Spatial Sensing of Stimulus Gradients Can Be Superior to Temporal Sensing for Free-Swimming Bacteria

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ABSTRACT Predictions of the minimal size an organism must have to swim along stimulus gradients were used to compare the relative advantages of sensory systems employing spatial (simultaneous) and temporal (sequential) gradient detection mechanisms for small free-swimming bacteria, leading to the following conclusions: 1) there are environmental conditions where spatial detection mechanisms can function for smaller organisms than can temporal mechanisms, 2) temporal mechanisms are superior (have a smaller size limit) for the difficult conditions of low concentration and shallow gradients, but 3) observed bacterial chemotaxis occurs mostly under conditions where spatial mechanisms have a smaller size limit, and 4) relevant conditions in the natural environment favor temporal mechanisms in some cases and spatial mechanisms in others. Thus, sensory ecology considerations do not preclude free-swimming bacteria from employing spatial detection mechanisms, as has been thought, and microbiologists should be on the lookout for them. If spatial mechanisms do not occur, the explanation should be sought elsewhere.

INTRODUCTION

Locomotion is of little use to organisms unless it can be directed in appropriate directions. For relatively simple organisms, the information for guiding locomotion is obtained by determining the orientation of a gradient of chemicals, light, or temperature. Information about the orientation of the gradient is obtained by comparing the intensity of stimulation at two or more locations in the stimulus field. To be successful, the difference in stimulation at these two positions must be greater than the noise in sensing stimulus intensity, and this requirement sets some clear limitations on what gradients can be sensed by an organism of particular design.

There are two fundamentally distinct mechanisms for detecting gradients (Dusenbery, 1992, pp. 414–416). Those employing spatial detection mechanisms simultaneously compare the intensity of stimulation of receptors in different parts of the organism, which allows the organism to turn in the appropriate direction (tropotaxis). Organisms employing sequential, or temporal, detection mechanisms compare the intensity of stimulation of receptors at different times, between which the organism moves from one location to another, and modulate the probability of changing their direction of locomotion (klinokinesis or klinotaxis). In either case, larger organisms are at an advantage for several reasons. They can reduce noise by averaging sensation over a larger volume (Berg and Purcell, 1977); they can make comparisons over larger distances because receptors can be further apart for spatial mechanisms or because larger organisms generally move faster for temporal mechanisms (Dusenbery and Snell, 1995); and most importantly, larger organisms have more time before Brownian motion randomizes their orientation (Berg and Purcell, 1977). The question addressed here is which mechanism is most appropriate–spatial or temporal?

The movement of the enteric bacteria *Escherichia coli* and *Salmonella typhimurium* in chemical gradients (chemotaxis) has been much studied (e.g., Adler, 1969, 1975; Macnab, 1978, 1987; Hazelbauer, 1988; Manson, 1992), and they clearly employ a purely temporal sensing mechanism (Block et al., 1982; Segall et al., 1986). The recent discovery that receptors may be unequally distributed between the two ends of *E. coli* (Maddock and Shapiro, 1993) has been shown to be of little consequence because the cells frequently switch which end is forward (Berg and Turner 1995).

In contrast, insects (Calenbuhr and Deneubourg, 1992) and ameboid cells, such as the slime mold (Segall, 1990) and leukocytes (Tranquillo, 1990), appear to use spatial mechanisms for orientation to chemical gradients, although a temporal component remains.

A consideration of chemoreception (DeLisi et al., 1982; Dusenbery, 1992, p. 430) suggests that spatial mechanisms are superior for organisms larger than a few microns in size and that temporal mechanisms are superior for smaller organisms. This is consistent with the above observations, and for the past 25 years it has been held that bacteria are too small for spatial mechanisms to be effective in chemotaxis (e.g., Macnab and Koshland, 1972; Adler, 1975; Macnab, 1978; Carlile, 1980; Jackson, 1987, 1989; Ford, 1992; Mitchell, 1995).

However, it will be shown here that there are natural conditions in which the size limit for employing spatial detection mechanisms is smaller than for temporal mechanisms among the smallest free-swimming organisms.

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THE MODEL

To see this, we adopt a simple model of a free-swimming, spherical microbe of variable size. See Dusenbery (1997) for details. The main distinction from previous models is that I assume that the power available for locomotion is proportional to the volume of the organism. Applying Stokes' law, it is found that speed is proportional to linear size and relative swimming speed (u) is independent of size (Dusenbery and Snell, 1995). With typical values for energy metabolism and estimated efficiencies, the model organism is predicted to swim at ~10 diameters/s, which is within an order of magnitude of the swimming speed of most organisms (Dusenbery, 1996, p. 45). Even at speeds as high as 100 diameters/s, Stokes' law is applicable for diameters up to 70 μm (Dusenbery, 1997). Consequently, all bacteria are within the size range to which the model applies.

For free-swimming microbes, the time available to make measurements is limited by the rate of random rotation caused by Brownian motion. Information from the past has no value if past positions are equally likely to be in any direction from the present position. Well known theory (e.g., Tanford 1961, pp. 432–7; Berg, 1993, p. 83) shows that the rotational time for Brownian motion (τ) varies as

$$\tau = 4\pi\eta r^3/kT, \quad (1)$$

where the symbols are defined in Table 1. Note that it varies in proportion to the third power of the radius (r). For a micron-sized object, this time is on the order of a second.

With this model, it is straightforward to calculate the signal-to-noise ratio for determining the direction of a gradient of chemicals, light, or temperature using well known physical and chemical relationships and assuming optimal arrangements of receptors within the spherical boundaries of the organism.

Table 1 shows the parameters used and the values assumed as standard. In this paper, formulas are presented in a condensed form, where **S** is the signal-to-noise ratio, **V** is a parameter proportional to viscosity, and u is the relative speed of swimming. Stimulus intensity is represented as **C**, **I**, or **H**, proportional to concentration, light intensity, or thermal conductivity, respectively. (The absolute intensity matters because it controls the minimal noise an organism of a given size can obtain by integrating over a limited time interval.) The steepness of the stimulus gradient is represented as the decay length L of an exponential gradient or equivalently as the reciprocal of the relative gradient, $(1/I)\,dI/dx$, for any distribution that changes little in intensity over the distances of interest. The parameter values listed in Table 1 were chosen because they represent well defined values appropriate for common natural situations or the optimal values known to be available to organisms. More detailed explanations of the choices are available in Dusenbery (1997).

The resulting formulas are shown in Table 2 and demonstrate that the signal-to-noise ratios vary as high powers (3–6) of the radius of the organism for both spatial and temporal mechanisms. None of the other parameters have more than a 7/4 power compared with the signal-to-noise ratio.

Comparing signal-to-noise ratios

To compare the performance of the spatial and temporal mechanisms, the formulas of Table 2 are used to calculate

TABLE 1 Parameters used

Symbol	Meaning	Value*	Units
C	Concentration of a chemical	1×10^{16}	molecules cm^{-3}
D	Diffusion coefficient for chemicals	1×10^{-5}	$cm^2\ s^{-1}$
f	Fraction of light absorbed by photoreceptor	0.0003	—
h	Viscosity of the environment	0.01	poise = erg s cm^{-3}
H_c	Heat capacity per unit volume	4.2×10^7	erg cm^{-3} °K^{-1}
H_T	Thermal conductivity	6.2×10^4	erg s^{-1} cm^{-1} °K^{-1}
I	Light intensity	1×10^{16}	photons s^{-1} cm^{-2}
k	Boltzmann's constant	1.4×10^{-16}	erg °K^{-1}
L	Decay length of spatial gradient[#]		cm
r	Radius of organism		cm
T	Absolute temperature	293	°K
τ	Time constant for loss of orientation		s
u	Speed relative to size	20	radii s^{-1}
		10	diameters s^{-1}
v	Absolute speed		cm s^{-1}
S	Signal-to-noise ratio	1	—
U	$4\pi\eta/kT$	$\sim 3.1 \times 10^{12}$	cm^{-3} s
C	$2\pi DC$	$\sim 6.3 \times 10^{11}$	molecules cm^{-1} s^{-1}
I	$4\pi If$	$\sim 1.9 \times 10^{13}$	photons cm^{-2} s^{-1}
H	$4\pi H_T\,(k^2 H_c)^{-1/3}$	$\sim 8.3 \times 10^{13}$	s^{-1}

*Values assumed in making the standard estimates.
[#]0.1 cm for chemical and light stimuli; 5×10^5 cm for temperature.

TABLE 2 Constraints on signal-to-noise ratio

Stimulus	Mechanism	Constraint formulas*
Chemical	Spatial	$\mathbf{S} \le 3\mathbf{U}^{1/2}\mathbf{C}^{1/2}L^{-1}r^3$
Chemical	Temporal	$\mathbf{S} \le u\mathbf{U}^{3/2}\mathbf{C}^{1/2}L^{-1}r^6$
Light	Spatial	$\mathbf{S} \le \sqrt{2}\mathbf{U}^{1/2}\mathbf{I}^{1/2}L^{-1}r^{7/2}$
Light	Temporal	$\mathbf{S} \le u\mathbf{U}^{3/2}\mathbf{I}^{1/2}L^{-1}r^{13/2}$
Temperature	Spatial	$\mathbf{S} \le 2\mathbf{U}^{3/4}\mathbf{H}^{3/4}L^{-1}r^{13/4}$
Temperature	Temporal	$\mathbf{S} \le u\mathbf{U}^{7/4}\mathbf{H}^{3/4}L^{-1}r^{25/4}$

*Modifications of formulas from Table 2 of Dusenbery (1997).

the ratio of the stimulus-to-noise ratio for the temporal (S_T) mechanism to that of the spatial (S_S) mechanism. The result is

$$\frac{\mathbf{S}_T}{\mathbf{S}_S} = \frac{\mathbf{U}r^3u}{n} = \frac{4\pi\eta r^3u}{nkT} = \frac{u\tau}{n}, \qquad (2)$$

where n is a numerical factor equal to 3, $\sqrt{2}$, or 2 for chemical, light, and temperature stimuli, respectively, τ is the time constant for loss of orientation (Eq. 1), and the other symbols are defined in Table 1. The ratio is approximately equal to half the number of radii traveled in the period of the time constant. Note that the ratio depends only on the environmental parameters temperature and viscosity and the organism's size and speed. Intensity and gradient have canceled out because they affect the signal-to-noise ratio in the same way for both mechanisms.

For an organism of radius 1 μm, the ratio is near unity (1, 3/2, or $3/\sqrt{2}$), and surprisingly, the two mechanisms are approximately equal in potential performance. Even more surprisingly, as organisms decrease in size, the spatial mechanism rapidly gains advantage. This is because the signal-to-noise ratio for the temporal mechanism is proportional to r raised to a power that is 3 more than the power in the spatial formula, for all stimuli (Table 2). However, this analysis may be comparing the relative advantages of two mechanisms that both have such low signal-to-noise ratios as to be useless. Consequently, I compare the minimal size limits for the two mechanisms.

Comparing minimal size limits

For all stimuli and either mechanism of gradient detection, signal-to-noise ratio declines sharply with size (Table 2), and there are size limits below which any particular method is not functional ($S < 1$). The equations for these limits are presented in Table 3. Note that the exponents on all of the parameters differ between spatial and temporal mechanisms, for all stimulus types. To see this more clearly, for each stimulus, I take the ratio of the equations for the size limit of spatial and temporal mechanisms to obtain formulas for the ratio of the limiting sizes (Table 4). It can be seen that none of the exponents is zero, which means that in principle spatial mechanisms can function in smaller organisms than can temporal mechanisms for one extreme or the other of any of the parameters.

To obtain a clearer view of the similarity of the exponents across parameters and stimulus type, the diverse fractional exponents have been converted to decimals in Table 5. Relative speed, gradient steepness, and signal-to-noise ratio have the strongest impact (powers in the range of 0.13–0.17), with viscosity and stimulus magnitude having somewhat less impact (0.049–0.111). Considering the range of variation in natural environments, the most important variables impacting the relative advantages of the two types of mechanism are gradient steepness and the concentration of chemical stimuli or the intensity of light.

How do the two mechanisms compare for realistic values of the parameters? The equations for the limiting sizes are plotted in Fig. 1 for a chemical stimulus of 0.5 mM and variable gradient, with the other parameters having their standard values. It is seen that the curves cross, and for sufficiently steep gradients (small gradient decay lengths), spatial mechanisms work for smaller organisms than do temporal comparisons.

The 0.5 mM concentration was chosen because data on the behavior of *S. typhimurium* in well defined chemical gradients is available at this concentration (Dahlquist et al., 1976, Fig. 1). It may be seen that *S. typhimurium* performs close to the predicted limits but loses effectiveness in their vicinity, which augments confidence in the model. Remarkably, the parameter domain for *S. typhimurium* is close to the region where spatial and temporal mechanisms are equal in size limit. So it is not clear-cut that temporal detection mechanisms are a superior choice for bacteria.

In Fig. 2, variation in both concentration and gradient are considered, and the $r_{CS} = r_{CT}$ boundary is plotted. On the side of this boundary with the more difficult conditions of low concentration and shallow gradients, temporal mechanisms function for smaller organisms than do spatial ($r_{CS} > r_{CT}$). On the other side, spatial mechanisms function for smaller organisms than do temporal ($r_{CS} < r_{CT}$).

TABLE 3 Constraints on size

Stimulus	Mechanism	Constraint formulas	Limit*
Chemical	Spatial	$r \ge \mathbf{S}^{1/3}\mathbf{U}^{-1/6}\mathbf{C}^{-1/6}L^{1/3}3^{-1/3} \equiv r_{CS}$	0.29 μm
Chemical	Temporal	$r \ge \mathbf{S}^{1/6}\mathbf{U}^{-1/4}\mathbf{C}^{-1/12}L^{1/6}u^{-1/6} \equiv r_{CT}$	0.32
Light	Spatial	$r \ge \mathbf{S}^{2/7}\mathbf{U}^{-1/7}\mathbf{I}^{-1/7}L^{2/7}2^{-1/7} \equiv r_{LS}$	0.89
Light	Temporal	$r \ge \mathbf{S}^{2/13}\mathbf{U}^{-3/13}\mathbf{I}^{-1/13}L^{2/13}u^{-2/13} \equiv r_{LT}$	0.53
Temperature	Spatial	$r \ge \mathbf{S}^{4/13}\mathbf{U}^{-3/13}\mathbf{H}^{-3/13}L^{4/13}2^{-4/13} \equiv r_{HS}$	0.37
Temperature	Temporal	$r \ge \mathbf{S}^{4/25}\mathbf{U}^{-7/25}\mathbf{H}^{-3/25}L^{4/25}u^{-4/25} \equiv r_{HT}$	0.34

*Limiting radius when all the other parameters have their standard values (Table 1).

TABLE 4 Equations for ratios of limiting sizes

Stimulus	Equation
Chemicals	$r_{CS}/r_{CT} = 3^{-1/3}\mathbf{S}^{1/6}\mathbf{U}^{1/12}\mathbf{C}^{-1/12}L^{1/6}u^{1/6}$
Light	$r_{LS}/r_{LT} = 2^{-1/7}\mathbf{S}^{12/91}\mathbf{U}^{8/91}\mathbf{I}^{-6/91}L^{12/91}u^{2/13}$
Temperature	$r_{HS}/r_{HT} = 2^{-4/13}\mathbf{S}^{48/325}\mathbf{U}^{16/325}\mathbf{H}^{-36/325}L^{48/325}u^{4/25}$

How does this boundary compare with the performance of actual bacteria? Also plotted in Fig. 2 are data on the chemotactic performance of *S. typhimurium* in well defined chemical gradients (Dahlquist et al., 1976). Two measures of performance are available from this work. One measure is the relative gradient (γ_0) at which the population of bacteria migrate at half their maximal possible rate. The reciprocal of this value is the gradient decay length, which is plotted ($1/\gamma_0$). The other measure of performance is the gradient decay length at which the trajectory of individual bacteria is doubled, on average (labeled b). These two measures parallel one another separated by a factor of 4. Remarkably, the two curves straddle the $r_{CS} = r_{CT}$ boundary and parallel it up to a concentration of $\sim 10^{-3}$ M, where saturation of the receptors is thought to begin (Dahlquist et al., 1976). (As the model assumes that receptors have optimal properties, deviation from the model under these conditions is expected.) This comparison demonstrates that chemotaxis in *S. typhimurium* functions under conditions where spatial and temporal mechanisms are both possible. Indeed, as these curves represent the limits of chemotactic function, most of the parameter space where the bacteria can follow a gradient is below the boundary, where spatial mechanisms function for smaller organisms ($r_{CS} < r_{CT}$).

How does the boundary compare with the needs of bacteria? Also plotted in Fig. 2 are data on the concentrations and gradients of nutrients naturally present in sediments. It is clear that these conditions commonly occur on both sides of the $r_{CS} = r_{CT}$ boundary. Consequently, there could be small free-swimming bacteria in some environments that would find a spatial detection mechanism advantageous.

DISCUSSION

It might be argued that available power is limited by the rate of nutrient diffusion to the cell, in which case available power would be proportional to r instead of r^3 as assumed here (Berg and Purcell, 1977). As speed is proportional to the square root of available power (Dusenbery and Snell, 1995), this would predict that speed is independent of size, which certainly contradicts the large-scale trends (Dusen-

TABLE 5 Exponents of parameters in the ratio of size limits using spatial detection mechanisms to size limits using temporal mechanisms

	Stimulus		
Parameter	Chemical	Light	Temperature
u	1/6 = 0.1667	2/13 = 0.1538	4/25 = 0.1600
L and **S**	1/6 = 0.1667	12/91 = 0.1319	48/325 = 0.1477
U	1/12 = 0.0833	8/91 = 0.0879	16/325 = 0.0492
C, **I**, or **H**	−1/12 = −0.0833	−6/91 = −0.0695	−36/325 = −0.1108

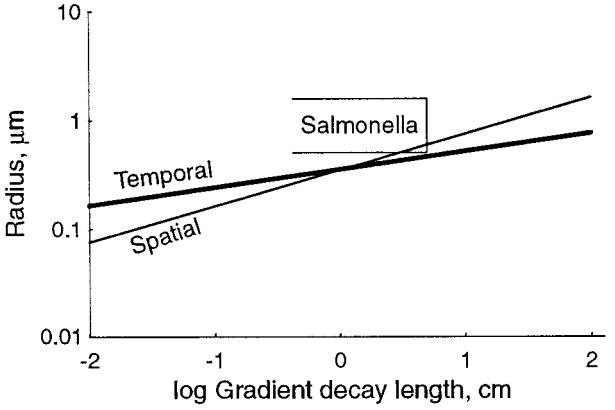

FIGURE 1 Minimal sizes for migration along a chemical gradient. The lines are the minimal radii (r_{CS} and r_{CT}) calculated from the first two equations of Table 3, assuming standard values (Table 1) except for a concentration of 0.5 mM, which was selected to allow comparison with observations. The box labeled Salmonella delineates the area of this plot in which observations of *S. typhimurium* fall. The horizontal extent of this box corresponds to the range of gradient decay lengths over which the bacteria were observed to migrate (Dahlquist et al., 1976, Fig. 1). The left side is open because no limit was observed on the steep (small decay length) side. The vertical extent corresponds to the geometric averages of the range of widths and the range of lengths reported for the genus in Bergey's Manual (Holt, 1984, p. 427).

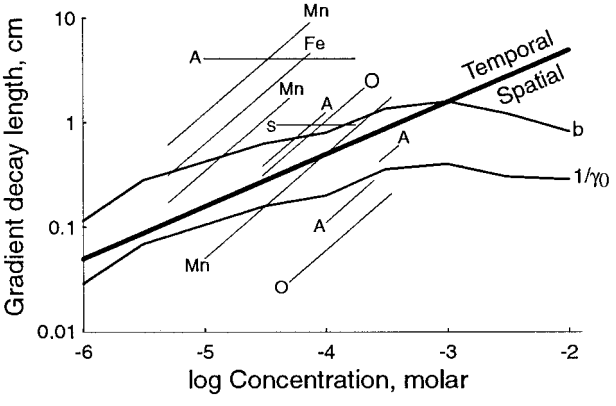

FIGURE 2 Chemical concentrations and gradients. The heavy line is the boundary where spatial and temporal gradient detection mechanisms have equal size limits ($r_{CS} = r_{CT}$). For the more difficult conditions of lower concentration and shallower gradients (larger gradient decay lengths), temporal mechanisms function for smaller organisms than spatial. For the less challenging conditions of higher concentration and steeper gradients, spatial mechanisms function for smaller organisms than temporal. The two irregular lines traversing the plot depict data on the limits of performance of *S. typhimurium* using two different criteria of performance (Dahlquist et al., 1976, Table 2). Half the maximal rate of migration of the population along the gradient occurred along the line labeled $1/\gamma_0$. The average lifetime of trajectories of individual bacteria doubled along the line labeled b. The short, straight lines represent the range of concentrations and gradients observed for nutrients in a sample of sediments (calculated from Sweerts et al., 1991, Figs. 3 and 4; Canfield et al., 1993, Fig. 3). The nutrients are ammonium (A), iron (Fe), manganese (Mn), oxygen (O), and sulfate (S).

bery, 1996, p. 45). Even so, replacing u by v/r in Eq. 2 would mean that the ratios of signal-to-noise would vary as r^2 rather than r^3; in the temporal equations of Table 3, the substitution at most changes the size limit from r to $r^{5/6}$. In both cases, this change has little impact on the conclusions.

Furthermore, studies of how oxygen consumption varies with size among single-cell organisms (Robinson et al., 1983) suggest that available power would scale as volume to the power 0.83 or $r^{2.49}$. This is much closer to the assumed proportionality to volume ($\propto r^3$) than to maximal nutrient flux ($\propto r$). The observed value of 2.49 could be incorporated into the model, but its uncertain appropriateness did not justify the increased complexity of the model, and it would not affect the general conclusions.

We see from Fig. 1 that the predictions of this model are consistent with the few observations available of bacterial behavior in defined chemical gradients. The analysis indicates that temporal detection mechanisms are favored (in the sense of $r_{CS} > r_{CT}$) under the difficult conditions of low concentration and shallow gradients (Table 4 and Figs. 1 and 2). Thus, the commonly held notion that temporal mechanisms are superior for organisms as small as bacteria is appropriate for these conditions but not for others. Surprisingly, commonly studied bacteria actually perform in conditions where spatial mechanisms function for smaller organisms ($r_{CS} < r_{CT}$) and reach the limits of their abilities in the region of $r_{CS} = r_{CT}$ (Figs. 1 and 2). So it would appear quite possible that some free-swimming bacteria may be found to rely on spatial detection mechanisms.

How did the notion arise that temporal mechanisms were so superior? Initial arguments suggested that the separation of the sites at which intensity was measured could be much greater with temporal stimulation ($vt \gg 2r$). However, this argument ignored the facts that the swimming path is not straight and that the time to integrate the signal is more limited for temporal mechanisms.

In a more rigorous analysis for chemical stimuli, Berg and Purcell (1977) concluded that spatial mechanisms were feasible on the basis of signal and noise considerations. However, they assumed that the comparison was between receptors on the forward edge and the trailing edge and that the organism absorbed the stimuli. They then pointed out that movement through a uniform concentration would result in stronger stimulation at the front and reduced stimulation at the rear and assumed that this distortion would preclude detection of the external gradient.

This complication does not arise for light or temperature gradients. In addition, in principle, the organism has all the information needed to correct for this effect, so it may not be an insurmountable problem. Indeed, biological mechanisms usually calibrate themselves by adaptive physiological processes rather than relying on the formation of identical receptors. Another way out of the problem would be for the organism to employ comparison across a lateral distribution of receptors rather than fore-and-aft. This occurs in the response of the cyanobacterium *Anabaena* to light (Häder, 1987). Thus, none of the arguments against the performance of spatial gradient detection mechanisms is very rigorous.

Are prokaryotes capable of evolving spatial detection mechanisms, even if they would be functional? The answer appears to be affirmative, because several cyanobacteria have been shown to respond to stimulation by light through spatial mechanisms (Häder, 1987). However, cyanobacteria are not free-swimming organisms but glide over surfaces. Consequently, they are not disoriented by Brownian motion and can usefully integrate stimuli over much longer time periods (minutes) than can free-swimming bacteria (seconds). Apparently, no prokaryote has been shown to employ spatial detection mechanisms on the rapid time scale required by a free-swimming bacterium. So it could be that it would be difficult to evolve such a mechanism. This might be the explanation for why spatial mechanisms have not been discovered among free-swimming microbes.

But, without invoking this assumption, can we explain why temporal mechanisms appear to be much more commonly used by bacteria? Examination of Fig. 1 suggests that using a temporal mechanism allows *S. typhimurium* to push its range of functional chemotaxis further into the difficult circumstance of shallow gradients than if it employed a spatial mechanism. This could be the important general reason that temporal mechanisms appear to be more common.

Another consideration is shape. Most bacteria are cylindrical rather than spherical, as assumed here. Does this matter? It will be shown in a forthcoming paper that elongation of the organism at constant volume can enormously increase the signal-to-noise ratio for the temporal mechanism, whereas spatial mechanisms are improved much less. This consequence of shape may be the strongest force favoring temporal mechanisms. Thus, the most likely type of bacteria to employ spatial mechanisms are spherical cells living in environments where the important chemicals occur at high concentrations with steep gradients.

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