A conjecture on the relationship of bacterial shape to motility in rod-shaped bacteria

Stephen Cooper [a],*, Mark W. Denny [b]

[a] Department of Microbiology and Immunology, University of Michigan Medical School, Ann Arbor, MI 48109-0620, USA
[b] Department of Biology, Stanford University, Hopkins Marine Station, Pacific Grove, CA 94950, USA

Abstract

We have calculated the optimal shape, i.e. the length-to-width ratio of a bacterial cell, that allows a bacterial cell to move most efficiently through liquid. For a cell of a given size, a minimum exists in the force required to move through any liquid when the length of the cell is approx. 3.7 times greater than the width. As this is in approximate agreement with the observed shape of bacteria such as the Enterobacteriaceae, we conjecture that the current observed shape of these bacteria may have been determined, in part, to obtain the most efficient shape for moving through liquids. It is also found that spherical cells are very inefficient in movement through liquid, while longer cells of a fixed size are still relatively efficient in moving through liquids. Since the optimal shape is independent of actual size (within large bounds), it is further proposed that hydrodynamic efficiency considerations support the proposal of constant shape over a range of sizes for rod-shaped bacteria.

Keywords: Cell shape; Motility; Bacteria; Escherichia coli; Hydrodynamic efficiency

1. Introduction

After we first notice that rod-shaped bacteria are somewhat longer than wide, we generally take no more notice of exactly why the observed length-to-width ratio is what it is. We now look more closely at bacterial shape and ask the question: 'Is there some logical or evolutionary reason why rod-shaped bacteria have the shape they do?' More specifically we ask, for example, why does Escherichia coli have the shape it does? Why isn't it longer or shorter?

* Corresponding author. Tel.: +1 (313) 764 4125; fax: +1 (313) 764 3562; e-mail: cooper@umich.edu

1.1. A priori considerations on cell shape

There are probably many reasons a cell is the shape it is. Perhaps there are physical constraints, such as the inability of peptidoglycan to bend in a certain way, or limitations due to the requirement that a cell accommodate its nucleoid. A bacterial cell can optimize its growth efficiency by maintaining a small size so that there is a relatively short distance between the external source of nutrients and the cell cytoplasm that will metabolize those nutrients. A small cell size means that for a given mass there will be a large surface-to-volume ratio, and thus an efficient and rapid incorporation of external nutrients. By adjusting its shape, a cell can make this

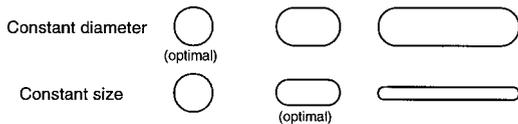Constant diameter ○ ⬭ ▭
(optimal)

Constant size ○ ⬭ ▭
(optimal)

Fig. 1. Comparison of elongation of cells with constant diameter and with constant size. With a given, fixed diameter, the least resistance is given by the most spherical cell. With constant size, there is an optimum shape that is elongated, with a larger surface area but a smaller cross-sectional face.

surface even more accessible to the external environment.

We do not propose to solve the entire problem of cell shape here. What we would like to do is merely to suggest one factor that may be important, and present our calculations on the relationship of shape to motility for rod-shaped organisms.

At the level of the single cell we can now ask what shape would continue this maximization of external resource utilization. As a first approximation we can propose that a spherical cell, with a minimum surface-to-volume ratio, is not optimal. Rather a flat or thin cell would be better. If a sheet-like shape (or a convoluted, wrinkled shape) is eliminated due to considerations of peptidoglycan structure (i.e., the peptidoglycan cannot bend in some particular way), we would expect that cells would be most efficient, metabolically, as extremely long and thin cells. Therefore, if increasing the surface to volume ratio was the only consideration, we would expect cells to tend to be very long and thin.

This, of course, is not the case. While *Escherichia coli* is not round, it is also not very long. We may imagine many reasons why cells are not extremely long, and consequently, not extremely thin. First, if a cell has a single compact genome, a very long, thin cell would have a significant portion of its cytoplasm a significant distance from the nucleoid. Ribosomes that are distant from the nucleoid would rarely meet a messenger RNA, and thus would be inefficient at synthesizing protein. This would not be beneficial for optimizing cell growth.

A second logical reason cells are not extremely thin is that the genome, in the light microscope, appears relatively compact. If it is compact, and relatively spherical, then this compact genome, in its approximately spherical shape, would not be compatible with a thin cell. If localized bulges are ruled

out, then the thinnest a cell could be would be no thinner than a cell with a width able to contain a compact nucleoid.

Finally, there may be structural reasons for not allowing an extremely thin shape, such as the impossibility of having a pole region with a curvature that would allow a thin cell. If the radius of curvature at the end of a cell cannot be smaller than a certain value, this would preclude cells below a certain width. Of course, this last argument would only mean that small cells would have a minimum thinness, while large cells should be able to be as thin as small cells. This would argue that cells would have a constant thinness, the minimum, and larger cells (such as those found in rich media) would be extremely long. Since cell shape is relatively constant, this argument is probably not valid.

1.2. Hydrodynamic considerations and cell shape

Let us now turn to a different type of consideration to understand cell shape, that of hydrodynamic efficiency. We have looked at the relationship of shape to the ability of a motile organism to move through water, and have modified the initial question to: 'Is there some optimal bacterial shape that is most efficient for motility through water?' When the analysis is performed in the proper manner, we find an optimal shape exists. Most gratifying, the optimal shape calculated is similar to that found by microscopic examination. The results imply that cell
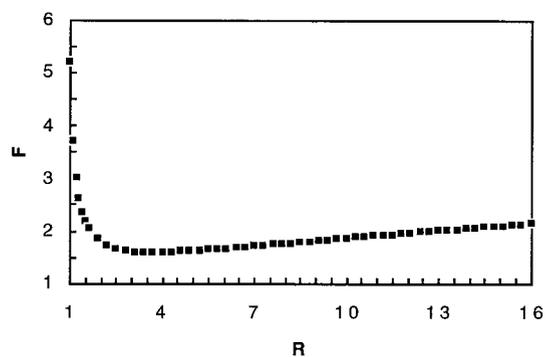
Fig. 2. Calculations of F, the force to required to move a rod-shaped cell through liquid, for various values of R ($R = a/b$), where a is the length in the long axis and b is the width of the cell). Note that there is a minimum at approx. 3.7. When $R = 136$, the value of F is the same as for an R of 1.0.

shape should be quite constant over a range of cell sizes.

Consider a spherical bacterium. It has a certain resistance to movement through liquid. This is given by the force, F, required to move the bacterium through water at a given velocity. The resistance is due to two components; one component is the fore-aft pressure difference across the bacterium (which leads to pressure drag), and the other component comes from the friction of the cell's movement through a viscous medium (the surface drag). Pressure drag is proportional to the cell's projected area, while surface drag is proportional to the total surface area of the cell. Now consider that we enlarge this bacterium into a rod-shaped cell while keeping the diameter (cross-sectional area) constant (upper part of Fig. 1). We assume the bacterium is moving through the liquid in a direction parallel to the long axis of the cell. Since the projected cross-sectional area is constant, and since the surface area is minimal in the coccus or sphere-shaped cell, we would expect that the resistance would continuously increase and no optimum rod-shape (with regard to the resistance property) would be obtained. The minimum F would be found for the initial sphere-shaped cell.

The mass of a bacterial cell is determined, in some way, by the cell mass or volume at initiation of DNA replication [1]. Given that the mass of the cell is determined by factors independent of those determining shape, we can rephrase the problem and investigate how the efficiency of movement through liquid changes when the shape changes with a cell constrained to a constant volume or mass (lower part of Fig. 1). Again consider a spherical cell that is successively lengthened, only this time as the cell elongates it must get thinner in order to preserve the constraint of constant mass. Here we have the cross-sectional area decreasing and the length or total surface area increasing. The decreasing cross-sectional area, by itself, leads to a lower F value, and the increasing surface area (because the minimum surface of a given volume is produced by a sphere) by itself, produces more surface drag that leads to a larger F value. We can now ask whether for these cells there is some optimum shape with a minimum F value. We find that there exists such a minimum.

2. Results

The volume of a prolate ellipsoid is

$$V = (4/3)\pi a^3 (1/R)^2 \qquad (1)$$

where a is one half of the long axis length of the ellipsoid and R is the ratio of this long axis to the minor axis; i.e., R is the aspect ratio for the bacterium.

The force required to push an ellipsoid through water parallel to its long axis is (to a first order approximation) [2]:

$$F = \mu u 4\pi a / ([\ln(2R)] - 1/2) \qquad (2)$$

where μ is the dynamic viscosity and u is velocity, and a and R are as defined in Eq. 1. [It should be realized that Eq. 2 is a first order approximation which can be refined with higher order approximations that are available (see [2]). But this added complexity does not change the fundamental conclusions reached here regarding the relationship of size, shape, and motility. The first order approximation used here may also be found in [3].

Solving Eq. 1 for a in terms of volume, V, and inserting that into Eq. 2, we see that

$$F = \mu u 4\pi (3V/4\pi)^{1/3} \cdot (R^{2/3} / ([\ln(2R)] - 1/2)) \qquad (3)$$

Thus, for any given μ, u, and V, the force (F) is given by:

$$F = k \cdot (R^{2/3} / ([\ln(2R)] - 1/2)) \qquad (4)$$

If we evaluate the differential of F with respect to R, and rearrange the terms, we find

$$dF/dR = ((2/3 \cdot k R^{-1/3}) \cdot [\ln 2R - 2]) / [\ln 2R - 1/2]^2 \qquad (5)$$

Solving for R when dF/dR is a minimum by setting dF/dR in Eq. 5 equal to zero, the only solution occurs when $(\ln 2R - 2) = 0$, thus,

$$\ln 2R_{(F_{min})} = 2 \qquad (6)$$

and

$$R_{(F_{min})} = e^2/2 \qquad (7)$$

and thus

$$R_{(\mathrm{F_{min}})} = 3.6945 \tag{8}$$

Therefore, the function (Eq. 4) has a minimum at approximately $R = 3.7$. This is shown graphically in Fig. 2. At the minimum the rod-shaped cell is approximately 5 times more efficient at motility than a spherical cell of the same mass or volume. Not until the length of a cell is 136 times the width (a very long filamentous cell) does the resistance (given as F) reach that of the original sphere. The force increases rapidly for $R < 3.7$ and more slowly for $R > 3.7$. Thus, long, thin bacteria may not be very inefficient in movement through liquid, but short round bacteria are much less efficient in motility.

Measurements of the shape of *E. coli* over a wide range of growth rates have been summarized (Table 6-1 in [1]), and an average of all of the shapes presented there is 3.93. This matches very well with the calculated optimal shape presented here. The evidence in this table also supports the proposal that over a range of growth rates the shape of the *E. coli* is relatively constant.

3. Discussion

It is satisfying to observe that the calculations performed here indicate that the optimum bacterial shape is approximately that found in nature. The calculation has only been presented for the idealized case of a prolate ellipsoid moving in the direction of its axis. A more accurate calculation would use the idealization of the cell as a cylinder capped by two hemispheres.

The calculation presented here constrained cells to be of constant mass as shape varied. This is more akin to comparing apples with apples because the size of the cell is determined by the need to have a certain mass at initiation of DNA replication. That is, the shape of the cell is determined within the constraint of a particular cell size which is determined by the rate of growth. (For a detailed analysis of this proposal, see [1].) When the calculation is performed with constant size constraints (i.e., calculating the optimal shape for a given size as we vary the shape), we find that the optimum shape of the

bacterial cell is a length-to-width ratio of 3.7. This is similar to that found by measurements.

Ideally, one would want calculate the optimal shape for cells growing from one length (at birth) to twice that length (at division) and with all lengths in between. The optimum would be determined by integrating the F value over all ages during the division cycle. In the absence of this calculation, we suggest that the initial results shown here are quite satisfying, and are not likely to be significantly changed by a more extensive calculation over a range of cell ages.

It has been proposed that the shape (defined as the ratio of length to width) of a given bacterial cell such as *E. coli* is constant or invariant even though there may be growth rate determined changes in cell size [1]. That is, for a given cell (specifically, *E. coli* in the original analysis) the length-to-width ratio is constant while cells change their size with growth rate. Here we show that from hydrodynamic considerations there is an optimal shape irrespective of cell size. Since there is no reason to imagine that the condition of optimality varies for cells of slightly different sizes, the analysis presented here may be taken as oblique support for the initial and experimentally supported proposal of constant shape for a bacterial cell [1]. Cells have a constant shape because the optimality conditions for motility are independent of cell size.

Motility considerations may not be the only determinant of cell shape. We realize that there may be many other reasons why cells are the shape they are. Different strains of *E. coli* do exhibit slightly different shapes. There may be constraints of peptidoglycan structure, constraints of enzymology, constraints on the biosynthesis of the cell structures, as well as other, unknown aspects of cell chemistry. Also, various historical and ecological conditions may have altered cells and compromised the ideal shape. We would note that at the region of the minimum, there is a broad range where variations from the minimum have little effect on motility. Thus, other considerations of growth and evolution may modify different strains of *E. coli* without compromising the basic considerations outlined here. Even more to the point, different bacteria may have different shapes. The hydrodynamic calculation presented here is not meant to be the final explanation of shape. Rather, we be-

lieve that shape is determined by the interaction of a large number of factors, physical, environmental, chemical, and energetic, and it is the integration of all of these factors that determines the final shape. Here we merely point out that the calculated optimal shape is close to that observed for a well-studied organism, and furthermore that this shape is proposed to be independent of cell size. Thus, the hydrodynamic considerations alone suggest that shape would be constant. That such a constancy of shape is found [1] is gratifying but in no way can it be taken as a proof that the shape is determined by hydrodynamic considerations alone.

What we wish to conjecture here is that the observed shape of cells is consistent with the proposal that this shape has evolved, in part, because of its greater efficiency in motility. Further, these considerations would lead to the expectation that cells would exhibit a constant shape as size varied due to growth conditions.

References

[1] Cooper, S. (1991) Bacterial Growth and Division: Biochemistry and Regulation of Prokaryotic and Eukaryotic Division Cycles, Academic Press, San Diego, CA.
[2] Tillet, J.P.K. (1970) Axial and transverse stokes flow past slender axisymmetric bodies. J. Fluid Mech. 44, 401–417.
[3] Lamb, H. (1932) Hydrodynamics, 6th edn., Cambridge University Press, Cambridge, UK.