

The velocity field of growing ear cartilage

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INTRODUCTION

At the whole body or organ level, growth may be estimated by the direct use of the relative (Huxley, 1972) or specific growth rate (Medawar, 1945). However, its counterpart at the tissue level, the rate of increase in size of a very small volume of material, is found indirectly and demands a knowledge of the velocity at a number of points of that tissue. Associated with growth of this order there is frequently morphological differentiation, which presents further problems of quantitative description. Stereological methods may allow an assessment of differentiating cellular or tissue components, but changes in these need to be related to the movement of the diminutive block of tissue in which they occur. For this, the velocity with which the tissue is moving is again essential.

Developing cartilage, and in particular the developing cartilage of the rabbit ear, is a convenient tissue for the examination of growth and morphological differentiation. It is assumed in the current work that the velocity vector field of the developing ear reflects the velocity of the underlying cartilage. The purpose of the present paper is to compute equations that describe this field. This information is a pre-requisite to studies, at the tissue level, of the specific growth rate and quantitative morphological differentiation of elastic cartilage.

MATERIALS AND METHODS

The ears of New Zealand White rabbits aged 10, 11, 12, 14 and 18 days were first shaved, and the remaining fine hair then removed with 'Immac' cream (Anne French, London, Paris, Milan) before transverse or longitudinal lines or rectangular grids were either painted or lightly tattooed on their dorsal surfaces. For painting, pyrogallol paint (Martindale, 1967) was used and for tattooing, a simple light instrument obtained from D. M. & F. Davis, Leigh-on-Sea, Essex was employed. The ear was treated as a two-dimensional structure and displacements, in two mutually perpendicular directions, of the lines and of intersections of the lines were noted. In the case of the 12 day old rabbit, whose detailed results are considered, the right ear was lightly tattooed with a square grid of approximately 0.5 cm spacing, the grid being orientated so that a straight line ran along the centre of the ear from the tip to the base. Two additional parallel lines were added on either side of this central line and approximately 0.2 cm from it. The *y*-axis was chosen as a line parallel to the central line but touching the most posterior point on the posterior margin of the ear and the *x*-axis as a line at right angles to the *y*-axis and touching the tip of the ear. The origin lay at the intersection of these two axes. The co-ordinates of the intersections of the grid, and of the points where it met the margins of the ear, were

measured with calipers. These co-ordinates were recorded at intervals from 12 days to 299 days. The co-ordinates in cm in the x and y directions were plotted separately against the time in days/10. Different types of curves such as polynomial, rational, exponential and logistic functions were fitted to these points, the exponential functions yielding the best fit judging from the residual mean squares of the fitted curves and the variance of the ordinate for a given value of the abscissa.

Differentiation of these empirical curves enabled the velocities at a given time to be calculated at different points. Then, by considering the velocities as functions of position at a given time, equations were fitted for the components of the velocity in cm/10 days in the x or, more precisely, the i direction, i.e. u components, and for the components in the y or, more precisely the j direction, i.e. v components. Logistic functions were fitted. These equations determined the velocity in quantity and direction at any point of the velocity field at a given time. The curve fitting was accomplished from a remote terminal using an ICL 4-70 computer and a program (MLP) for fitting standard, non-linear models to data by maximum likelihood or least squares.

RESULTS

It soon became apparent that, as the ear grew, the individual transverse and longitudinal lines, and the grid lines, remained approximately parallel with their original positions in the five rabbits. Unfortunately, it was not always possible to draw absolutely straight and parallel lines, this being particularly so when constructing the grid for the right ear of the 12 day old rabbit. However, by considering each point as describing a separate path line it was decided that a more accurate picture of the velocity field could be obtained. The co-ordinates at intervals from 12 to 299 days, for the right ear of this rabbit, yielded 106 equations when their measurements in cm were expressed as functions of the time in days/10 (t). There were 57 equations in the i direction of the form

$$x = a + b \exp(-kt) \quad (1)$$

and 42 in the j direction of the form

$$y = c + d \exp(-lt). \quad (2)$$

The values of the assigned asymptotes a and c , and of the parameters b , k , d and l and their standard errors, together with P , the co-ordinates of the starting points at 12 days ($t = 1.2$), are given in Tables 1 and 2. The standard errors are given in brackets in columns 2 and 3. In addition, there were 7 points on or near the posterior margin of the ear where the abscissa in the i direction remained approximately constant. The two-dimensional path lines of 35 points are included in the 106 equations and, of the remaining points, the movements of 29 are restricted to equations of displacement in the i direction and of 7 in the j direction.

Differentiation of the equations with respect to t (days/10), and evaluation of the gradients for given values of t , provide the velocity components in the i and j directions at a number of points (x, y) . Since the grid lines remain approximately parallel with their original positions, the velocity components in the i and j directions have been assumed to be independent of y and x respectively. Consequently, the velocity component in the i direction (u) is considered as a function of x and t and the velocity component in the j direction (v) as a function of y and t . For t constant, u and v fit the logistic curves

$$u = \frac{f}{1 + \exp(-m(x-r))} \quad (3)$$

Table 1. *Parameters of path lines*

<i>a</i>	<i>b</i>	<i>k</i>	<i>P</i>
0.55	-0.6 (0.2)	0.5 (0.1)	(0.20, 0.95)
1.30	-1.5 (0.2)	0.45 (0.05)	(0.40, 0.45)
1.50	-1.6 (0.1)	0.50 (0.04)	(0.60, 0.45)
1.50	-1.6 (0.1)	0.50 (0.04)	(0.60, 0.95)
1.50	-1.6 (0.1)	0.50 (0.04)	(0.60, 1.45)
1.55	-1.6 (0.2)	0.51 (0.05)	(0.65, 1.95)
1.50	-1.6 (0.1)	0.50 (0.04)	(0.60, 2.55)
1.50	-1.6 (0.1)	0.50 (0.04)	(0.60, 3.00)
1.50	-1.6 (0.1)	0.49 (0.04)	(0.60, 3.50)
1.50	-1.5 (0.1)	0.47 (0.04)	(0.65, 4.00)
2.00	-2.2 (0.2)	0.49 (0.04)	(0.85, 0.45)
2.20	-2.3 (0.3)	0.47 (0.05)	(0.90, 0.95)
2.40	-2.1 (0.3)	0.36 (0.05)	(0.90, 1.45)
2.50	-2.7 (0.3)	0.49 (0.05)	(0.95, 2.00)
2.45	-2.7 (0.2)	0.46 (0.04)	(0.95, 2.60)
2.40	-2.8 (0.3)	0.49 (0.04)	(0.90, 3.05)
2.20	-2.5 (0.2)	0.53 (0.04)	(1.00, 3.55)
2.40	-2.1 (0.2)	0.34 (0.03)	(1.05, 4.00)
2.50	-2.8 (0.2)	0.53 (0.04)	(1.05, 0.45)
2.65	-3.0 (0.2)	0.49 (0.03)	(1.05, 0.95)
2.90	-3.1 (0.3)	0.46 (0.04)	(1.10, 1.45)
3.15	-3.3 (0.3)	0.46 (0.03)	(1.20, 2.00)
3.20	-3.3 (0.2)	0.40 (0.03)	(1.20, 2.60)
3.00	-3.3 (0.2)	0.44 (0.03)	(1.15, 3.05)
2.70	-2.9 (0.2)	0.50 (0.04)	(1.25, 3.55)
2.80	-2.5 (0.2)	0.38 (0.03)	(1.30, 4.00)
3.20	-3.7 (0.2)	0.51 (0.03)	(1.25, 0.45)
3.55	-3.7 (0.3)	0.42 (0.04)	(1.30, 0.95)
3.70	-4.4 (0.4)	0.51 (0.04)	(1.35, 1.45)
3.95	-4.7 (0.3)	0.50 (0.03)	(1.40, 2.00)
3.90	-4.4 (0.3)	0.44 (0.03)	(1.40, 2.60)
3.60	-4.1 (0.3)	0.46 (0.03)	(1.40, 3.05)
3.15	-3.4 (0.3)	0.50 (0.05)	(1.50, 3.55)
3.10	-2.9 (0.3)	0.43 (0.04)	(1.55, 4.05)
3.85	-4.4 (0.3)	0.51 (0.03)	(1.55, 0.45)
4.05	-4.5 (0.3)	0.48 (0.03)	(1.55, 0.95)
4.20	-4.8 (0.3)	0.49 (0.03)	(1.60, 1.45)
4.75	-5.1 (0.4)	0.44 (0.03)	(1.70, 2.05)
4.70	-5.0 (0.3)	0.41 (0.03)	(1.70, 2.65)
4.55	-4.8 (0.3)	0.42 (0.02)	(1.85, 3.20)
3.80	-4.1 (0.5)	0.50 (0.05)	(1.90, 3.70)
3.70	-3.5 (0.3)	0.41 (0.03)	(1.80, 4.15)
4.15	-4.7 (0.3)	0.52 (0.03)	(1.80, 0.45)
5.15	-5.5 (0.2)	0.49 (0.02)	(2.15, 0.95)
4.85	-5.4 (0.3)	0.47 (0.02)	(1.85, 0.95)
5.35	-5.8 (0.3)	0.45 (0.02)	(2.00, 1.45)
5.70	-6.0 (0.4)	0.45 (0.02)	(2.15, 2.10)
6.00	-6.7 (0.4)	0.45 (0.02)	(2.25, 2.60)
5.70	-5.8 (0.3)	0.41 (0.02)	(2.40, 3.15)
4.90	-5.0 (0.5)	0.48 (0.04)	(2.45, 3.70)
4.55	-4.9 (0.5)	0.51 (0.04)	(2.25, 4.20)
6.05	-6.5 (0.3)	0.47 (0.02)	(2.40, 1.45)
7.10	-7.2 (0.3)	0.44 (0.02)	(2.75, 2.10)
7.50	-7.7 (0.3)	0.44 (0.02)	(3.05, 2.60)
6.30	-5.4 (0.6)	0.39 (0.04)	(3.25, 4.20)
7.35	-7.3 (0.5)	0.44 (0.03)	(3.40, 3.15)
6.60	-6.3 (0.5)	0.46 (0.04)	(3.45, 3.20)

Table 2. *Parameters of path lines*

<i>c</i>	<i>d</i>	<i>l</i>	<i>P</i>
0.70	-0.7 (0.1)	0.28 (0.06)	(1.80, 0.15)
0.75	-0.73 (0.03)	0.38 (0.05)	(0.70, 0.25)
1.10	-0.70 (0.03)	0.36 (0.04)	(0.60, 0.45)
1.10	-0.70 (0.03)	0.36 (0.04)	(1.05, 0.45)
1.10	-0.70 (0.03)	0.36 (0.04)	(1.55, 0.45)
1.65	-2.0 (0.2)	0.46 (0.04)	(2.10, 0.65)
2.45	-2.7 (0.2)	0.47 (0.03)	(0.60, 0.95)
2.45	-2.5 (0.2)	0.42 (0.03)	(1.05, 0.95)
2.70	-2.5 (0.2)	0.31 (0.03)	(1.55, 0.95)
2.45	-2.5 (0.2)	0.42 (0.03)	(1.85, 0.95)
4.20	-3.9 (0.3)	0.33 (0.03)	(0.30, 1.45)
3.95	-4.4 (0.3)	0.45 (0.03)	(0.60, 1.45)
4.20	-3.9 (0.3)	0.33 (0.03)	(1.10, 1.45)
4.40	-4.3 (0.3)	0.33 (0.02)	(1.60, 1.45)
3.90	-3.8 (0.3)	0.38 (0.03)	(2.00, 1.45)
5.60	-5.3 (0.4)	0.36 (0.03)	(0.20, 1.95)
5.35	-5.6 (0.3)	0.42 (0.03)	(0.65, 1.95)
5.60	-5.4 (0.4)	0.39 (0.03)	(1.20, 2.00)
6.15	-6.1 (0.4)	0.36 (0.02)	(1.70, 2.05)
5.70	-6.3 (0.4)	0.45 (0.03)	(2.15, 2.10)
7.40	-7.5 (0.5)	0.38 (0.03)	(0.20, 2.50)
7.15	-7.5 (0.4)	0.41 (0.02)	(0.60, 2.55)
7.40	-7.3 (0.5)	0.38 (0.03)	(1.20, 2.60)
7.95	-7.9 (0.5)	0.36 (0.02)	(1.70, 2.65)
7.25	-7.4 (0.4)	0.40 (0.02)	(2.25, 2.60)
8.60	-8.8 (0.6)	0.39 (0.03)	(0.30, 2.95)
8.50	-8.8 (0.4)	0.40 (0.02)	(0.60, 3.00)
9.00	-8.8 (0.5)	0.37 (0.02)	(1.15, 3.05)
9.75	-9.7 (0.6)	0.35 (0.02)	(1.85, 3.20)
8.85	-9.1 (0.5)	0.40 (0.02)	(2.40, 3.15)
10.15	-10.5 (0.5)	0.38 (0.02)	(0.60, 3.50)
10.70	-10.1 (0.6)	0.33 (0.02)	(1.25, 3.55)
11.45	-11.0 (0.7)	0.32 (0.02)	(1.90, 3.70)
10.60	-10.7 (0.5)	0.38 (0.02)	(2.45, 3.70)
11.45	-12.2 (0.5)	0.39 (0.02)	(0.65, 4.00)
12.00	-11.2 (0.6)	0.31 (0.02)	(1.30, 4.00)
12.80	-12.0 (0.7)	0.30 (0.02)	(1.80, 4.15)
12.15	-11.4 (0.6)	0.32 (0.02)	(2.25, 4.20)
12.05	-12.4 (0.5)	0.39 (0.02)	(0.65, 4.50)
12.60	-11.4 (0.6)	0.31 (0.02)	(1.30, 4.50)
13.40	-12.2 (0.7)	0.30 (0.02)	(1.30, 4.65)
12.75	-11.6 (0.7)	0.33 (0.02)	(2.25, 4.70)

and

$$v = \frac{g}{1 + \exp(-n(y-s))}. \quad (4)$$

The values of the parameters f , g , m , n , r and s and their standard errors, for t equal to 1.5, 2.0, 2.8, 3.6, 4.9, 5.9 and 8.7, are shown in Tables 3 and 4. The standard errors are given in brackets in columns 2, 3 and 4. Each of these common curves involves either 65 sets of co-ordinates (x, u) or 43 sets of co-ordinates (y, v) , the origin being included in each case. From values such as those given in Tables 3 and 4 it is possible to express f , g , m , n , r and s as exponential functions of t , viz.

$$f = 2.75 \exp(-0.431 t), \quad (5)$$

with standard errors of the parameters, 0.01 and 0.003 respectively,

$$m = 1.05 + 6.7 \exp(-1.01 t), \quad (6)$$

Table 3. Parameters of components of velocity

<i>t</i>	<i>f</i>	<i>m</i>	<i>r</i>
1.5	1.45 (0.05)	2.4 (0.2)	1.39 (0.05)
2.0	1.67 (0.04)	1.9 (0.1)	1.75 (0.06)
2.8	0.82 (0.03)	1.5 (0.1)	2.20 (0.07)
3.6	0.58 (0.02)	1.30 (0.08)	2.54 (0.09)
4.9	0.33 (0.01)	1.12 (0.08)	2.9 (0.1)
5.9	0.216 (0.009)	1.04 (0.08)	3.2 (0.1)
8.7	0.063 (0.004)	1.0 (0.1)	3.5 (0.2)

Table 4. Parameters of components of velocity

<i>t</i>	<i>g</i>	<i>n</i>	<i>s</i>
1.5	2.31 (0.07)	1.5 (0.1)	2.4 (0.1)
2.0	1.97 (0.06)	1.14 (0.08)	3.1 (0.1)
2.8	1.53 (0.05)	0.88 (0.06)	3.9 (0.2)
3.6	1.19 (0.04)	0.73 (0.05)	4.7 (0.2)
4.9	0.80 (0.04)	0.60 (0.05)	5.8 (0.3)
5.9	0.60 (0.03)	0.54 (0.05)	6.6 (0.3)
8.7	0.29 (0.04)	0.41 (0.05)	8.9 (0.8)

with standard errors of the parameters, 0.05, 0.6 and 0.08 respectively,

$$r = 3.65 - 3.80 \exp(-0.344 t), \tag{7}$$

with standard errors of the parameters, 0.01, 0.01 and 0.004 respectively,

$$g = 3.68 \exp(-0.310 t), \tag{8}$$

with standard errors of the parameters, 0.03 and 0.004 respectively,

$$n = 0.50 + 3.6 \exp(-0.83 t), \tag{9}$$

with standard errors of the parameters, 0.04, 0.4 and 0.09 respectively, and

$$s = 18 - 17 \exp(-0.08 t), \tag{10}$$

with standard errors of the parameters, 3, 3 and 0.02 respectively. While Tables 3 and 4 and equations (3) and (4) define the velocity vector field for certain values of *t*, equations (3)–(10) allow the velocity to be calculated at any point (*x*, *y*) at any time between 12 and 87 days, the velocity being of the form

$$\mathbf{q}(x, y, t) = u(x, t)\mathbf{i} + v(y, t)\mathbf{j}. \tag{11}$$

The existence of these expressions also corroborates that the velocity at any point on the ear is a continuous function of time.

The components of the vorticity or curl of the velocity in two dimensions reduce to

$$\frac{\partial v}{\partial x} - \frac{\partial u}{\partial y}.$$

However, $u = u(x, t)$ and $v = v(y, t)$, so that

$$\frac{\partial v}{\partial x} - \frac{\partial u}{\partial y} = 0$$

and $\text{curl } \mathbf{q} = 0$. This confirms that the growth of the rabbit ear may be regarded as an irrotational flow of material. The vanishing of the curl of the velocity is the

necessary and sufficient condition for the existence of a scalar function ϕ , the velocity potential, such that

$$\mathbf{q} = \nabla\phi.$$

It follows that stream lines and velocity equipotential lines may be calculated. For t constant, the stream lines, in two dimensions, are the solutions of the differential equation

$$\frac{dx}{u} = \frac{dy}{v}$$

and the velocity equipotential lines the solutions of

$$u dx + v dy = 0.$$

For convenience, the velocity component curves have been computed with the axes given above, but they may be translated to other axes. A translation to new parallel axes whose origins are approximately at the tip of the ear may be achieved with the following transformations:

$$x = X + r, \quad (12)$$

$$y = Y, \quad (13)$$

$$u = U + f/2, \quad (14)$$

and

$$v = V, \quad (15)$$

where (X, U) and (Y, V) are the co-ordinates referred to the new sets of axes. In this particular case the stream lines are the solutions of

$$\frac{dX}{\frac{f}{1 + \exp(-mX)} - \frac{f}{2}} = \frac{dY}{\frac{g}{1 + \exp(-n(Y-s))}}. \quad (16)$$

Integrals that satisfy this equation are

$$Y - \frac{1}{n} \exp(-n(Y-s)) = \frac{2g}{f} \left(\frac{2}{m} \ln(\exp(mX) - 1) - X \right) + gG, \quad (17)$$

where G is the constant of integration and $X > 0$,

$$Y - \frac{1}{n} \exp(-n(Y-s)) = \frac{2g}{f} \left(\frac{2}{m} \ln(1 - \exp(mX)) - X \right) + gG, \quad (18)$$

where $X < 0$, and

$$X = 0. \quad (19)$$

The corresponding velocity equipotential lines satisfy

$$\left(\frac{f}{1 + \exp(-mX)} - \frac{f}{2} \right) dX + \left(\frac{g}{1 + \exp(-n(Y-s))} \right) dY = 0. \quad (20)$$

Integration yields an implicit solution

$$\left(1 + \exp(mX) \right)^{\frac{f}{m}} \left(1 + \exp(n(Y-s)) \right)^{\frac{g}{n}} = \exp\left(\frac{fX}{2} + \phi\right), \quad (21)$$

where ϕ is the constant of integration and the value of the velocity potential.

Using the parameters in Tables 3 and 4, the Newton-Raphson iterative procedure, and a simple Fortran program, it is possible to calculate co-ordinates that satisfy (17) and (18) and to draw the stream lines for the associated values of t . Those for $t = 1.5, 2.8, 4.9$ and 8.7 are shown in Figures 1-4. The corresponding velocity

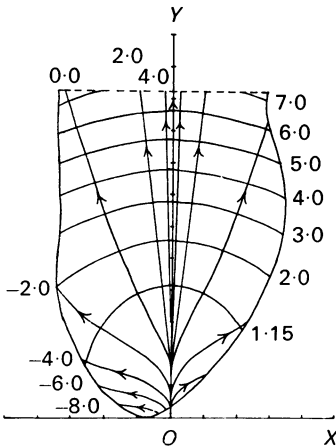


Fig. 1

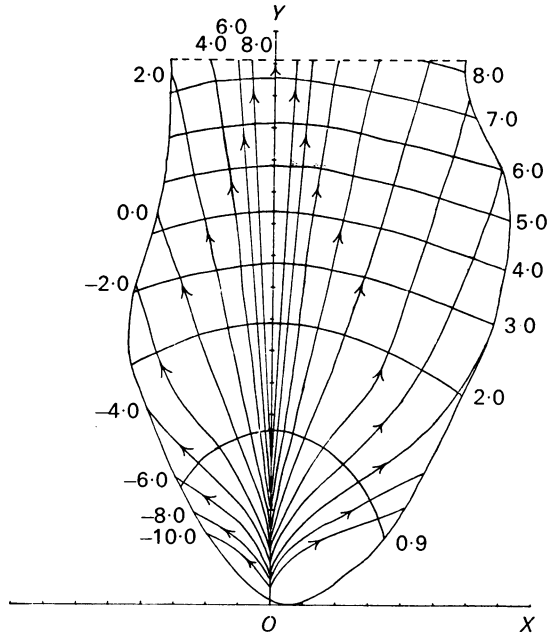


Fig. 2

Fig. 1. Stream lines and velocity equipotential lines for the growing right ear of a 15 day old rabbit ($t = 1.5$). The numbers on the right are the values of the velocity potential (ϕ) and those on the left of the constants of integration (G). The X and Y units are 0.5 cm.

Fig. 2. Stream lines and velocity equipotential lines for the growing right ear of the same rabbit at 28 days ($t = 2.8$).

equipotential lines, obtained from (21) by the use of a simple Fortran program, are also sketched.

A further consequence of the velocity vector field given by equation (11) is that

$$\nabla q = q \nabla,$$

i.e. the dyadic is self-conjugate. Similarly,

$$\nabla Q = Q \nabla,$$

where Q is the transformation of q to the new origin and axes, and the grad is interpreted in the same sense.

DISCUSSION

One of the most important vector fields in fluid dynamics is the field of the fluid velocity. The situation is somewhat analogous in the study of biological growth. Since the velocity, together with most of the other parameters, depends upon time as well as upon position, there is continual change at any point of the growing ear cartilage. As a consequence, the velocity vector field has been calculated above for given values of t . The equations computed allow the velocity to be defined at any point of the growing ear and, by implication, of its cartilage, between 12 and 87 days. The curl of the velocity being zero, the tissue movement must be regarded as irrotational. There is thus no tendency for the minute volumes of moving cartilage to form vorticular or whorled patterns during growth, as occur, for example, with some

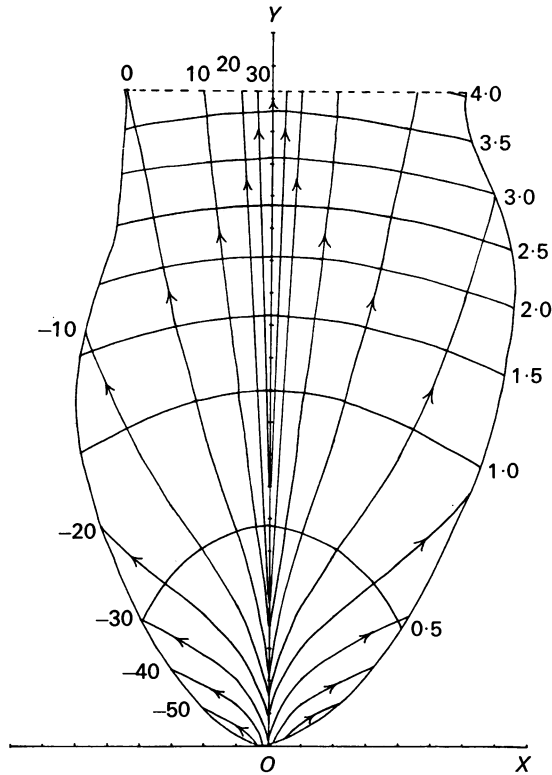


Fig. 3. Stream lines and velocity equipotential lines for the growing right ear of the same rabbit at 49 days ($t = 4.9$).

neoplasms. Moreover, the irrotational motion of growing cartilage has less kinetic energy than any other possible motion that has the same normal component of velocity on the boundary and the same distribution of specific growth rate throughout the cartilage. Irrotational motion is, therefore, the most economical as regards the work done during tissue movement. The velocity field may be visualized by the use of stream lines and velocity equipotential lines, for stated values of t . At all points of the field the velocity is tangential to the stream lines, which reveal the direction of tissue movement, at a given instant, from the point of view of an observer at the tip of the ear. No tissue crosses the stream lines, which are at right angles to the equipotential lines. The velocity potential is constant on any equipotential line and the velocity varies with the gradient of the potential. The value of the potential rises and the equipotential lines become progressively closer together from the tip to the base (Figs 1-4), showing that the velocity is increasing in magnitude. An element of cartilage near the edge of the ear would have a greater velocity than one on the same stream line but nearer the tip. The edge fragment has received contributions to its velocity from the tissue behind it. At the microscopic level, these contributions are due to the presence of numerous cartilage cells which by virtue of their enlargement, cell division and production of collagen, elastic tissue and ground substance behave as multiple, active sources and increase the tissue movement; the latter may also be influenced by active cell movement and by cell degeneration. The velocity potential varies with time, reaching a value of 7 in the 5.1 cm long, 15 day old ear, ascending

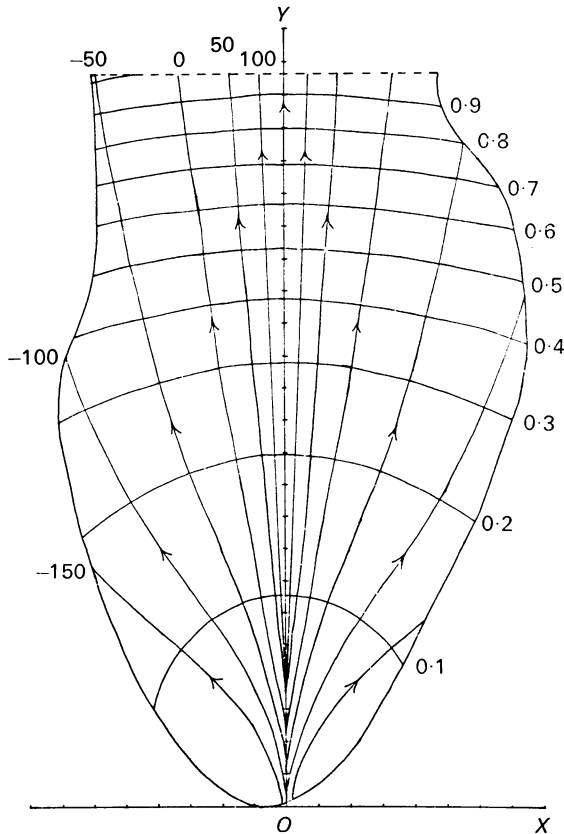


Fig. 4. Stream lines and velocity equipotential lines for the growing right ear of the same rabbit at 87 days ($t = 8.7$).

to 8 in the 8.5 cm long, 28 day old ear and descending to 4 in the 10.1 cm, 49 day old ear and to 1 only in the 11.3 cm long, 87 day old ear. The stream lines become more widely separated as they pass from the tip towards the base (Figs 1–4) and yet the equipotential lines establish that the velocity is increasing. This may also be explained by the presence of chondroblasts acting as active sources in the manner described above. While these individual cellular sources are not directly detectable by the technique used, their physical scale being small compared with the tattoo marks, their distribution may be disclosed by calculating the divergence of the velocity. The alterations in the patterns of stream lines and equipotential lines with time provide an exact illustration of tissue movement during growth (Figs 1–4). Notwithstanding these changes, the stream line along the midline of the ear maintains its direction, a characteristic which commends the midline as a site for investigating tissue differentiation, since the velocity in one direction only needs to be considered. Some studies of the morphology in this region have been undertaken (Cox & Peacock, 1977).

As far as can be ascertained, previous investigations of the velocity field of developing cartilage have not been made. However, the use of stream lines in studying change of shape was emphasized by Thompson (1942), who adopted systems of orthogonal co-ordinates, some of which he considered represented stream lines and

'isothermals'. By transforming these sets of lines he sought to compare related biological forms. Medawar (1944, 1945) employed Thompson's approach in a more general manner in examining human shape as a function of time, and Richards & Riley (1937) applied the method descriptively in analysing the growth of *Amblystoma punctatum* larvae. Nevertheless, Richards & Kavanagh (1943, 1945) commented that few studies of growth were sufficiently complete to provide the basic measurements for a detailed growth analysis. These authors obtained their data from Avery's (1933) investigations of the growth of the tobacco leaf and calculated ratios of growth rates at the same stage of development. Unfortunately, there was no record of time, so that they could neither derive true velocity vector fields nor compare velocities at different stages.

The object of the present paper has been to provide measurements of the velocity field of growing cartilage. Although these have been used to describe the type of tissue movement occurring, other applications of the velocity data are even more interesting. These will, therefore, be discussed briefly.

First, the divergence of the velocity yields an estimate of the specific growth rate in volume, i.e. the time rate of increase in volume per unit volume, of a minute, elementary volume of tissue at any point, at a given time (Richards & Kavanagh, 1943, 1945). As such, the divergence of the velocity is important in many equations involving cellular differentiation and growth. Level lines of the specific growth rate and field lines of the gradient of the specific growth rate demonstrate where the growth rate is maximum, and the direction of its change (Cox & Peacock, 1978). These results show that, with time, a single centre of maximum specific growth rate moves, approximately, along the midline of the ear from the tip towards the base. In the early stages, mitotic activity would be important in the cellular increase at this migrating centre, but subsequently, cell hypertrophy would appear to be dominant (Cox & Peacock, 1977). The intercellular material produced would be collagen, elastic tissue and ground substance. Although the overall production rate of cellular and intercellular material is maximum at the site mentioned, it does not follow that the centres for maximum rates of production of intercellular material and cellular material coincide with that site or with one another (Cox & Peacock, 1978).

Secondly, the grad of the velocity may provide information about the principal axes of the rate of strain during growth. The grad of the velocity of the ear cartilage is self-conjugate, is equal to the rate of strain dyadic or tensor and indicates a pure straining motion without rotation; the principal axes of the rate of strain have directions parallel to the X and Y axes. The specific growth rate in length (Richards & Kavanagh, 1943), i.e. the time rate of increase in length per unit length in a direction \hat{p} , is equal to $\hat{p} \cdot \nabla Q \cdot \hat{p}$, where \hat{p} is a unit vector. In two dimensions this is equal to

$$\cos^2\theta \frac{\partial U}{\partial X} + \sin^2\theta \frac{\partial V}{\partial Y},$$

where θ is the angle that the direction of the elementary unit of length makes with the i direction. The effect is to convert a minute element of tissue which is initially circular into an ellipse with principal axes that do not rotate and whose rates of extension are $\partial U/\partial X$ and $\partial V/\partial Y$.

Thirdly, the velocity is an essential term in the expression for the material rate of change of many cell and tissue components. Cox & Peacock (1977) have described the developing elastic cartilage of the rabbit ear and have noted variations, which may be related to position as well as time, in the intercellular matrix, cell surface

area, intracellular lipid and other features at the cellular level. In order to express better the changes in these constituents, it is valuable to consider an extremely small, elementary volume of cartilage and the quantitative alterations that occur in its cell and tissue components as it actually moves from the tip towards the base of the ear during the processes of growth and differentiation. This measure of tissue differentiation is given by the material derivative of the component, viz.

$$\frac{dV_{V_f}}{dt} = \frac{\partial V_{V_f}}{\partial t} + \mathbf{Q} \cdot \nabla V_{V_f},$$

where V_{V_f} is, for example, the volume fraction of intracellular lipid. Although the V_{V_f} may be found stereologically, the velocity is still required. The results of the examinations of morphological differentiation will be treated elsewhere.

Finally, the velocity is one of a number of terms necessary for the determination of an equation of motion or growth for developing cartilage. In quantitative formulations of cartilage growth and morphological differentiation at the cellular level the velocity term is ubiquitous. A knowledge of the velocity vector field of developing cartilage is, therefore, germane to many inquiries and it is surprising that so little attention has been given to it.

SUMMARY

The velocity vector field of the growing rabbit ear cartilage has been investigated between 12 and 299 days. Empirical curves have been computed for path lines and for velocities between 12 and 87 days. The tissue movement has been found to behave as an irrotational flow of material. Stream lines and velocity equipotential lines have been calculated and provide a kinematic description of the changes during growth. The importance of a knowledge of the velocity vector in physical descriptions of growth and morphological differentiation at the tissue and cellular levels is emphasized.

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REFERENCES

- AVERY, G. S. (1933). Structure and development of the tobacco leaf. *American Journal of Botany* **20**, 565-592.
- COX, R. W. & PEACOCK, M. A. (1977). The fine structure of developing elastic cartilage. *Journal of Anatomy* **123**, 283-296.
- COX, R. W. & PEACOCK, M. A. (1978). The growth of elastic cartilage. *Journal of Anatomy* (in the Press).
- HUXLEY, J. S. (1972). *Problems of Relative Growth*, 2nd ed. New York: Dover Publications.
- MARTINDALE, W. (1967). *Extra Pharmacopoeia*, 25th ed. (ed. R. G. Todd), pp. 1408. London: Pharmaceutical Press.
- MEDAWAR, P. B. (1944). The shape of the human being as a function of time. *Proceedings of the Royal Society B* **132**, 133-141.
- MEDAWAR, P. B. (1945). Size, shape and age. *Essays on Growth and Form* (ed. W. E. Le Gros Clark and P. B. Medawar), pp. 157-187. Oxford: Oxford University Press.
- RICHARDS, O. W. & KAVANAGH, A. J. (1943). The analysis of the relative growth gradients and changing form of growing organisms illustrated by the tobacco leaf. *The American Naturalist* **77**, 385-399.

- RICHARDS, O. W. & KAVANAGH, A. J. (1945). The analysis of growing form. *Essays on Growth and Form* (ed. W. E. Le Gros Clark and P. B. Medawar), pp. 188–229. Oxford: Oxford University Press.
- RICHARDS, O. W. & RILEY, A. G. (1937). The growth of amphibian larvae illustrated by transformed coordinates. *Journal of Experimental Zoology* **77**, 159–167.
- THOMPSON, D'A. W. (1942). *On Growth and Form*, 2nd ed. Cambridge: Cambridge University Press.