Eur Biophys J (1989) 17:237–243

European Biophysics Journal

Periodicity and chaos in the response of *Halobacterium* to temporal light gradients

A. Schimz* and E. Hildebrand

Institut für Biologische Informationsverarbeitung der Kernforschungsanlage Jülich GmbH, Postfach 1913, D-5170 Jülich, Federal Republic of Germany

Received January 3, 1989/Accepted in revised form July 26, 1989

Abstract. Halobacteria spontaneously reverse their swimming direction about every 10 s. This periodicity can be altered by light stimuli. We found that temporal exponential changes in light intensity, depending on wavelength and sign, lengthened or shortened the intervals between reversals. Within a limited range of steepness, light gradients enforced a new stable periodicity upon the system. Outside this range, they caused period doubling or induced a sequence of reversal events without any obvious regularity. An analysis of a functional relationship between apparently irregular periods by plotting each period as a function of the preceding one yielded a clearly discernible non-random structure, which shows some similarities to the one obtained by a model calculation for a periodically perturbed limit cycle oscillator. These results indicate that external forcing of the system may generate chaos. When the decay of intracellular sensory signals is delayed by inhibition of protein methylation the transition from periodic to aperiodic behavior occurs at a lower steepness of the gradient. We therefore assume that the generation of either periodic or deterministic chaotic behavior is determined by the relation between the signal lifetime and the frequency of stimulus inputs. The strong indications for transitions from periodic to chaotic behavior can be regarded as a further support of our hypothesis that the behavioral pattern of *Halobacterium* is controlled by an endogeneous oscillator.

Key words: Oscillation, chaotic behavior, photosensing, signal processing, *Halobacterium*

Introduction

Halobacteria swim by means of polarly inserted flagella. Owing to a change of flagellar rotation from clockwise (CW) to counterclockwise (CCW) or vice versa, the cells spontaneously reverse their swimming direction about every 10 s on the average (Alam and Oesterhelt 1984; Schimz and Hildebrand 1985).

In *Halobacterium*, three sensory photosystems, PS 565, PS 370 (Hildebrand and Dencher 1975), and PS 480 (Takahashi et al. 1985; Wolff et al. 1986; Marwan and Oesterhelt 1987) are known. Changes of light intensity act as external stimuli and transiently disturb the behavioral pattern. A sudden increase of yellow-green light prolongs a swimming interval, independently of whether the flagella are rotating CW or CCW. This response is defined as the attractant response. An increase of UV or blue light leads to a shortened interval, which is defined as the repellent response. A decrease of yellow-green (attractant) light, on the other hand, elicits a repellent response, whereas a decrease of UV or blue (repellent) light leads to an attractant response (Hildebrand and Dencher 1975; Spudich and Stoeckenius 1979; Hildebrand and Schimz 1983; Takahashi et al. 1985; Wolff et al. 1986; Marwan and Oesterhelt 1987). After one changed swimming interval the bacteria normally resume their autonomous reversal rhythm (Schimz and Hildebrand 1985).

The frequency distribution of interval lengths can be fitted by a log normal distribution which points to a regulated process rather than to a stochastic one (Schimz and Hildebrand 1985). We have proposed an oscillatory mechanism as the basis of the rhythmic reversals for the following reasons: *1.* The responsiveness during an interval is not constant. Stimulation at different times yields a saw-tooth shaped phase response curve (Schimz and Hildebrand 1985, 1987); *2.* The system can be entrained by periodic stimulation. UV-light pulses enforce a new faster reversal rhythm upon the system, which, in a limited frequency range, matches the stimulation frequency (phase-locking), and becomes aperiodic above this frequency range (Schimz and Hildebrand 1986); *3.* Weak stimuli cause normal or inverted responses in a phase-depen-

* To whom offprint requests should be sent

dent manner (Hildebrand and Schimz 1987). Our model assumes that an oscillating regulatory component controls the directional changes of flagellar rotation (Schimz and Hildebrand 1985). Cellular attractant and repellent signals would shift the phase of oscillation in one or the other direction to delay or advance the next reversal (Hildebrand and Schimz 1986; Schimz and Hildebrand 1987). On the basis of this model one would expect that repetitive stimulation by attractants can lead to a slower reversal rhythm. The present paper shows that halobacteria respond to temporal gradients of light intensity, attractants as well as repellents. Temporal gradients can be regarded as a borderline case of periodic stimulation, which, depending on their steepness, lead to new stable periodicities or to chaotic behavior.

Materials and methods

Halobacterium halobium, "wild type" strain WS, was used for experiments. Cells in a suspension were observed through a microscope connected to a video system (Hildebrand and Schimz 1986). A single bacterium was chosen, and successive intervals between reversals of the swimming direction were measured with an electronic stopwatch connected to a printer. The behavior of the same cell was registered before, during, and after its exposure to temporal gradients of light intensity. Exponential gradients of different steepness were obtained by driving an optical wedge through the beam of stimulating light at given rates. A linear gradient was achieved by using an arrangement of small strips of a film which had been exposed for different times to obtain a linearly increasing optical transmission.

The three photosystems differ in their absolute sensitivity (Hildebrand and Dencher 1975). Therefore, for exponential gradients, the total change in fluence rate was from 4×10^{10} to 1×10^{14} photons $\times$ mm^{-2} s^{-1} at 565 nm wavelength, from 1.4×10^{10} to 3×10^{13} at 480 nm, and from 4.7×10^{8} to 2.8×10^{12} at 380 nm. For linear gradients, it was from 1×10^{13} to 8×10^{13} photons $\times$ mm^{-2} s^{-1} at 565 nm, and from 3×10^{11} to 3.4×10^{12} at 380 nm. Observation light was white light, 250 μW $\times$ mm^{-2}, in the case of stimulation at 565 nm and 380 nm, and red light >715 nm during stimulation at 480 nm. Temperature was 22 °C.

Inhibition of protein methylation was achieved by suspending the cells in peptone-free medium containing 10 mmol/l of DL-homocysteine obtained from Fluka. The intracellular level of cyclic GMP was increased by addition of N^2-2′-O-dibutyrylguanosine 3′:5′-cyclic monophosphate (Sigma) dissolved in ethanol, to the cell suspension. The final concentration was 50 µmol/l.

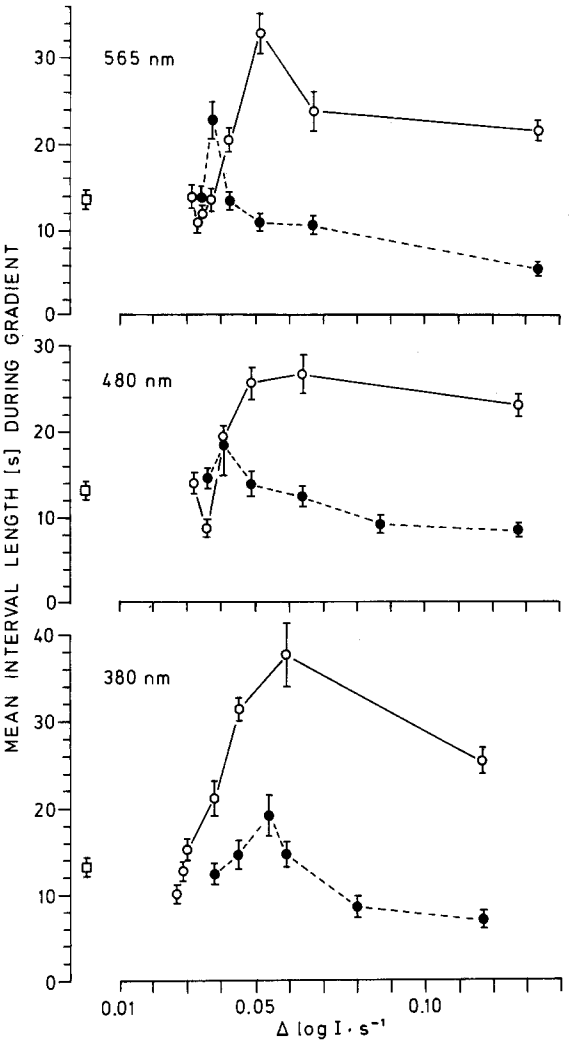

Fig. 1. Mean length of swimming intervals as a function of the steepness of temporal exponential light gradients. Attractant gradients (*solid lines*) were realized by an increase of fluence rate at 565 nm, or a decrease of fluence rate at 480 and 380 nm. Repellent gradients (*dashed lines*) were a decrease of fluence rate at 565 nm, or an increase at 480 and 380 nm. The steepness of the gradient is given in $\Delta \log I \times s^{-1}$ (I = intensity in photons $\times$ mm^{-2} s^{-1}). During the application of gradients, successive intervals between reversals of the swimming direction of a single cell were measured, and the data obtained from several cells were averaged. *Squares* indicate spontaneous interval lengths in the absence of a light gradient. Each point is the mean $\pm$ SEM of 30–100 intervals

Results and discussion

Mean length of swimming intervals as a function of the steepness of temporal exponential gradients of light intensity

With attractant gradients (either light increase at 565 nm or light decrease at 480 and 380 nm), the first detectable response occurred when the steepness of the gradient, given in $\Delta \log I \times s^{-1}$, reached about 0.03 (Fig. 1, solid lines). The resulting interval lengths were

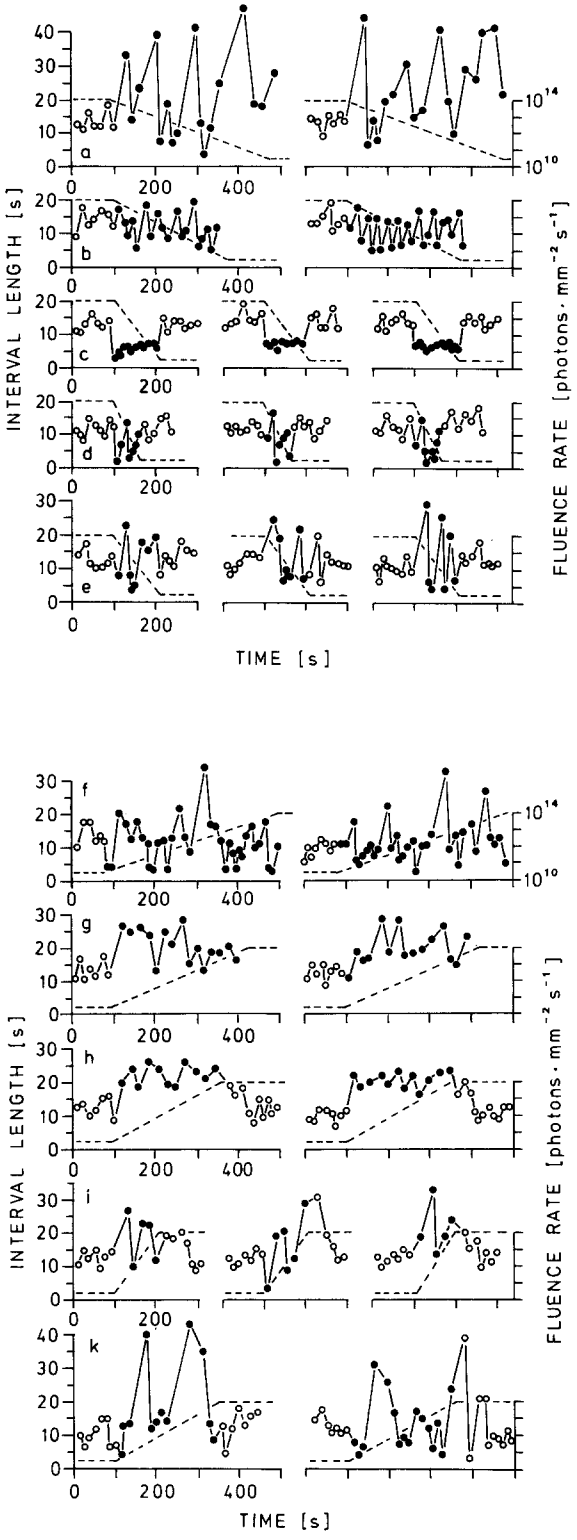

Fig. 2a–k. Length of successive intervals during application of exponential gradients. Successive swimming intervals of a single bacterium were measured before, during, and after a gradient. For each gradient two to three runs with different cells out of 4 to 10 runs are shown. *Open circles* give the intervals before or after the gradient, *closed circles* the intervals during the gradient. The gradients were turned on immediately after a spontaneous reversal. The *dashed lines* indicate the change in light intensity. Repellent gradients were achieved by decreasing the fluence rate at 565 nm. The steepness of the gradient expressed in $\Delta \log I \times s^{-1}$ was (**a**) 0.037, (**b**) 0.050, (**c**) 0.132, (**d**) 0.230, (**e**) 0.132, after protein methylation had been inhibited. Similar results were obtained with an increasing fluence rate at 480 or 380 nm. Attractant gradients were an increase of fluence rate at 565 nm. The steepness of the gradient was (**f**) 0.032, (**g**) 0.042, (**h**) 0.050, (**i**) 0.132, (**k**) 0.050, after protein methylation had been inhibited. Similar results were obtained with a decreasing fluence rate at 480 or 380 nm

shorter than the spontaneous intervals (repellent responses). Such inverse responses have also been observed for weak step-like stimuli (Hildebrand and Schimz 1987). A further increase of the gradient changed the response into an attractant one; the intervals became longer until the maximal length was reached at a steepness of about 0.05 to 0.06. Additional increase in the steepness resulted in a slight decrease of the mean interval lengths.

The threshold for repellent gradients (Fig. 1, dashed lines) was slightly higher. Again the first detectable response, which occurred at a steepness of about 0.035 to 0.045 was an "inverse" response. Increasing the gradient changed the response into a repellent one. Neither with attractant nor with repellent gradients was the response, i.e. the interval lengths during the gradient, a linear function of the steepness, as has been shown for the response of *Escherichia coli* to exponential gradients of chemical substances (Block et al. 1983).

Length of successive intervals during application of exponential gradients

During application of a relatively low repellent gradient the fluctuations of the interval lengths became much larger than in the spontaneous case; very long and short intervals occurred without any obvious regularity (Fig. 2a). A slight increase of the gradient resulted in a fairly regular sequence of alternating short and medium length intervals (Fig. 2b). When a repellent gradient of a steepness of $\Delta \log I \times s^{-1} = 0.132$ was turned on, the interval length was immediately cut in half and persisted so for the duration of the gradient (Fig. 2c). After the gradient had ended, the cell returned to its autonomous periodicity within about 10 s. A further increase of the steepness did not further shorten the intervals but caused aperiodic behavior (Fig. 2d).

Stable periodicity during a repellent gradient occurred only when the interval length was about cut in half. This is in accordance with our previous data obtained with periodic repellent light pulses (Schimz and Hildebrand 1986). Under the latter conditions, the periodicity was also stable when the period length became cut in half, and it became aperiodic at higher

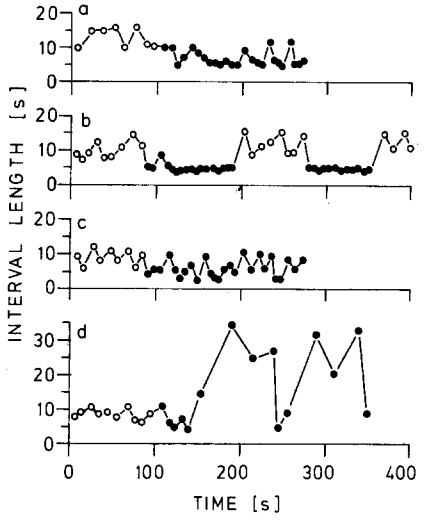

Fig. 3a–d. Length of successive intervals during stimulation with periodic UV-pulses. Light pulses of 1 s duration at 370 nm (1×10^{13} photons $\times$ mm^{-2} s^{-1}) were applied with given frequencies: **(a)** $0.17 \times s^{-1}$, **(b)** $0.2 \times s^{-1}$, **(c)** $0.3 \times s^{-1}$, **(d)** $0.4 \times s^{-1}$. Each set shows data of a single cell; (•) during stimulation, (o) without stimulation

stimulation frequencies (Fig. 3). We therefore assume that an exponential temporal change in light intensity can be regarded as a borderline case of periodic stimulation which acts as a *Zeitgeber* for the system within a limited range.

The effect of repetitive attractant stimuli cannot be measured by use of periodic pulses because a light pulse consists of an attractant and a repellent flank, and the bacterium always integrates two subsequent opposite stimuli to give a net repellent response (Hildebrand and Schimz 1986). Experiments with attractant stimuli, therefore, were done with light gradients only.

A low exponential attractant gradient also caused large fluctuations in the interval lengths (Fig. 2f). An increase of the steepness increased and stabilized the interval lengths (Fig. 2g) until, at a steepness of $\Delta \log I \times s^{-1}$ of 0.05 the interval lengths were doubled and remained rather regular during the gradient (Fig. 2h). When the gradient was turned off, other than after a repellent gradient it lasted for about 50 s until the interval length had gradually decreased to the autonomous value (Fig. 2h). A further increase of the gradient again caused aperiodic behavior (Fig. 2i).

The results show that an exponential attractant gradient could also enforce a stable periodicity upon the system, in this case in the range where it caused the interval length to be doubled. Outside this range, the gradient induced aperiodic behavior.

As we could show, the lifetime of the intracellular attractant signal is about 3 times as long as that of the repellent signal (submitted for publication). Consequently, the cell can integrate repetitive attractant stimuli over a longer period of time. This may account for the observation that the threshold for attractant gradients was lower than for repellent gradients (Fig. 1), which has also been reported for *E. coli* exposed to gradients of chemical substances (Block et al. 1983). It may also be the reason for the finding that a small increase in the steepness of an attractant gradient was sufficient to cause the interval length to be doubled while a much higher repellent gradient was required to cut the interval length in half. The lifetime both of the repellent (Schimz and Hildebrand 1987) and of the attractant signal (submitted) can be significantly extended by inhibition of protein methylation. Under these conditions the spontaneous intervals remain unchanged, but a repellent (Fig. 2e) or an attractant gradient (Fig. 2k), which normally caused a stable periodicity, now led to aperiodic behavior. Extending the signal lifetime thus had a similar effect as a strong increase in the steepness of the gradient.

The induction of stable periodicity or aperiodic sequences required an exponential change in light intensity. This became obvious when linear temporal gradients were used instead. A linear increase of repellent light caused a gradual decrease of the interval lengths (Fig. 4a), while a linear increase of attractant light resulted in a gradual increase of the interval length (Fig. 4b). These input-output relations are supposed to be caused by the mode of signal transduction at the receptor level, since a logarithmic increase of incident light would lead to a linear increase of photon absorption. Similar conclusions have been drawn for the chemoreceptors of *E. coli* (Block et al. 1983).

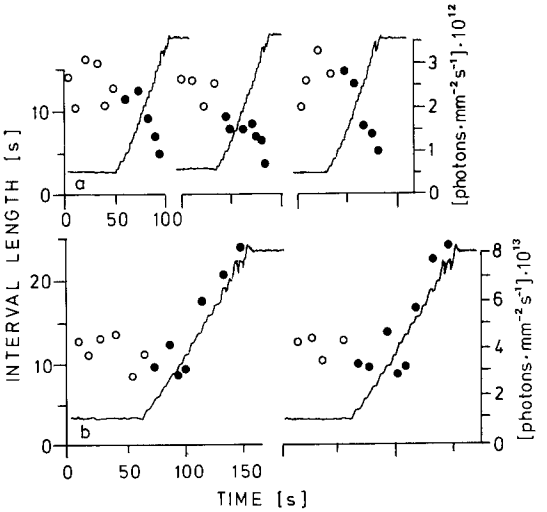

Fig. 4a and b. Length of successive intervals during application of linear light intensity gradients. Experiments were done as in Fig. 2. *Open circles* give the intervals before the gradient, *closed circles* the intervals during the gradient. The *solid lines* show the recorded change in light intensity. **a** Repellent gradient, light increase 380 nm; **b** attractant gradient, light increase 565 nm

Evidence for the generation of chaos at certain magnitudes of exponential gradients

We have reported previously that the frequency distribution of spontaneous interval lengths can be fitted by a log normal distribution (Schimz and Hildebrand 1985). Also the interval lengths obtained during exponential gradients which cause a new stable periodicity (Fig. 2c and h) can be described by a log normal distribution (data not shown). We suggest that under these conditions we have to deal with periodic oscillations of the system, comparable to the phase-locking observed with periodic UV-pulses (Schimz and Hildebrand 1986).

The aperiodic intervals occuring during gradients of lower or higher steepness can be fitted neither by a log normal distribution nor by a Poisson distribution. Our hypothesis of an oscillatory mechanism suggests that even under these conditions the behavior may have some functional regularity, i.e. that it may be chaotic. It seems to be the rule rather than the exception that exposing an oscillator to repetitive perturbations causes the oscillation to be chaotic (Tomita 1982). A stable predictable periodicity can be described by a simple 2-dimensional limit cycle of two variables, e.g. the concentration changes of two chemical components of the oscillator system. By addition of periodic perturbations a third variable is added, and the limit cycle can be changed into a "strange attractor" of a complex geometrical structure (Rössler 1976a and b; Tomita 1982) which gives rise to deterministic chaos, i.e. to a cyclic phenomenon without a fixed period, which nevertheless does not develop at random but according to certain laws based on feedback loops (Decroly and Goldbeter 1982; Olsen 1984; Markus and Hess 1984).

Periodic and chaotic oscillations have been observed in several biological systems (for review see Olsen and Degn 1985). In order to diagnose chaos without having a mathematical model of the system, one important sign to look for is period doubling, i.e. bifurcation from a fixed interval into two alternating intervals. There is a good chance that changing a parameter in the direction of period doubling will lead to chaos. If under these conditions a sequence of events without any obvious regularity is measured, one can see if there is a functional relationship between successive periods by plotting each period as a function of the preceding one. If this "next period plot" is a well defined curve or shows some non-random structure the system is most probably governed by a deterministic dynamical law. A period-one oscillatory behavior, on the other hand, would become a single point in this plot (for review see Shaw 1984; Olsen and Degn 1985).

In our system distinct period doubling was caused by the exponential repellent gradient at a certain steepness (Fig. 2b). The next period plot of these data (Fig. 5b) shows two distinct spots. A decrease in the steepness of the gradient (Fig. 2a) or a strong increase (Fig. 2d) led to aperiodic interval lengths. This could be interpreted as a period doubling route to chaotic oscillations. The next period plots of the data from Fig. 2a and d are shown in Fig. 5a and d, where a non-random structure is discernible. Attractant gradients could, depending on their steepness, also cause aperiodic behavior. The next period plot of the data in Fig. 2f (low gradient) is shown in Fig. 5f, that of the data from Fig. 2i (high gradient) in Fig. 5i. In both cases the plot shows a clearly discernible structure. For some of the data the three-dimensional representation of the next period plots is given in Fig. 6.

We have shown that an increase in the intracellular level of cGMP increases the interval length in the absence of stimulus inputs (Schimz and Hildebrand 1987). Successive spontaneous intervals measured under these conditions also yielded a discernible structure in the next period plot (Fig. 5m). We have proposed previously that cGMP may be a component of the oscillatory system (Schimz and Hildebrand 1987).

According to these data we suggest that in halobacterial behavior chaos may arise as a consequence of periodic perturbation of a limit cycle oscillation. Such a phenomenon can be described by the following model, which is a linear approximation to the nonlinear system (Olsen and Degn 1985):

$$p_{n+1} = A(p_n - 0.5) + 0.5 + R \sin(2\pi F t_n),$$

$$t_{n+1} = t_n + p_{n+1},$$

where p is the period (corresponding to the swimming interval), t is the time, and A is a constant which determines the stability of the limit cycle oscillation. R denotes the strength and F the frequency of the perturbation.

The model calculation given in Fig. 7a shows chaotic behavior, the parameters being $A = -0.2$; $R = 0.21$; $F = 2.5$. When Gaussian noise is added multiplicatively to p_n and t_n, the fine structure of the plot changes, whereas the overall structure is generally preserved (Fig. 7b). Small amounts of noise obviously do not obscure the chaotic structure, but create some additional structure which looks similar to the structures in Fig. 5i, k, and m. The structural similarities of the experimental data and the calculated plot can be taken as a further indication that a functional regularity exists also in the aperiodic and apparently irregular regions. The question whether the aperiodic behavior is caused by a noisy chaotic motion or by a higher period limit cycle oscillation, which, by addition of noise, can assume a motion similar to chaos, cannot be decided from the present data. In the latter case, the motion is not chaotic in a strict mathematical sense, but there are nearby parameters, which will yield

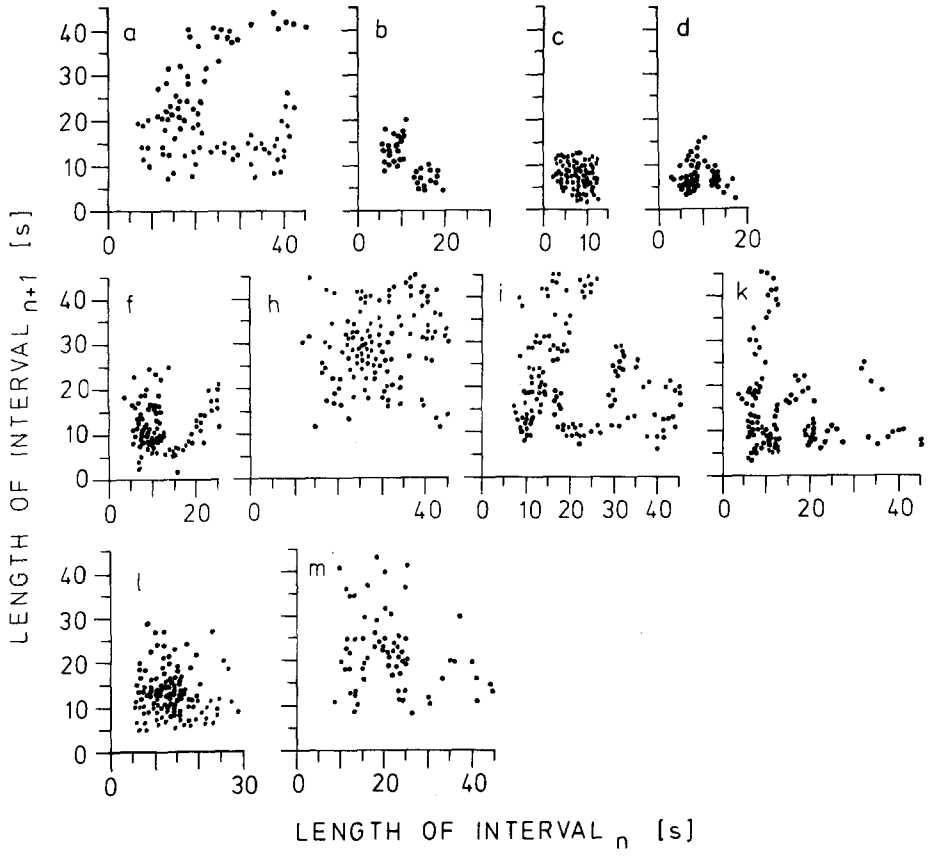

Fig. 5a–m. Next period plots of successive intervals. Each interval was plotted as a function of the preceding interval. Each plot contains data from 4–10 bacteria. Repellent gradients were an exponential decrease, attractant gradients an exponential increase of light at 565 nm. **a** Intervals during repellent gradient, steepness: $\Delta \log I \times s^{-1} = 0.037$; **b** repellent gradient, 0.050; **c** repellent gradient, 0.132; **d** repellent gradient, 0.230; **f** attractant gradient, 0.032; **h** attractant gradient, 0.050; **i** attractant gradient, 0.132; **k** attractant gradient, 0.050, after inhibition of protein methylation; **l** spontaneous intervals; **m** spontaneous intervals, after increase of the level of cGMP

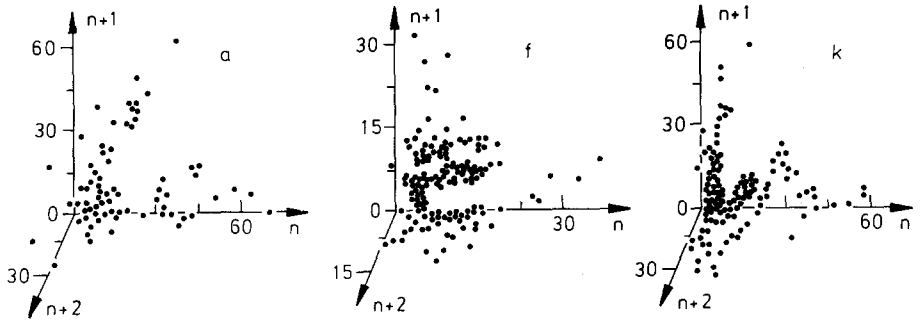

Fig. 6a, f, and k. Three-dimensional next period plot of successive intervals. Each interval n (horizontal coordinate) is plotted versus the following interval $n+1$ (vertical coordinate), and versus the next but one, $n+2$ (coordinate projecting out of the plane). **a** Data from Fig. 5a; **f** from Fig. 5f; **k** from Fig. 5k

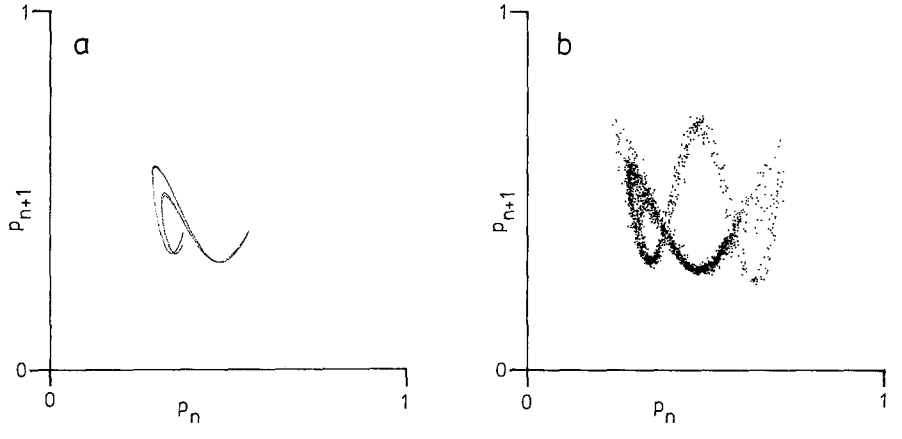

Fig. 7a and b. Model calculations of next period plots for a periodically perturbed limit cycle oscillation (Olsen and Degn 1985). For details see text. **a** Without noise; **b** with 2% noise

chaotic motion, and thus the motion can be called "prechaotic" (Schaffer et al. 1986).

For spontaneous intervals, unless the level of cGMP was increased, no clear structure was observable (Fig. 5l). Also the data obtained during gradients which led to a stable division in half of the period length (Fig. 2c) or to a doubling (Fig. 2h) lacked a structure in the next period plot (Fig. 5a and h). Especially in Fig. 5c the fluctuations were very small. Chaotic motion is rather stable against noise, in contrast to limit cycle oscillations which can readily be destroyed by noise (Schaffer et al. 1986). The absence of structure in Fig. 5c, h, and l could therefore be explained by the assumption that the oscillation is periodic under these conditions, and that the fluctuations are caused by stochastic processes due to additional steps in the transduction chain, which may be located between the oscillator and the flagellar motor. Kinetic models for transitions between different states of the flagellar motor have been proposed (Marwan and Oesterhelt 1987; McCain et al. 1987) which include one deterministic and 2 to 3 stochastic steps.

The data presented here suggest that exponential attractant and repellent light gradients, within a limited range of steepness, can enforce highly predictable periodic dynamics upon the system. Outside this range the predictability is lost due to either chaotic or prechaotic motion, but the functional regularity is still preserved.

We have proposed that methylation of specific membrane proteins is a feedback loop to extinguish the cellular sensory signals and thereby to allow the system to return to its autonomous reversal rhythm (Schimz and Hildebrand 1987). When the decay of the signal was delayed biochemically by inhibition of methylation, a lower gradient was sufficient to induce chaotic behavior (Figs. 5k and 6k). The change from periodic to chaotic oscillations therefore may be determined by a relation between the rate of stimulation and the signal lifetime.

We take the indications for chaotic behavior as a further support of our hypothesis that in *Halobacterium* reversal events are determined by an oscillator or a system of coupled oscillators.

Acknowledgements. We thank the unknown referee who suggested the application of the mathematical model, and Dr. F. Drepper, Jülich, for the computer calculations and for reading the manuscript. This work was supported by the Deutsche Forschungsgemeinschaft (SFB 160 and grant Hi 414/1-1).

References

Alam M, Oesterhelt D (1984) Morphology, function and isolation of halobacterial flagella. J Mol Biol 176:459–475

Block SM, Segall JE, Berg HC (1983) Adaptation kinetics in bacterial chemotaxis. J Bacteriol 154:312–323

Decroly O, Goldbeter A (1982) Birhythmicity, chaos and other patterns of temporal self-organization in a multiply regulated biochemical system. Proc Natl Acad Sci USA 79: 6917–6921

Hildebrand E, Dencher N (1975) Two photosystems controlling behavioural responses of *Halobacterium halobium*. Nature 257:46–48

Hildebrand E, Schimz A (1983) Photosensory behavior of a bacteriorhodopsin-deficient mutant, ET-15, of *Halobacterium halobium*. Photochem Photobiol 37:581–584

Hildebrand E, Schimz A (1986) Integration of photosensory signals in *Halobacterium halobium*. J Bacteriol 167:305–311

Hildebrand E, Schimz A (1987) Role of the response oscillator in inverse responses of *Halobacterium halobium* to weak light stimuli. J Bacteriol 169:254–259

Markus M, Hess B (1984) Transition between oscillatory modes in a glycolytic model system. Proc Natl Acad Sci USA 81: 4394–4398

Marwan W, Oesterhelt D (1987) Signal formation in the halobacterial photophobic response mediated by a fourth retinal protein (P_{480}). J Mol Biol 195:333–342

McCain DA, Amici LA, Spudich JL (1987) Kinetically resolved states of the *Halobacterium halobium* flagellar motor switch and modulation of the switch by sensory rhodopsin I. J Bacteriol 169:4750–4758

Olsen LF (1984) The enzyme and the strange attractor-comparisons of experimental and numerical data for an enzyme reaction with chaotic motion. In: Schuster P (ed) Stochastic phenomena and chaotic behavior in complex systems. Springer, Berlin Heidelberg New York, pp 110–123

Olsen LF, Degn H (1985) Chaos in biological systems. Q Rev Biophys 18:165–225

Rössler OE (1976a) An equation for continuous chaos. Phys Lett 57A:397–398

Rössler OE (1976b) Chaotic behaviour in simple reaction systems. Z Naturforsch 31a:259–264

Schaffer WM, Ellner S, Kot M (1986) Effects of noise on some dynamical models in ecology. J Math Biol 24:479–523

Schimz A, Hildebrand E (1985) Response regulation and sensory control in *Halobacterium halobium* based on an oscillator. Nature 317:641–643

Schimz A, Hildebrand E (1986) Entrainment and temperature dependence of the response oscillator in *Halobacterium halobium*. J Bacteriol 166:689–692

Schimz A, Hildebrand E (1987) Effects of cGMP, calcium and reversible methylation on sensory signal processing in halobacteria. Biochim Biophys Acta 923:222–232

Shaw R (1984) The dripping faucet as a model chaotic system. The Science Frontier Express Series, Aerial Press, Santa Cruz

Spudich JL, Stoeckenius W (1979) Photosensory and chemosensory behavior of *Halobacterium halobium*. Photobiochem Photobiophys 1:43–53

Takahashi T, Tomioka H, Kamo N, Kobatake Y (1985) A photosystem other than PS 370 also mediates the negative phototaxis of *Halobacterium halobium*. FEBS Microbiol Lett 28:161–164

Tomita K (1982) Chaotic responses of non-linear oscillators. Phys Rep 86:113–167

Wolff EK, Bogomolni RA, Scherrer P, Hess B, Stoeckenius W (1986) Color discrimination in halobacteria: Spectroscopic characterization of a second sensory receptor covering the blue-green region of the spectrum. Proc Natl Acad Sci USA 83:7272–7276