DIFFUSION IN BRANCHING REGIONS

By J. C. JAEGER

Received 13 January 1959

ABSTRACT. The problem of diffusion from an instantaneous point source in a thin plane sheet which is intersected by one or more other thin plane sheets of the same material is considered. This problem arises in the study of the diffusion of packets of transmitter substance in synaptic clefts, and some numerical results for the amphibian neuro-muscular junction are presented. A similar discussion applies to branching rods and to cases where there is loss of diffusing substance at the surfaces of the sheets.

1. *Introduction.* Conduction of heat or diffusion in branching regions is frequently of considerable importance. In conduction of heat, such problems usually arise in connexion with the cooling fins attached to surfaces to assist in the removal of heat. The theory of these has been confined almost entirely to that of a single fin under steady-state conditions. The present analysis is the basic transient theory for some simple complexes of such fins (assumed to be thin). It also applies to problems on thin wires with branches which occur in some systems involving heated wires or thermocouples.

The particular problem which suggested the present investigation is the physiological one of the diffusion of transmitter substance in the synaptic cleft. Such clefts occur at the junctions of nerve fibres with other cells and play an essential part in the transmission of electrical impulses through such a system. They usually take the form of thin sheets, a few hundred Ångstroms in thickness, containing liquid. (For a description of some typical systems, see Eccles and Jaeger (7).) At one surface of the cleft (the presynaptic membrane) a nerve impulse causes the synaptic transmitter substance to be liberated and this substance diffuses through the liquid in the cleft. At the other surface of the cleft (the subsynaptic membrane) the molecules of transmitter substance become attached to the membrane and cause a large change in its ionic permeability; this allows a flow of current across the subsynaptic membrane. Thus the synaptic cleft is a complicated mechanism by means of which a nerve impulse terminating in the presynaptic membrane causes electric current to flow in the region containing the subsynaptic membrane.

It is now known ((2), (3), (4), (8), (9)) that the transmitter substance is not liberated uniformly over the surface of the presynaptic membrane but is liberated quantally, packets of a few hundred molecules being released suddenly at a definite point and time, and subsequently diffusing through the liquid in the cleft. Clearly, such problems must be among the most perfect realizations in nature of the Green's functions (instantaneous sources) of the mathematical theory of conduction of heat. The electrical properties of the cleft at any time are determined by the concentration of transmitter substance at the active regions of the surface of the subsynaptic membrane, and thus the study of diffusion in the cleft is an essential preliminary for a study of the variation of the electrical behaviour with time. When the cleft has a simple form such as a thin disc or a long thin sheet, the necessary results are available in the

https://doi.org/10.1017/S0305004100034289 Published online by Cambridge University Press

literature (Carslaw and Jaeger (1), Chap. XIV), but it is now known (cf. Eccles and Jaeger (7)) that much more complex forms are common, in particular that the cleft frequently has a large number of puckers or folds in the subsynaptic membrane whose effect is to increase its area. The general form of the cleft is that of a thin sheet which occasionally divides into other thin sheets, not necessarily of the same thickness. The object of the present paper is to study diffusion from a point source in such a system.

As a typical example the amphibian neuro-muscular junction may be considered. This takes the form of (half) a long circular cylinder whose cross-section is shown in Fig. 1 and is precisely that of a finned cylinder barrel (Eccles and Jaeger (7), Robertson (10), Couteaux and Taxi (5)). Suppose now that a packet of transmitter substance is instantaneously liberated at a point S: it is desired to be able to follow the course of its

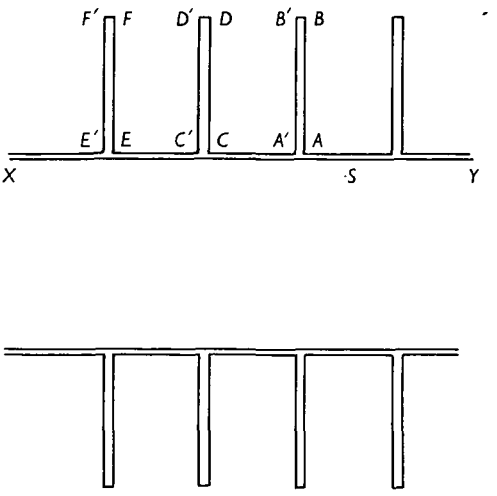


Fig 1. Schematic cross-section of the amphibian neuro-muscular junction.

diffusion into the fins $ABB'A'$, $CDD'C'$, etc., and in particular to see how many of these may be affected. While a solution could, in principle, be given for this rather complicated system, the effect of the curvature and thickness of the cleft are negligible in this and many other practical cases, and it is sufficient to consider problems on diffusion in thin plane sheets which are joined along their lines of intersection (which will be called *branch lines*). It will be shown in § 2 that a very simple solution exists for the case in which three semi-infinite thin plane sheets are joined along a single branch line, and in § 4 some discussion of the physiological implications of this solution will be given. Some problems with two branch lines are discussed in § 3. In § 6 it is shown that the preceding results, with simple modifications, apply also to the case of thin rods with branches.

As a first approximation it may be taken that there is no loss of transmitter substance from the cleft. However, when the decay of the excitation has to be studied, it is found that two mechanisms for the removal of the transmitter substance from the cleft are operative and have to be considered: first, the transmitter substance may diffuse from the cleft into the surrounding medium into which it opens, a process considered in § 5;

https://doi.org/10.1017/S0305004100034289 Published online by Cambridge University Press

secondly, the transmitter substance may be removed from the surface of the subsynaptic membrane by enzyme action, an effect which is taken into account in § 7 by assuming that the transmitter substance is removed at the surface of the sheet at a rate proportional to its concentration (the 'radiation' boundary condition of conduction of heat).

In all cases the diffusion constant D is assumed to be the same in all branches: if it is not, the problem becomes more difficult. While problems are stated in terms of diffusion, they may be taken over immediately to conduction of heat by taking D as the thermal diffusivity and $Q\rho c$ as the quantity of heat liberated, where ρ is the density and c the specific heat of the material.

Finally, it may be remarked that the method, involving the simplifying assumption stated in § 2 (ii), is applicable to cases in which more than three sheets intersect in

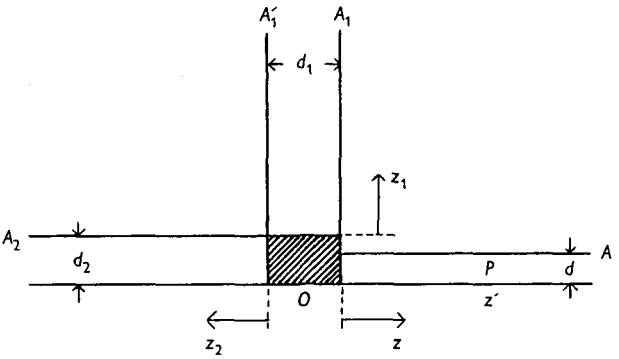


Fig. 2. Cross-section of three semi-infinite sheets intersecting in one branch line.

a branch line and also to cases in which the system of sheets is multiply connected. It may also be applied to sheets of variable cross-section, and, in particular, to the important case of a sheet opening into a half-space. A problem of the latter type has been discussed by Eccles and Jaeger (7) in this way. The simpler results of §§ 2, 3 may be derived by the method of images, but the Laplace transformation method will be used here since it applies in the same manner to systems of any degree of complexity.

2. *An instantaneous point source in a thin plane sheet with one branch line.* The sheet is supposed to be of thickness d and to run perpendicular to the paper in Fig. 2, OA being its intersection with the paper. At O it branches into two sheets OA_1, OA_2, perpendicular to the paper, of thicknesses d_1 and d_2. The essential assumptions made in the calculation are: (i) that the sheets are so thin that the concentration of transmitter substance is uniform across their thickness, and, (ii), that the effect of the small region at O (shown black in Fig. 2) at which the branches meet can be neglected, so that the boundary conditions along the line of intersection through O can be taken to be continuity of concentration and continuity of flow in the z-direction. With this assumption, the sheets OA, OA_1, OA_2 need not be perpendicular as shown schematically in Fig. 2 but may make any angles with one another. As stated in § 1 it will be assumed for the present that there is no flow of transmitter substance across the surfaces of the sheets and that the coefficient D of diffusion of transmitter substance in the material of the sheets is the same for all sheets.

https://doi.org/10.1017/S0305004100034289 Published online by Cambridge University Press

We take a coordinate system in which the x-axis is perpendicular to the plane of the paper, and coordinates z, z_1, z_2 in the sheets are as shown in Fig. 2 so that the sheets OA, OA_1, OA_2 are $-\infty < x < \infty$, $z > 0$; $-\infty < x < \infty$, $z_1 > 0$; $-\infty < x < \infty, z_2 > 0$ respectively. We assume that, at time $t = 0$, an amount Q of transmitter substance is liberated at the point P, $z = z'$, $x = 0$, in the region OA.

If a quantity Q of transmitter substance is liberated at $t = 0$ at the point $(0, z')$ of an infinite sheet $-\infty < x < \infty$, $-\infty < z < \infty$, of small thickness d, the concentration $u(x, z-z', t)$ at (x, z) at time t is known to be ((1), § 10·3; (6), § 3·2)

$$u(x, z-z', t) = \frac{Q}{4\pi Dtd} \exp\left\{-\frac{x^2+(z-z')^2}{4Dt}\right\}. \tag{1}$$

Most of the results of the present paper will be expressed in terms of this fundamental function. In the present problem we require the values $C(x, z, t)$, $C_1(x, z_1, t)$, $C_2(x, z_2, t)$ of the concentrations in the regions OA, OA_1, OA_2 for times $t > 0$. C, C_1, C_2 have to satisfy the equation of diffusion,

$$\frac{\partial^2 C}{\partial x^2} + \frac{\partial^2 C}{\partial z^2} - \frac{1}{D}\frac{\partial C}{\partial t} = 0, \tag{2}$$

and the boundary conditions assumed above, which are

$$[C]_{z=0} = [C_1]_{z_1=0} = [C_2]_{z_2=0}, \tag{3}$$

$$d\left[\frac{\partial C}{\partial z}\right]_{z=0} + d_1\left[\frac{\partial C_1}{\partial z_1}\right]_{z_1=0} + d_2\left[\frac{\partial C_2}{\partial z_2}\right]_{z_2=0} = 0. \tag{4}$$

Also, C, C_1, C_2 have to vanish at infinity. The calculation now follows the lines of Carslaw and Jaeger (1), § 14·10. The Laplace transform $\bar{u}$ of the fundamental source solution u defined in (1) is

$$\bar{u} = \int_0^\infty e^{-pt} u\, dt = \frac{Q}{2\pi Dd} K_0\{q[x^2+(z-z')^2]^{\frac{1}{2}}\} \tag{5}$$

$$= \frac{Q}{2\pi Dd}\int_0^\infty \exp[-\eta\,|z-z'|]\frac{\cos\xi x}{\eta}\,d\xi, \tag{6}$$

where

$$q^2 = p/D, \quad \eta = [q^2+\xi^2]^{\frac{1}{2}}, \tag{7}$$

$K_0(x)$ is the modified Bessel function of the second kind of order zero, and (6) follows from (5) by equation (2) of Watson (11), p. 416. We then assume

$$\bar{C} = \frac{Q}{2\pi Dd}\int_0^\infty [\exp[-\eta\,|z-z'|] + A(\xi)\,e^{-\eta z}]\frac{\cos\xi x}{\eta}\,d\xi, \tag{8}$$

$$\bar{C}_1 = \frac{Q}{2\pi Dd}\int_0^\infty A_1(\xi)\,e^{-\eta z_1}\frac{\cos\xi x}{\eta}\,d\xi, \tag{9}$$

$$\bar{C}_2 = \frac{Q}{2\pi Dd}\int_0^\infty A_2(\xi)\,e^{-\eta z_2}\frac{\cos\xi x}{\eta}\,d\xi, \tag{10}$$

https://doi.org/10.1017/S0305004100034289 Published online by Cambridge University Press

where $A(\xi)$, $A_1(\xi)$, $A_2(\xi)$ are functions of ξ to be determined by substituting (8) to (10) in the Laplace transforms of the continuity conditions (3), (4), which are seen to be satisfied for all values of x. The results are

$$A_1(\xi) = A_2(\xi) = \frac{2d}{d+d_1+d_2} e^{-\eta z'}, \quad A(\xi) = \frac{d-d_1-d_2}{d+d_1+d_2} e^{-\eta z'}. \tag{11}$$

Inserting these values in (8) to (10) and using (6) gives, in the notation of (1),

$$C = u(x, z-z', t) - \frac{d_1+d_2-d}{d_1+d_2+d} u(x, z+z', t), \tag{12}$$

$$C_1 = \frac{2d}{d+d_1+d_2} u(x, z_1+z', t), \tag{13}$$

$$C_2 = \frac{2d}{d+d_1+d_2} u(x, z_2+z', t). \tag{14}$$

Thus the concentration C_2 at z_2 in OA_2 is just $2d/(d+d_1+d_2)$ times the value at the same distance $[x^2+(z_2+z')^2]^{\frac{1}{2}}$ from a source of the same strength in an infinite sheet of uniform thickness d. The same result holds for C_1. Thus the whole time-course of diffusion in the branches OA_1, OA_2 is precisely the same as that in a single sheet except for multiplication by the factor $2d/(d+d_1+d_2)$. It follows from (12) that if $d_1+d_2 > d$ the concentration C in OA is reduced by an amount which increases with (d_1+d_2-d) and which becomes larger the nearer the source is to O.

A number of useful results follow immediately from (12) to (14). First, the concentration on the junction $z = 0$ is

$$\frac{2d}{d+d_1+d_2} u(x, z', t) = \frac{Q}{2\pi(d+d_1+d_2)tD} \exp[-(x^2+z'^2)/4Dt], \tag{15}$$

or $2d/(d+d_1+d_2)$ times its value for a uniform sheet. Secondly, the concentration at the source point $z = z'$, $x = 0$ is, by (12),

$$\frac{Q}{4\pi Dtd}\left\{1 - \frac{d_1+d_2-d}{d_1+d_2+d} \exp[-z'^2/4Dt]\right\}; \tag{16}$$

for very small values of the time the concentration here is not changed, but for large values of the time it is $2d/(d+d_1+d_2)$ times the value for a uniform sheet.

Finally, the total amount of transmitter substance in any sheet at any time may be written down. In OA_2 it is, by (14)

$$\frac{Qd_2}{2\pi Dt(d+d_1+d_2)} \int_{-\infty}^{\infty} \exp[-x^2/4Dt]\, dx \int_0^{\infty} \exp[(-z_2+z')^2/4Dt]\, dz_2 = \frac{Qd_2}{d+d_1+d_2} \operatorname{erfc} \frac{z'}{2(Dt)^{\frac{1}{2}}}, \tag{17}$$

where $\operatorname{erfc} x = 1 - \operatorname{erf} x$, and $\operatorname{erf} x$ is the tabulated error function. Similarly, the total quantity in OA_1 is

$$\frac{Qd_1}{d+d_1+d_2} \operatorname{erfc} \frac{z'}{2(Dt)^{\frac{1}{2}}}, \tag{18}$$

https://doi.org/10.1017/S0305004100034289 Published online by Cambridge University Press

and in OA it is

$$Q - \frac{Q(d_1+d_2)}{d+d_1+d_2}\operatorname{erfc}\frac{z'}{2(Dt)^{\frac{1}{2}}}. \tag{19}$$

For large values of the time the total amounts in OA, OA_1, OA_2 are in the ratios $d:d_1:d_2$.

3. *Extension to cases of two branching lines or to branches of finite length.* In order to see how far the simple results derived in § 2 for the simple system of Fig. 2 may be applied to more complicated systems such as that of Fig. 1 it is useful to study typical slightly more complicated systems. Explicit results for those of Figs. 3 and 4 are given below.

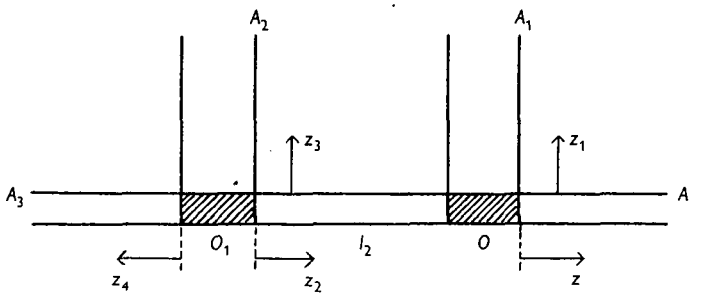


Fig. 3. Cross-section of a system of sheets with two branch lines.

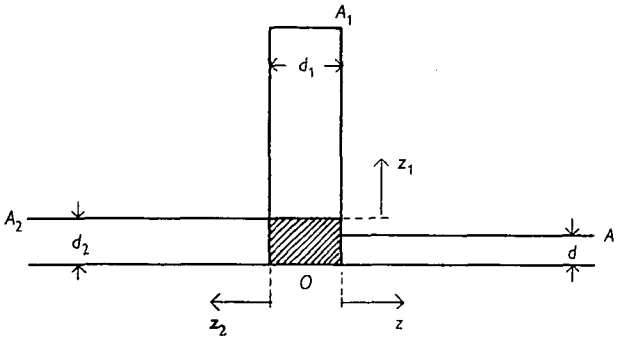


Fig. 4. Cross-section of a system consisting of an infinite strip and two semi-infinite sheets intersecting in one branch line.

(i) *The system of Fig.* 3 *with two branching lines at O and* O_1 *distant* l_2 *apart. Source* Q *at* $z = z'$ *in* OA. For simplicity we take OA, OO_1 and O_1A_3 all to have thickness d, and OA_1 and O_1A_2 to have thickness d_1. Then with the coordinate system shown in Fig. 3, the concentration C_4 at z_4 in O_1A_3 is given by

$$C_4 = \frac{4d^2}{(2d+d_1)^2}\sum_{n=0}^{\infty}\left(\frac{d_1}{2d+d_1}\right)^{2n} u(x, z_4+z'+(2n+1)\,l_2, t), \tag{20}$$

where u is defined in (1).

(ii) *The system of* (i) *except that the source is at* $z_2 = z_2'$ *in the region* O_1O.

$$C_4 = \frac{2d}{2d+d_1}u(x, z_4+z_2', t) + \frac{2d}{2d+d_1}\sum_{n=1}^{\infty}\left\{\left(\frac{d_1}{2d+d_1}\right)^{2n} u(x, z_4+z_2'+2nl_2, t) - \left(\frac{d_1}{2d+d_1}\right)^{2n-1} u(x, z_4-z_2'+2nl_2, t)\right\}. \tag{21}$$

https://doi.org/10.1017/S0305004100034289 Published online by Cambridge University Press

The first term of (21) corresponds to (14), and the series of smaller terms represents a reduction due to the presence of the additional sheet OA_1.

(iii) *The problem of* § 2 *except that the fin* OA_1 *is of finite length* l_1. *Source* Q *at* $z = z'$ *in* OA.

$$C_1 = \frac{2d}{d+d_1+d_2} \sum_{n=0}^{\infty} \alpha^n [u(x, z'+z_1+2nl_1, t) + u(x, z'-z_1+2(n+1)\,l_1, t)], \tag{22}$$

$$C_2 = \frac{2d}{d+d_1+d_2} \left\{ u(x, z_2+z', t) + (\alpha+1) \sum_{n=0}^{\infty} \alpha^n u(x, z_2+z'+2(n+1)\,l_1, t) \right\}, \tag{23}$$

where
$$\alpha = (d_1-d-d_2)/(d_1+d+d_2). \tag{24}$$

(iv) *The problem of* (iii) *but with the source* Q *at* $z_1 = z_1'$ *in* OA_1.

$$C_2 = \frac{2d}{d+d_1+d_2} \sum_{n=0}^{\infty} \alpha^n \{u(x, 2nl_1+z_1'+z_2, t) + u(x, 2(n+1)\,l_1+z_2-z_1', t)\}, \tag{25}$$

where α is defined in (24).

4. *Numerical discussion.* In order to see how far the simple results of § 2 may be applied to complicated systems such as that of Fig. 1 some numerical results will be given for the problems of §§ 2, 3, taking values for the parameters which are of the order of those for the amphibian neuro-muscular junction, namely, $d = d_2 = 4 \times 10^{-6}$ cm., $d_1 = 10^{-5}$ cm., and, when they occur, $l_1 = 6 \times 10^{-5}$ cm., $l_2 = 4 \times 10^{-5}$ cm. For D, the value $7{\cdot}6 \times 10^{-6}$ cm^2/sec. for acetylcholine will be used.

Considering first the system of Fig. 2, it appears that the effect of the branching is to reduce the concentrations in OA_1 and OA_2 to $2d/(d+d_1+d_2) = 0{\cdot}44$ times the value in a single unbranched sheet. In the neuro-muscular junction the effect, then, is to expose three surfaces of the subsynaptic membrane (OA_1, OA_1', OA_2 in Fig. 2) to rather less than half the concentration which would exist in a single unbranched sheet. The variation of concentration with time at the point $O, x = 0, z = 0$, of the branch line, for $z' = 2 \times 10^{-5}$ cm., in the presence and absence of branches is shown in Curves I and II respectively of Fig. 5. In all the curves of Fig. 5, $\log_{10}(4\pi DdC/Q)$ is plotted against $\log_{10} T$, where T is the time in milli-seconds and C is the concentration at the point under consideration.

Next, we consider how this result is affected if the branch OA_1 has a finite length $l_1 = 6 \times 10^{-5}$ cm. In this case the appropriate result is (23) with $\alpha = \frac{1}{9}$. The first term is that previously discussed, and, because of the small value of α, terms of the series after the first have little effect. It should be noticed, however, that since $u(x, z, t)$ has a maximum value of $Q/\pi d[x^2+z^2]$ when

$$t = [x^2+z^2]/4D$$

the later terms become important at progressively later times. In Fig. 5, Curves III and IV, respectively, the variation of concentration with time at the branch line, $z_1 = 0$, and at the end of the branch, $z_1 = l_1$, are shown. For large values of the time these curves tend to that for a point source in a single sheet.

The fact that in Fig. 1 the source lies between two branch lines may be taken into account by using (21). In the present case, the first term is that previously discussed, and since $d_1/(2d+d_1) = 0{\cdot}55$ the later terms of the series are not of great importance.

https://doi.org/10.1017/S0305004100034289 Published online by Cambridge University Press

Comparison of Curve V of Fig. 5 for $z_2 = 0, l_2 = 4 \times 10^{-5}$ cm., $z_2' = 2 \times 10^{-5}$ with Curve I shows the magnitude of the effect.

Finally, the concentration beyond two branch lines may be studied from (20). Since the effect of one branch is to reduce the concentration beyond it in the ratio $2d:(2d+d_1)$ it might be expected that beyond two branches the concentration would be reduced in the ratio $(2d)^2:(2d+d_1)^2$. This corresponds to the first term of (20); the effect of ignoring later terms may be seen by comparing the complete result for the case $z_4 = 0$, $l_2' = 4 \times 10^{-5}, z' = 2 \times 10^{-5}$, Fig. 5, Curve VI, with the first term only, Fig. 5, Curve VII.

In general, it may be concluded that for a source in a region such as Fig. 1 with many branches, reasonably high concentrations only occur in the two branches nearest to the source, but that approximate values in further branches may be estimated as above if desired.

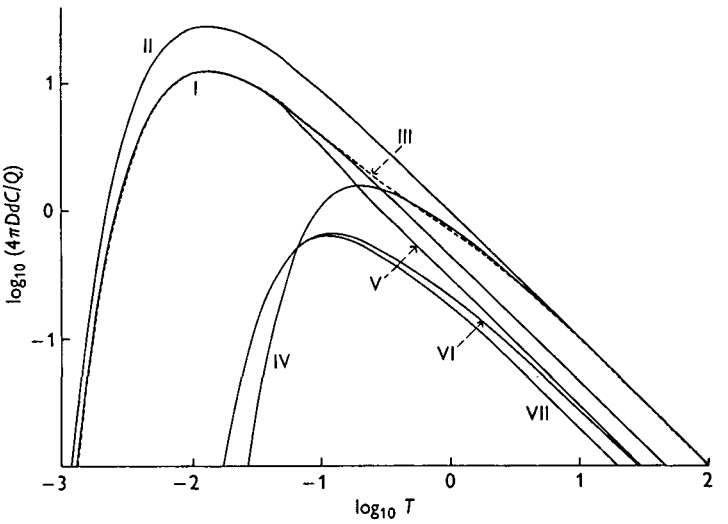


Fig. 5. Variation of concentration with time T (msec.) due to an instantaneous point source. Curve I, at a single branch line. Curve II, at the same distance from the source in a single sheet. Curve III (dotted), at a single branch line when one branch is of finite length. Curve IV at the closed end of a branch of finite length. Curve V, at a branch line when the source is midway between two branch lines. Curve VI, at a branch line when the source lies beyond a second branch line. Curve VII, the approximation to Curve VI obtained by using only the first term of the series.

5. *The case in which the sheets are quarter-infinite or strips.* In the preceding discussion it has been assumed that all the sheets extend to infinity in the region $-\infty < x < \infty$. If they are all semi-infinite, $x > 0$, with either no flow or zero concentration when $x = 0$, results may be obtained by adding the appropriate images. For example, for the problem of § 2 in the region $x > 0$ with zero concentration at $x = 0$ and transmitter substance liberated at (x', z'), the results corresponding to (12) and (13) are

$$C = u(x-x', z-z', t) - u(x+x', z-z', t) - \frac{d_1+d_2-d}{d_1+d_2+d}[u(x-x', z+z', t) - u(x+x', z+z', t)], \tag{26}$$

$$C_1 = \frac{2d}{d+d_1+d_2}[u(x-x', z_1+z', t) - u(x+x', z_1+z', t)]. \tag{27}$$

https://doi.org/10.1017/S0305004100034289 Published online by Cambridge University Press

If all the sheets are strips of width l, $0 < x < l$, an infinite series of images can be constructed in the usual way.

Results of this type are needed in problems such as that of the amphibian neuromuscular junction, Fig. 1, in which the fins run round half a cylinder, ending on a diametral plane at which they open into a surrounding infinite region and so the concentration is effectively zero. In this case, if the transmitter substance is liberated near the diametral plane, the effect of loss to the surrounding medium may be taken into account by adding an image as in (26) and (27).

6. *The case of a thin rod with branches.* For an infinite thin rod $-\infty < z < \infty$ of area d, the temperature at the point z at time t due to liberation of a quantity Q of transmitter substance at the point z' at zero time is

$$U(z-z',t) = \frac{Q}{2d(\pi Dt)^{\frac{1}{2}}} \exp\left\{-\frac{(z-z')^2}{4Dt}\right\}. \tag{28}$$

This replaces the quantity u defined in (1). Problems on branching rods may be treated by a method similar to that used above, and the results are found to be the same as those given in (12)–(25) with $u(x, z-z', t)$ replaced by $U(z-z', t)$.

7. *The case of removal of transmitter substance at the surfaces of the sheet.* The only simple assumption is the 'radiation' boundary condition of conduction of heat; that is, that the substance is removed at the surface at a rate proportional to its concentration, or

$$\frac{\partial C}{\partial n} + hC = 0,$$

where h is a constant. In this case the fundamental source solution (1) is replaced by

$$u^*(x, z-z', t) = \frac{Q}{4\pi Ddt} \exp\left\{-k^2 Dt - \frac{x^2 + (z-z')^2}{4Dt}\right\}, \tag{29}$$

where $k^2 = 2h/D$, and all results (12) ... (25) remain valid with u replaced by u^*, that is, multiplied by $\exp(-k^2 Dt)$.

8. *Acknowledgements.* The writer is indebted to Professors J. C. Eccles and B. Katz for suggesting the problem and for much valuable discussion.

REFERENCES

(1) Carslaw, H. S. and Jaeger, J. C. *Conduction of heat in solids*, 2nd ed. (Oxford, 1959).
(2) Castillo, J. del and Katz, B. *J. Physiol.* 124 (1954), 553.
(3) Castillo, J. del and Katz, B. *J. Physiol.* 125 (1954), 546.
(4) Castillo, J. del and Katz, B. *Microphysiologie comparée des éléments excitables.* (Colloques Internationaux du Centre National de la recherche scientifique, no. 67, 1957), p. 245.
(5) Couteaux, R. and Taxi, J. *Arch. Anat. micr. morph. exp.* 41 (1952), 352.
(6) Crank, J. *The mathematics of diffusion* (Oxford, 1956).
(7) Eccles, J. C. and Jaeger, J. C. *Proc. Roy. Soc.* B, 148 (1957), 38.
(8) Fatt, P. and Katz, B. *J. Physiol.* 117 (1952), 109.
(9) Fatt, P. and Katz, B. *Acta physiol. scand.* 29 (1953), 117.
(10) Robertson, J. D. *J. biophys. biochem. Cytol.* 2 (1956), 381.
(11) Watson, G. N. *Theory of Bessel Functions*, 2nd ed. (Cambridge, 1944).

Australian National University
Canberra
Australia

https://doi.org/10.1017/S0305004100034289 Published online by Cambridge University Press