n)}}{\partial r}(k,1,\theta) = 0.$$

The solution to (55) is

(56) 
$$\psi_1^{(n)}(k,r) = -\frac{2\delta_{0n}}{k^2} - I_n(kR) \frac{K'_n(k)}{I'_n(k)} I_n(kr) + \begin{cases} K_n(kR)I_n(kr), & 0 \le r \le R, \\ K_n(kr)I_n(kR), & R \le r \le 1. \end{cases}$$

Taking the inverse transform (54) of (56) and substituting the result in (52), we obtain

(57) 
$$V_{1}(x, r, \theta) = -\frac{|x|}{2\pi} + \frac{1}{4\pi} (x^{2} + r^{2} + R^{2} - 2rR\cos\theta)^{-1/2} - \frac{1}{2\pi^{2}} \sum_{n=-\infty}^{\infty} e^{in\theta} \int_{0}^{\infty} dk \cos(kx) \left[ \frac{K'_{n}(k)}{I'_{n}(k)} I_{n}(kR) I_{n}(kr) + \frac{2\delta_{0n}}{k^{2}} \right].$$

The integral over k in (57) can be replaced by an equivalent sum by considering the integral in (57) as a portion of a contour integral, so that

(58) 
$$V_{1}(x, r, \theta) = -\frac{|x|}{2\pi} - \frac{1}{2\pi} \sum_{n=-\infty}^{\infty} e^{in\theta} \sum_{s=1}^{\infty} e^{-\lambda_{ns}|x|} \frac{J_{n}(\lambda_{ns}R)J_{n}(\lambda_{ns}r)}{\lambda_{ns} \left(\frac{n^{2}}{\lambda_{ns}^{2}} - 1\right)J_{n}^{2}(\lambda_{ns})}$$

where  $\lambda_{ns}$  is the sth zero of  $J'_n(\lambda)$  excluding the one at  $\lambda = 0$ . Using (58), we can see that as  $|x| \to \infty$ ,  $V_1 \to -|x|/(2\pi)$  plus terms which are exponentially small in |x|, and hence the solution (57) or (58) is the required solution to (41).

Equation (58) is useful for computing the O(1) part of the potential, except for small values of |x|. As  $x \to 0$ , the convergence rate becomes progressively slower. A more general expansion has been obtained elsewhere [5], which contains an adjustable parameter for making the convergence rate rapid at any x, including x = 0, and for two special values of the parameter, reduces to (57) or (58).

We now turn to the  $V_3$  problem and evaluate the constant B. Integrating the Laplacian in (43) over the volume of a large cylinder extending from -x to x, and using the divergence theorem, we have

(59) 
$$0 = \lim_{|x| \to r} \int_{-x}^{x} dx \int_{0}^{1} r \, dr \int_{0}^{2\pi} d\theta \, \nabla^{2} V_{3}$$
$$= \lim_{|x| \to r} \left[ \int_{-x}^{x} dx \int_{0}^{2\pi} d\theta \, \frac{\partial V_{3}}{\partial x}(x, 1, \theta) + \int_{0}^{1} r \, dr \int_{0}^{2\pi} d\theta \, \frac{\partial V_{3}}{\partial x}(x, r, \theta) \right].$$

Using the boundary condition in (43), and (52), and the transform (54) for  $V_1$ , we see that the first integral in (59) becomes

(60) 
$$-\lim_{|x| \to \infty} \int_{-\infty}^{x} dx \int_{0}^{2\pi} d\theta \ V_{1}(x, 1, \theta)$$

$$= x^{2} - \frac{1}{\pi} \int_{-\infty}^{x} dx \int_{0}^{x} dk \cos(kx) \psi_{1}^{(0)}(k, 1)$$

$$= x^{2} - \psi_{1}^{(0)}(0, 1).$$

From (56), we obtain, using the Wronskian of  $I_n$  and  $K_n$  and the power series expansion of  $I_n(k)$ ,

(61) 
$$\psi_1^{(0)}(0, 1) = \lim_{k \to 0} \left( -\frac{2}{k^2} + \frac{I_0(kR)}{kI_1(k)} \right)$$
$$= \frac{1}{2}(R^2 - \frac{1}{2}).$$

Using the asymptotic form for large |x| for  $V_3$  from (43), we see that the second integral in (59) becomes

(62) 
$$\int_0^1 r \, dr \int_0^{2\pi} d\theta \, 2\sqrt{2} \left[ A \left( \frac{1}{8} - x^2 + \frac{r^2}{2} \right) - B \right] = 2\pi \sqrt{2} \left[ A \left( \frac{3}{8} - x^2 \right) - B \right].$$

Combining (59) -(62) and using (50) for A yields an equation which may be solved to give

(63) 
$$B = \frac{\sqrt{2}}{4\pi} \left( \frac{5}{8} - \frac{R^2}{2} \right).$$

As a consequence of (63),  $W_1$  and  $V_2$  depend on R, the distance from the source to the axis of the cylinder, whereas lower order terms do not.

Having evaluated A and B in (50) and (63), we have now obtained the near field and far field up to terms of  $O(\varepsilon^{1/2})$ , i.e., we have obtained  $V_0$ ,  $V_1$ ,  $V_2$ ,  $W_0$  and  $W_1$ . These terms represent that part of the potential which is numerically significant in a physiological experiment: all higher order terms are too small to detect anywhere in a cylindrical cell. Nevertheless, it is of some mathematical interest to carry out the calculation further in order to demonstrate that the process can be continued indefinitely, although it clearly soon becomes quite tedious. We continue as far as necessary to calculate the constant C, and will discuss the results at that point.

In order to obtain C, we must proceed in solving the problem for  $V_3$ . The method employed is identical to that applied to the  $V_1$  problem, namely, a new potential,  $\Phi_3$ , is defined which approaches zero for large |x|. Thus

(64) 
$$V_3(x, r, \theta) = \Phi_3(x, r, \theta) + \frac{|x|}{4\pi} \left( R^2 + r^2 - 1 - \frac{2}{3} x^2 \right),$$

where we have used the expressions (50) and (63) for A and B in the asymptotic form of  $V_3$  given in (43).

Substituting (64) and the definition of  $\Phi_1$ , (52), in the problem for  $V_3$ , (43) yields the problem for  $\Phi_3$ :

(65) 
$$\nabla^2 \Phi_3 = -\frac{1}{2\pi} (R^2 + r^2 - 1) \, \delta(x),$$

$$\frac{\partial \Phi_3}{\partial r} = -\Phi_1,$$

$$\Phi_3(\pm \infty, r, \theta) = 0.$$

The source term in (65) is a nonuniform distribution of current on the disc at x = 0, plus the current crossing the membrane given by the r = 1 boundary condition.

It can be verified easily that the algebraic term in (64) satisfies Laplace's equation for |x| > 0, as well as the r = 1 boundary condition in (43). It has a discontinuous derivative at x = 0, however, and so is not a solution to (43) at x = 0. The function  $\Phi_3$ , which has a source at x = 0, must be added to the algebraic term to obtain a solution valid everywhere. The discontinuity in the derivative of  $\Phi_3$  will be just the negative of the discontinuity in the derivative of the algebraic term

As in the  $\Phi_1$  problem,  $\Phi_3$  is an even function of x and  $\theta$ , and we define the double Fourier cosine transform of  $\theta_3$  as in (54), with subscript 1 replaced by 3. The problem (65) thus becomes, in Fourier transform space,

(66) 
$$\frac{1}{r} \frac{\partial}{\partial r} \left( r \frac{\partial \psi_3^{(n)}}{\partial r} \right) - \left( k^2 + \frac{n^2}{r^2} \right) \psi_3^{(n)} = -(R^2 + r^2 - 1) \delta_{0n}.$$

$$\frac{\partial \psi_3^{(n)}}{\partial r} (k, 1) = -\psi_1^{(n)} (k, 1) = 2 \frac{\delta_{0n}}{k^2} - \frac{I_n(kR)}{kI'(k)},$$

where we have substituted for  $\psi_1^{(n)}(k, 1)$  from (56) and used the Wronskian of  $I_n$  and  $K_n$ . The solution to (66) is

(67) 
$$\psi_3^{(n)}(k,r) = \frac{\delta_{0n}}{k^2} \left( R^2 + r^2 - 1 + \frac{4}{k^2} \right) - \frac{I_n(kR)I_n(kr)}{[kI'_n(k)]^2}.$$

 $V_3(x,r,\theta)$ 

Taking the two inverse transforms of (67), and using (64), we obtain

(68) 
$$= \frac{|x|}{4\pi} \left( R^2 + r^2 - 1 - \frac{2}{3} x^2 \right)$$

$$- \frac{1}{2\pi^2} \sum_{n=-\infty}^{\infty} e^{in\theta} \int_0^{\infty} dk \frac{\cos kx}{k^2} \left[ \frac{I_n(kR)I_n(kr)}{[I'_n(k)]^2} - \left( R^2 + r^2 - 1 + \frac{4}{k^2} \right) \delta_{0n} \right].$$

By relating the integral in (68) to a contour integral, the integral can be converted to a sum. The result is given elsewhere [7] and from it we can show that  $V_3 \to (R^2 + r^2 - \frac{2}{3}x^2 - 1)|x|/(4\pi)$  plus terms which are exponentially small as  $|x| \to \infty$ .

The constant B was determined by considering the volume integral of the  $V_3$  problem (43), and was seen to be related to the large-|x| behavior of  $V_3$  and  $V_1$ , and to  $\psi_1^{(0)}(0,1)$ . In exactly the same way, by considering the volume integral of the  $V_5$  problem (45), (without actually solving for  $V_5$ ), we can determine C from our present knowledge of the large-|x| behavior of  $V_5$  and  $V_3$ , and of  $\psi_3^{(0)}(0,1)$ . Having determined C, we will then have  $V_4(x,r)$  and  $W_2(x^*,r)$ . The details are given elsewhere [7]. The result is

(69) 
$$C = \frac{\sqrt{2}}{64\pi} \left[ \frac{25}{24} - 3R^2 + R^4 \right].$$

5. Summary and discussion of results. We have now calculated all the coefficients appearing in the first three terms in the far-field expansion, and in the first five terms in the near-field expansion. This permits us to write expressions for the potential (far- or near-field) to  $O(\varepsilon^{3/2})$ . Substituting the results for A, B and C from (50), (63) and (69) in the expressions for  $W_0$ ,  $W_1$ , and  $W_2$  given in (22), (29) and (35) and then substituting these plus  $\zeta_0$  from (38) in the expansion (36) we obtain the expression for the far-field potential,

$$W(x^*, r, \theta; \varepsilon) = \varepsilon^{-1/2} W_0(x^*, r) + \varepsilon^{1/2} W_1(x^*, r) + \varepsilon^{3/2} W_2(x^*, r) + O(\varepsilon^{5/2})$$

$$= \frac{\sqrt{2}}{4\pi} e^{-\sqrt{2}|x^*|} \left[ \varepsilon^{-1/2} + \frac{1}{2} \varepsilon^{1/2} \left\{ \frac{5}{4} - (r^2 + R^2) \right\} + \frac{1}{16} \varepsilon^{3/2} \left\{ \frac{25}{24} - 3(r^2 + R^2) + r^4 + 4r^2 R^2 + R^4 \right\} + O(\varepsilon^{5/2}) \right],$$

where the far-field axial variable is

(34) 
$$x^* = \sqrt{\varepsilon} x \left[ 1 - \frac{1}{8} \varepsilon + \frac{5}{384} \varepsilon^2 + O(\varepsilon^3) \right].$$

Similarly, if we substitute the results for A, B and C in the near-field expressions for  $V_0$ ,  $V_2$ , and  $V_4$  given by (46), (47) and (48) and then substitute these plus  $V_1$  and  $V_3$  given by (57) and (68) in (39) we obtain the expression for the near-field potential,

$$V(x, r, \theta; \varepsilon) = \varepsilon^{-1/2} V_0(x, r, \theta) + V_1(x, r, \theta) + \varepsilon^{1/2} V_2(x, r, \theta) + \varepsilon V_3(x, r, \theta) + \varepsilon^{3/2} V_4(x, r, \theta) + O(\varepsilon^2)$$

$$= \varepsilon^{-1/2} \frac{\sqrt{2}}{4\pi} - \frac{|x|}{2\pi} + \frac{1}{4\pi} (x^2 + r^2 + R^2 - 2rR\cos\theta)^{-1/2}$$

$$- \frac{1}{2\pi^2} \sum_{n=-\infty}^{\infty} e^{in\theta} \int_0^{\infty} dk \cos kx \left\{ \frac{K'_n(k)}{I'_n(k)} I_n(kR) I_n(kr) + \frac{2\delta_{0n}}{k^2} \right\} + \varepsilon^{1/2} \frac{\sqrt{2}}{8\pi} \left[ \frac{5}{4} + 2x^2 - (r^2 + R^2) \right]$$
(cont'd.)

$$+ \varepsilon \left[ \frac{|x|}{4\pi} \left( r^2 + R^2 - \frac{2}{3} x^2 - 1 \right) \right]$$

$$- \frac{1}{2\pi^2} \sum_{n=-\infty}^{\infty} e^{in\theta} \int_0^{\infty} dk \frac{\cos kx}{k^2} \left\{ \frac{I_n(kR)I_n(kr)}{\left[I_n(k)\right]^2} - \left( r^2 + R^2 - 1 + \frac{4}{k^2} \right) \delta_{0n} \right\} \right]$$

$$+ \varepsilon^{\frac{3}{2}} \frac{\sqrt{2}}{64\pi} \left[ \frac{1}{24} (25 + 144x^2 + 64x^4) - (r^2 + R^2)(3 + 8x^2) + r^4 + 4r^2R^2 + R^4 \right] + O(\varepsilon^2).$$

The two k integrals in (71) can be replaced by the equivalent representations (58) and (C.9), of [7], respectively.

The leading terms in the far-field expansion (70) and in the near-field expansion (71) are each of order  $\varepsilon^{-1/2}$ . In the near field, the leading term is a constant. Thus, near the point source, the interior of the cylinder is raised to a large, constant potential, relative to the zero potential at infinity. The physical basis for the large potential is that the membrane permits only a small fraction of the current to leave the cylinder per unit length. Consequently, most of the current flows a long distance before getting out, and a large potential drop is required to force this current down the cylinder. The existence of this large constant potential, and its magnitude of  $O(\varepsilon^{-1/2})$ , could only be deduced from considerations of the far field.

The leading term in the far field decays as  $\exp{(-\sqrt{2\epsilon} |x|)}$ . Consequently, to lowest order, 1/e of the current leaves the cylinder in a distance of  $1/\sqrt{2\epsilon}$ . The corresponding potential required to drive a current this distance is of  $O(\epsilon^{-1/2})$ , which is the physical basis for the order of the large potential in the near field. The precise numerical values of the leading terms in (70) and (71) was determined by requiring in the limit  $|x| \to \infty$ ,  $x^* \to 0$ , that the two terms be identical to the lowest order in  $\epsilon$ . In the far far field, i.e.,  $x^* = x\sqrt{\epsilon}(1 - \epsilon/8 + \cdots) \to \infty$ , the potential is seen to approach zero exponentially.

The leading term in the far-field expansion (70) is independent of r and  $\theta$ . Thus, to the lowest order, the far-field current is distributed uniformly over the circular cross section of the cylinder. The leading term in (70) is the known result of one-dimensional cable theory [8, eq. (14)]. The high order terms are all independent of the polar angle  $\theta$ . They do, however, depend on the radial coordinate r. The dependence is in the form of a polynomial in  $r^2$ , the degree of the polynomial increasing by one in each successive term. We also see that the higher order terms also depend on R, the radial distance between the source and the axis of the cylinder. The potential is seen to be symmetric with respect to an interchange of r and R. This must be so because the potential is the Green's function (with source at x = 0,  $\theta = 0$ ) for the cylindrical problem [4, p. 808].

Successive terms in the far-field expansion decrease in powers of  $\varepsilon$ , whereas in the near-field expansion they decrease in powers of  $\sqrt{\varepsilon}$ .

The second, O(1), term in the near-field expansion, as written in (71) contains three parts. It is the solution to the problem (41) in which no current crosses

the membrane, i.e.,  $\partial V_1/\partial r = 0$  at r = 1. The first part of this term decreases linearly with increasing |x|. It corresponds to the potential required to drive a constant current parallel to the axis of the cylinder in the interior of the cylindrical cell. It is the appearance of this term in the expansion which led us to conclude that an expansion of the form (71) could not describe the potential for all x, since we could not satisfy the boundary condition at  $|x| = \infty$  with such a term present.

The second part of the O(1) term is the free-space potential of a point source. It is the only singular part of the solution, accounting fully for the singularity at the location (0, R, 0) of the delta function source. The third part is more complicated. When added to the first two parts, it satisfies the boundary condition at r = 1, and removes the discontinuity in the x-derivatives of the potential at x = 0, arising from the first part.

The third,  $O(\varepsilon^{1/2})$ , term in the near-field expansion is a polynomial of second degree in x, r and R. In general, each term of  $O(\varepsilon^{(2n+1)/2})$ , n an integer, are simply polynomials of degree 2n + 2. The  $O(\varepsilon^{1/2})$  term was required as a consequence of the  $O(\varepsilon^{-1/2})$  term and the coupling between orders given in the sequence of problems (40)–(45), and matching to the far field.

The fourth,  $O(\varepsilon)$ , term [specified by (43)], and subsequently all higher terms of  $O(\varepsilon^n)$ , contain a polynomial of degree 2n+1, in |x|, r, and R and a more complicated infinite sum, infinite integral term. Higher order terms are determined by solving the appropriate partial differential equation [analogous to (45)] and boundary conditions.

The first two terms in the far field,  $W_0$  and  $W_1$ , and the first three terms in the near field,  $V_0$ ,  $V_1$ , and  $V_2$ , represent the physiologically significant part of the potential. Higher order terms are too small to be detectable at any location in a cylindrical biological cell. The higher order terms  $W_2$ ,  $V_3$  and  $V_4$  are given to illustrate their interesting mathematical properties, and to provide a precise measure of the magnitude of the error introduced by using only the preceding terms.

A single expression which is uniformly valid in x can be written down. We saw in § 4 that the polynomial parts of the near field are exactly equal to the respective terms in the expansion (37) of the far field in near-field coordinates. The two complicated infinite sum and infinite integral terms in the near field are exponentially small in the far field. Consequently, the potential everywhere can be obtained from the single representation

$$V(x, r, \theta; \varepsilon) = \frac{\sqrt{2}}{4\pi} \exp\left\{-\sqrt{2\varepsilon} |x| \left(1 - \frac{\varepsilon}{8} + \frac{5\varepsilon^2}{384} - O(\varepsilon^3)\right)\right\}$$

$$-\varepsilon^{-1/2} \left[1 + \frac{\varepsilon}{2} \left\{\frac{5}{4} - (r^2 + R^2)\right\} + \frac{\varepsilon^2}{16} \left\{\frac{25}{24} - 3(r^2 + R^2) + r^4 + 4r^2R^2 + R^4\right\} + O(\varepsilon^3)\right]$$

$$+ \frac{1}{4\pi} (x^2 + r^2 + R^2 - 2rR\cos\theta)^{-1/2}$$
(cont'd.)

(72)(cont'd.) 
$$-\frac{1}{2\pi^2} \sum_{n=-\infty}^{\infty} e^{in\theta} \int_0^{\infty} dk \cos kx \left[ \frac{K_n'(k)}{I_n'(k)} I_n(kR) I_n(kR) + \frac{2\delta_{0n}}{k^2} + \frac{\varepsilon}{k^2} \left\{ \frac{I_n(kR) I_n(kr)}{\left[I_n'(k)\right]^2} - \left(r^2 + R^2 - 1 + \frac{4}{k^2}\right) \delta_{0n} \right\} + O(\varepsilon^2) \right],$$

which is asymptotic to (70) in the limit  $\varepsilon \to 0$  with  $x\sqrt{\varepsilon}$  held fixed, and to (71) in the limit  $\varepsilon \to 0$  with x held fixed. Again, we can replace the two integrals by using (58) and (C.9) of reference [7]. Equation (72) is more compact than (70) and (71), but the latter two have the advantage of clearly separating the terms according to their order in  $\varepsilon$  in the regions  $x \gg \varepsilon^{-1/2}$  and  $x \ll \varepsilon^{-1/2}$  respectively, and each order of  $\varepsilon$  is related to a simple physical problem. This solution is closely related to the solution derived by Barcilon, Cole and Eisenberg [1] using another technique of singular perturbation theory, multiple scaling. It can also be obtained from the eigenfunction expansion of the solution to (1) for arbitrary  $\varepsilon$ , by expanding in powers of  $\varepsilon$  [5].

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<sup>&</sup>lt;sup>1</sup> The result of the multiple scale analysis [1] differs from (72) because [1] contains a sign error and a secular term in  $V^{(3)}$  which has not been removed. If these errors are corrected, and the infinite sum over Bessel functions is written in closed form, the multiple scale result, the expansion of the exact solution, and the present results are identical.