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Photosensory Behavior in Procaryotes

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INTRODUCTION

Most motile microorganisms actively search for a suitable environment for survival and growth by using external factors such as photic (121, 189), magnetic (201), mechanical (246), chemical (26), thermal (117, 164), galvanic (278), and gravitational (25) stimuli as clues for directional migration. It is trivial to state that light is the single most important factor for photosynthetic organisms, which depend on the availability of visible (in some cases also near-ultraviolet [UV] or infrared) radiation (190). However, the photoreceptor pigments for orientation are not necessarily identical to the pigments for light harvesting, comprising only a subset of the photosynthetic pigments in some cases and being totally different in others (94, 185, 186). Some nonphotosynthetic microorganisms also use light as a reference for orientation (119, 123, 266). In these organisms the selection advantage of photoorientation is not always obvious.

Although movement responses in motile microorganisms controlled by light were first observed and described more than a century ago, the biophysical and molecular mechanisms underlying photoreception, signal transduction, and control of the motor apparatus are still obscure in most cases. Treviranus (273) is believed to have been one of the first to describe photomovement of eucaryotic flagellates, and Cohn (54) and Engelmann (73, 74) were among the first to observe light-dependent movement of procaryotes. In spite of the fact that the basic phenomena were already described and analyzed by the beginning of this century (38, 58, 214), the phenomenological characterization of the response and the terminology of the behavior are still controversial in some cases. Therefore, without going into the historical development of the terminology and its controversial usage (see reference 185), a set of currently widely accepted definitions of light-dependent motor responses are given here (61).

(i) Phototaxis (formerly also called phototopotaxis) describes a movement oriented with respect to light direction. Like many eucaryotic organisms, cyanobacteria show a directed movement toward the light source (positive phototaxis) at low fluence rates (measured in watts per square meter] and a movement away from the light source (negative phototaxis) at high fluence rates (68). At intermediate fluence rates, populations often split into subpopulations moving in either direction. Pieper (211) found a movement perpendicular to the incident light rays which is called diaphototaxis. Recently, a number of authors have used the term phototaxis in a wider sense to describe a photomovement unrelated to direction of the incident light (250, 264): *Halobacterium halobium* has been found to respond to sudden changes in the fluence rate (125), which is defined as a photophobic response but which may lead to accumulation of cells in a light field or an orientation in a light gradient (188). This usage of the term is in parallel to the usage of "chemotaxis" for bacteria which move up or down a chemical gradient by a trial-and-error mechanism but not by directed movement (4).

(ii) Photokinesis describes the dependence of the speed of movement on the fluence rate of irradiation. In this case the direction of the light beam is irrelevant and the organisms detect the absolute, steady-state irradiation (183). When an organism moves faster at a given fluence rate than in the dark control, this behavior is defined as positive photokinesis; when it moves slower, it is called negative photokinesis (94). Some organisms stop in darkness or at very high fluence rates.

(iii) A sudden change in the fluence rate (dI/dt) causes a photophobic response in many organisms. The individual response is species specific and may constitute a reversal of movement, a temporary stop, or a directional change (148, 186, 190). Either a step-up or a step-down in the fluence rate can cause a photophobic reaction. Some organisms respond to a step-down at low fluence rates and to a step-up at high fluence rates (99, 184, 279; D.-P. Häder, *in* P. Fay and C. Van Baalen, ed., *Cyanobacteria, Current Research*, in press). The two responses may be mediated by the same or by different photoreceptor systems (126). The photophobic response can be induced by either a temporal change in the

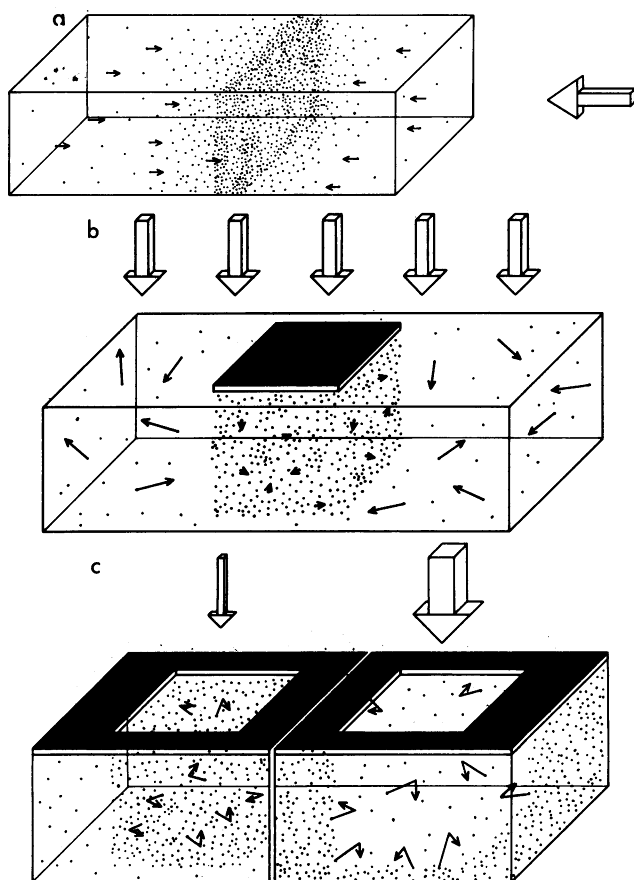

FIG. 1. Schematic representation of the three photomovement responses found in motile microorganisms. (a) Positive phototaxis at low fluence rates causes movement toward the light source and negative phototaxis at high fluence rates causes movement away from the light source, resulting in a band of organisms at an intermediate fluence rate. (b) Positive photokinesis causes microorganisms to accumulate in a shaded area, since their velocity is higher in light than that in darkness. (c) Accumulation of organisms in light fields by repetitive step-down photophobic responses at low fluence rates (left) and dispersal by step-up photophobic responses at high fluence rates (right) are shown.

fluence rate (e.g., by inserting a neutral density filter into the microscope beam) or a spatial one (e.g., by forcing the organisms to cross a light/dark boundary) (89).

Each of these three light-induced responses can lead to a migration of a population in a light field. Phototaxis causes a directional movement toward or away from the light source, and organisms often accumulate at an intermediate fluence rate resulting from the antagonistic responses (Fig. 1a). Positive photokinesis causes a population to accumulate in shaded areas where they spend more time due to their lower speed, while they transverse brighter areas with a higher speed (Fig. 1b); negative photokinesis results in the opposite behavior. Photophobic responses are effective mechanisms to accumulate organisms in areas of suitable fluence rates and disperse them from fields with adverse light conditions (Fig. 1c): step-down responses cause an accumulation in a light field because the organisms can enter the field but cannot leave it. Step-up responses result in a dispersal from the light field because the organisms are prevented from entering it and those initially in it eventually leave by random movement (51).

Whatever the physical property of light detected by the organism, the signal must be processed to control the motor apparatus (Fig. 2). The primary event is the absorption of a quantum of light at suitable wavelength by the photoreceptor pigment(s), which thereby enters an excited singlet or triplet state. Procaryotes utilize a wide range of photoreceptors, while higher eucaryotes generally use only a rather restricted set of photoreceptors for light-dependent orientation (120, 251).

Photoreceptor molecules are usually identified by action spectroscopy: the experimenter tries to align the spectral sensitivity curve of a response with the absorption spectrum of a (set of) pigment in vivo or in vitro. This procedure has a number of pitfalls. The action spectrum should be based on fluence rate response curves. Ideally these curves are parallel at all wavelengths; if not, more than one species of photoreceptor molecules or different photochemical reactions are involved. The action spectrum should be calculated from values in the linear portion of the fluence rate response curves to avoid distortions which can be substantial, especially when the response is saturated or near the threshold value.

Problems also arise when several pigments absorb in the same spectral region. In those cases only genetic analysis yields an unambiguous answer: mutants are needed which produce no or altered photoreceptor molecules; such mutant strains should lack the photoresponse under consideration. However, in many cases mutations affecting subsequent signal-processing aspects, rather than photoreceptor functions, are selected. When the photoreceptor molecule also serves another vital biochemical function in the cell, a photoreceptor mutation may be lethal. Another source of confusion is the existence of accessory pigments. When the photoreceptor pigment is present at a low concentration, and the photoactive radiation is absorbed mainly by accessory pigments (which transfer their energy to the photochemically active pigment), the absorption of the latter may be too small to be detected in the action spectrum: the bulk pigments are prominent.

To be effective, the absorbed energy is converted into another form, for example, electrical or chemical energy. With the exception of photokinesis, the initial signal is too small to influence directly the motor apparatus; it must be amplified. In cyanobacteria, for instance, the zero threshold for photophobic responses has been measured to be as low as 0.03 lx (178) and that for phototaxis is between 0.05 and 5 lx (118, 176). (One lux is the illuminance produced by a candle at 1-m distance; in full sunlight at noon, about 80,000 lx can be measured.) In procaryotes, several biophysical and biochemical mechanisms have evolved to accomplish the needed amplification; they are discussed below.

Photoreceptor molecules are probably always membrane

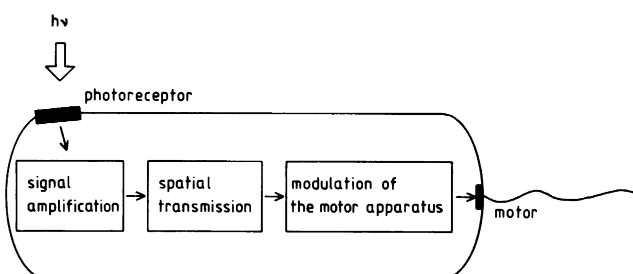

FIG. 2. Diagram of the sensory transduction chain in a procaryotic motile microorganism.

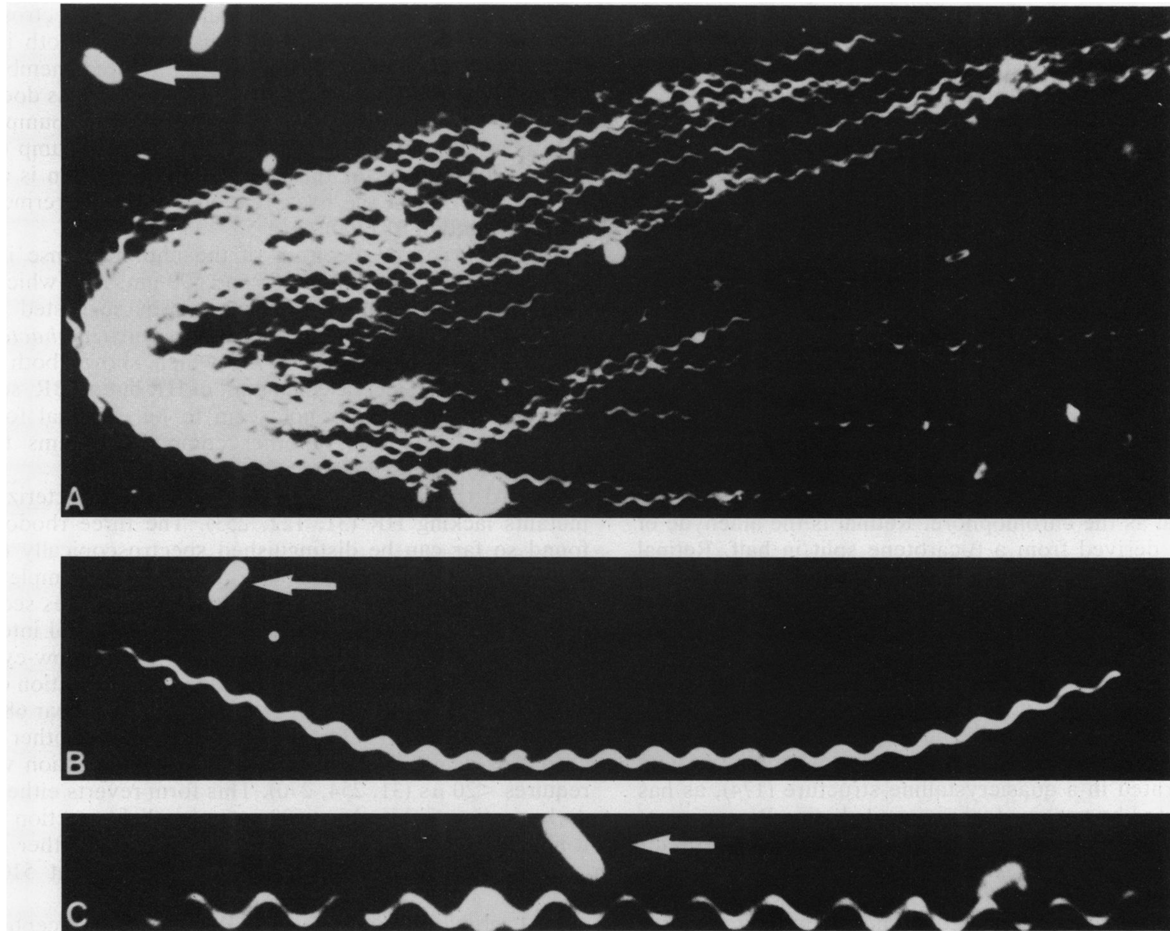

FIG. 3. Dark-field microphotographs of superflagella of *H. halobium* (reprinted from J. Mol. Biol. **176**:459–475 [1984] [reference 6] with kind permission from Academic Press, Inc. [London], Ltd., London).

bound (217). Because the photoreceptor site usually is different from the effector site, the signal needs to be relayed spatially either within a single cell or (in multicellular organisms) throughout the organism. Several possible mechanisms of signal transmission have been discussed, including electrical gradients (91, 171), diffusible low-molecular-weight substances or ionic gradients (94, 108, 170), and specific transmitter proteins (237).

The final step in the sensory transduction chain is the control of the cellular motor organelle. While the structural elements of the basal body in flagellated bacteria have been revealed to a certain extent (152), our knowledge about the motor apparatus in gliding cyanobacteria is very limited (45, 111). In no case have the molecular events controlling the motor activity been fully analyzed (27, 223).

FLAGELLATED BACTERIA

Photomovement in several taxonomically different groups of flagellated bacteria has been studied extensively. Light-induced behavior was observed in photosynthetic bacteria, including the purple and green bacteria, about a century ago (73, 74; cf. review in reference 52). In contrast, photoresponses of *Halobacterium* spp. have been analyzed only recently (59, 124, 125). In addition, there are some reports on photomovement in other groups (153).

Halobacterium spp.

The halophilic archaebacterium *H. halobium* is unique in several respects (267). It is adapted to high (even saturated) NaCl concentrations (3.5 to 5 M) such as can be found in the Dead Sea, in salines, or in brine ponds. The cells of this bacterium lyse when transferred to lower salt concentrations; the ribosomes and the cell wall are unstable at lower concentrations. The whole biochemical apparatus of the cell is tailored to these extreme conditions: most enzymes show optimum activity at concentrations above 2 M NaCl. The high external concentration of NaCl is compensated by an equally high internal concentration of KCl.

These organisms are procaryotes because they lack an organized nucleus and endoplasmic membranes. They swim by means of typical bacterial flagella located in a bundle at one end when young and at both ends when older (6). Under certain conditions, the flagella can be extremely long, several times the cell length, and can be visualized in a strong xenon lamp light beam (Fig. 3). In contrast to other bacteria, they lack a murein layer; they also lack the widely distributed lipoproteins. Instead the cell wall is composed of a single species of glycoproteins with a molecular weight of 200,000. Also, the chemical structure of ferredoxin and details in the protein biosynthesis resemble those found in eucaryotes. The usual fatty acid-glycerol esters are substi-

tuted by isoprenoid glycerol esters. Polyamines also have not been detected in these cells (48, 255).

Halobacterium spp. show two types of photobehavior: when entering a UV or blue light field or leaving an area irradiated with green light, cells reverse direction (123, 125). These typical step-up and step-down photophobic responses (however, for terminology see above) result in photodispersal from blue/UV fields and accumulations in green fields (188). Since the action spectrum of the step-down response closely resembles the absorption spectrum of bacteriorhodopsin (BR), this pigment was initially proposed to be the primary photoreceptor at least for the step-up photophobic response (123, 245), an intriguing observation because closely related rhodopsins occur in vertebrates and invertebrates as visual pigments (259), and recently a rhodopsin has been supposed to be the functional photoreceptor for phototaxis in the unicellular flagellate *Chlamydomonas* sp. (77).

BR is a protein with a molecular weight of about 26,000, with retinal as the chromophore. Retinal is the aldehyde of vitamin A derived from a β-carotene split in half. Retinal does not absorb in the visible region but has a broad absorption maximum at around 380 nm. By linking the chromophore to a lysine in the opsin via a Schiff's base, the absorption maximum is shifted to about 570 nm. The protein is arranged in trimers, with each unit spanning the membrane seven times (243). It is formed under low-oxygen partial pressure and is the only protein component of the so-called purple membrane, areas of the membrane where the protein is incorporated in a quasicrystalline structure (174), as has been detected by various techniques including Raman spectroscopy (8, 205), electron and neutron diffraction studies (136, 276), and monoclonal antibodies (204, 271).

The main function of BR seems to be light energy fixation: Stoeckenius demonstrated that the molecule operates as a light-driven proton pump (24, 258) undergoing a branched photocycle similar to the one found in visual pigments, including several intermediates with different absorption maxima (24). During the photocycle, protons are extruded from the cell forming an electrical and a pH gradient across the cytoplasmic membrane (65, 149). The primary photoreaction may result in a rotation of BR (5) and a large-scale structural alteration of the membrane (66). During the photocycle, retinal undergoes a *trans*/13*cis* isomerization (47). Ion concentrations and pH exert major effects on the partial reactions of the photocycle (219). The primary photochemistry and proton pumping also function when BR is incorporated into artificial vesicles (166). The vectorial transport seems to be correlated with a reduction of the Schiff base and is not affected by the C-terminal region (1); retinal can be substituted for by artificially altered chromophores (63). It is interesting to note that the visual rhodopsins also take up protons when irradiated (229).

Proton gradients can be either converted into other ionic gradients (23, 36) or used for adenosine triphosphate (ATP) production in a mechanism described by the Mitchell chemiosmotic hypothesis (86, 163) utilizing an adenosine triphosphatase (76, 81).

Although it was an intriguing proposal that BR also serves as the photoreceptor pigment for photophobic responses, this concept was discarded because mutant strains which lack the pigment retain the photophobic responses (127). In these mutants a second retinal pigment, called halorhodopsin (HR), was found (26, 159). This pigment also undergoes a photocycle with intermediates absorbing at different wavelengths (146, 200, 202). The structure of the chromophore has been analyzed by resonance Raman spectroscopy (9), and the molecule has been characterized both in the native membrane (32, 249) and in black lipid membranes (18); it also undergoes a *cis-trans* isomerization, as does BR (145). Unlike BR, which is light-driven proton pump, HR acts as a light-dependent electrogenic chloride pump (233). The quantum yield for the primary photoreaction is about 0.34, while that of the back reation from the intermediate HR410 is only 0.01 (200).

Since the action spectrum of the photoresponse in the visible range is maximal at 565 and 590 nm, HR, which has an absorption maximum at 588 nm, was suggested to be involved in the photosensory responses in *Halobacterium* spp. (272). Mutant strain L-33, which shows both light reactions, has an increased amount of HR but no BR, so that the latter pigment does not seem to be essential for the photoresponses. Thus, another component seems to be responsible at least for the activity at 565 nm.

A third rhodopsin has been found and characterized in mutants lacking HR (31, 122, 253). The three rhodopsins found so far can be distinguished spectroscopically (252). While the photocycle of the other rhodopsins is completed in the millisecond range, this retinyl pigment requires seconds to complete its cycle, which also involves several intermediates (30, 270); therefore, it has been called slow-cycling rhodopsin (SR). The first intermediate after irradiation of the initial form with 587 nm is a product absorbing near 680 nm (S680). This intermediate is transformed into another form absorbing near 373 nm (222) during a dark reaction which requires <20 μs (31, 254, 270). This form reverts either in a dark reaction within about 500 ms or in a light reaction when it absorbs a UV quantum (near 373 nm) via another intermediate with an absorption maximum of about 510 nm (SB510).

This retinyl pigment could well be the photoreceptor for one or both photoresponses found in *Halobacterium* spp. There are two conflicting schools of thought. Spudich and Stoeckenius proposed that SR in its 587-nm-absorbing form is the photoreceptor for step-down photophobic responses. After being transformed into the 373-nm-absorbing form the same photochromic pigment could act as a photoreceptor for the UV/blue response (31, 254, 263). This intriguing concept is supported by the finding that the UV/blue response is enhanced when the organisms have been preirradiated with green light. This observation is interpreted by assuming that the UV-absorbing component is formed by the green radiation previously (or simultaneously) administered (30, 254). This effect was not noticed in earlier microscopic studies since the necessary background irradiation served the function of partially phototransforming HR. Another indication that the same (group of) pigment(s) is responsible for both step-up and step-down responses is the fact that mutants exist that are impaired in both photoresponses while chemotaxis is normal (225).

Hildebrand and his group hold a different position claiming that the UV/blue response is mediated by a different photoreceptor molecule (PS370) (128, 228). Both photosystems are thought to contain retinal as chromophore. In addition, carotenoids may serve as accessory pigments for PS370. The strongest argument against assuming only one photochromic pigment is the finding that the response mediated by PS370 is developed earlier than the one initiated by PS570 in a freshly inoculated culture (128). The development of PS565 can even be inhibited by the addition of the protein synthesis blocker puromycin. In this case the cells do not show the step-down response, only the step-up reaction. As an alter-

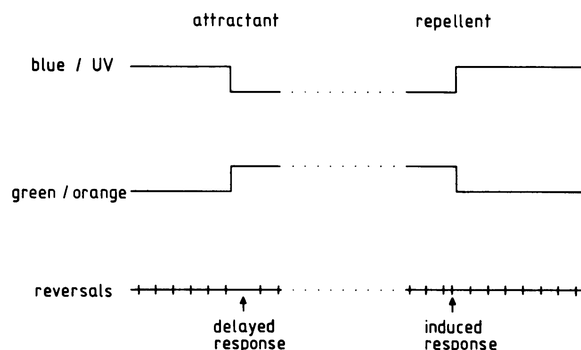

FIG. 4. Effect of attractant and repellent signals in *H. halobium*. An attractant signal (step-up of green/orange light or step-down of blue/UV light) delays the spontaneous reversal, and a repellent signal (step-down of green/orange light or step-up of blue/UV light) induces an instantaneous reversal in *Halobacterium*.

native model it has been proposed that a photosystem other than PS370 mediates the UV/blue responses in *H. halobium* (265). It can be assumed that at least the yellow/green light response is mediated by a retinyl chromophore because substitution of the retinal by analogs, which are incorporated into BR, HR, and SR565, shifts the peaks in the action spectrum of the step-down response by about the same amount to longer wavelengths as the absorption maxima (227). In addition, there may be another pigment (P475) responsible for the blue-light phobic response.

Recently, attempts have been made to develop a unified sensory model that combines both photobehavior and chemotaxis (128, 279). Actually, the photobehavior can be regarded as a modulation of the autonomous reversal of movement rather than a single reversal induced by a step-up or step-down in the fluence rate.

Chemotaxis in bacteria can be defined as a modulation of a three-dimensional random walk. Certain bacteria, including *Escherichia coli*, alternate runs of smooth swimming (when the flagella rotate counterclockwise) with tumbles, during which the flagella rotate clockwise and the bacterium changes the direction of movement. The orientation in a chemotactic gradient is brought about by an increase in the tumble frequency or by an increase in the mean path length of a smooth run (152). When a bacterium senses an increase in an attractant, which indicates that it is swimming up a gradient of an attracting substance, tumbles are suppressed. When the bacterium swims away from the attractant, the decrease in the concentration increases the probability of a tumble. In a repellent gradient the response is reversed (4). Cell envelopes of certain chemotaxis mutants of *E. coli* rotate their flagella constantly counterclockwise (218). The chemotactic signal can be replaced by a high-intensity, blue-light pulse, in e.g., *Salmonella* spp., which induces a tumble indistinguishable from a response to a repellent signal (265).

Examination of the behavior of *Halobacterium* spp. revealed a similar swimming pattern, but periods of runs are not separated by tumbles; instead, the cells swim equally well in both directions. The frequency of reversal has been supposed to be governed by an internal oscillator (226) with 10- to 20-s intervals between reversals dependent on strain (262). Yellow-green light pulses (or an increase in the fluence rate) can be compared with an attractant stimulus since it prolongs the time interval until the next spontaneous reversal (Fig. 4). A decrease in the fluence rate of a UV irradiation has the same effect, and therefore UV/blue radiation can be regarded as a repellent. A sudden decrease in the attractant light fluence rate or an increase in the repellent light fluence rate has an opposite effect: these signals induce an instantaneous reversal (226). Afterwards the normal frequency is resumed. Thus, the cells rapidly adapt to new light conditions (263).

There is another parallel between photobehavior of halobacteria and chemotaxis of other bacteria. The adaptation mechanism in the sensory transduction chain seems to involve a methylation and demethylation of methyl-accepting chemotaxis proteins (MCPs) (139, 247). A methionine-requiring step was found in the regulation of *Halobacterium* photoresponses (20, 224): methyl incorporation was considerably higher in the presence of a chemical attractant (glucose) or an attractant light stimulus (565 nm) and could be significantly inhibited by the addition of puromycin (224).

Another component in the sensory transduction chain of photoresponses in *Halobacterium* spp. seems to be calcium ions, which also plays an important role in the sensory processes of many other procaryotic and eucaryotic systems (70, 158, 236, 286). Incubation of the cells in the Ca^{2+} ionophore A23187 and ethylene glycol-bis(β-aminoethyl ether)-*N*, *N*, *N'*,*N'*-tetraacetic acid decreased the rate of spontaneous and photo-induced reversals. Therefore, it has been speculated that Ca^{2+} is involved in the control of flagellar rotation (19).

Recently, it was found that light regulates the phosphorylation of at least three different phosphoproteins in *H. halobium* (248). In darkness, ^{32}P is incorporated into the proteins; in light, the label is released. The photoreceptor seems to be BR. The function of this molecular mechanism could be control of the proton motive force (PMF)-generating process and thus would be independent of the photosensory transduction. However, Skulachev's group reports that *H. halobium* senses changes in the proton gradient (21); thus, light regulation of phosphoproteins could also play a role in the photobehavior of these organisms. This assumption is supported by the finding that attractant light stimuli affect the electrical membrane potential measured by studying the distribution of tetraphenylphosphonium ions. UV irradiation had no effect on the electrical potential, indicating a different mechanism of photoperception (22).

A model proposed recently assumes that a step-down in green light is sensed in terms of a decrease in the PMF. The transduction is mediated via a specific MCP. An increase in the UV fluence rate is sensed by P370 (independent of PMF changes) and relayed via another MCP. Chemical attractants and repellents are detected by specific chemoreceptors which control a number of other MCPs. The integrated status of the MCPs is relayed by the *che* gene products, eventually modulating the concentration of free intracellular Ca^{2+}, which ultimately controls the direction of flagellar rotation (20). In bacterial chemotaxis it is still controversial whether or not changes in the membrane potential are involved in the sensory transduction. Voltage clamp effects indicate that the information transduction to the flagellar motors does not require electrical steps (157).

Purple Bacteria

The flagellation of most purple bacteria is similar to that of halobacteria: the cells have bundles of flagella at both poles and swim in either direction with equal probability.

Engelmann was probably the first to observe light-dependent responses in a *Chromatium* species, which he called *Bacterium photometricum* (73, 74). When cells swam into a dark zone under the microscope, they reversed the direction of movement and swam back as if frightened (photophobic response). Crude action spectra of the response revealed the involvement of a substance initially called bacteriopurpurin (37, 74). Later the photoreceptor was identified as bacteriochlorophyll *a* (155). Depending on the culture conditions, carotenoids (especially spirilloxanthin) also can be involved in the light perception (268).

Photokinesis. Whether purple bacteria are capable of a phototactic orientation is questionable, but several purple bacteria including *Rhodospirillum* spp. show a pronounced photokinetic effect (269). That the photoreceptor pigments are identical to the energy-harvesting pigments suggests that there is a close correlation between photosynthesis and photomovement in purple bacteria (155).

Inhibitors of the photosynthetic electron transport chain such as *o*-phenanthroline, antimycin A, and atebrine drastically impair photokinesis of *Rhodospirillum rubrum* (269). The classical inhibitor 3-(3,4-dichlorophenyl)-1,1-dimethyl urea (DCMU), however, is not effective in photosynthetic bacteria. These results could indicate that the photokinetic effect is due to a linkage of the response to the photosynthetic electron transport chain. However, uncouplers such as dinitrophenol, imidazole, or desaspidin, which leave the electron transport intact while they impair the generation of a proton gradient and the photophosphorylation connected to this, also inhibit protokinesis effectively. These results suggest that the additional energy supply in light directly activates the flagellar motors. This notion was further supported by the fact that externally applied ATP induces a more rapid swimming speed in darkness (198).

According to the current interpretation, ATP may not directly power the flagellar motor of bacteria. Rather, it may act as an energy storage while the energy supporting motility is derived from ion or proton gradients across the cytoplasmic membrane. The excitation energy absorbed by accessory pigments is channeled into a reaction center and is utilized to form a membrane potential (64, 277). There are spectral indications that the accessory carotenoids undergo a photoisomerization, as do the rhodopsins, when irradiated with suitable wavelengths (33). The effect of the inhibitors and uncouplers could be interpreted as an inhibition of the light-dependent generation of the membrane potential (143).

Photophobic responses. The photophobic response has an action spectrum similar to that of the photokinetic effect and the absorption spectrum of *R. rubrum* (49, 50). Unlike photokinesis, the photophobic response is inhibited by the addition of external ATP (or adenosine diphosphate [286]). Inhibitors of the photosynthetic electron transport chain impair photophobic responses while uncouplers stimulate them (270), which indicates a coupling between photophobic responses and the photosynthetic electron transport chain. It is difficult, however, to explain phobic responses found at rather low fluence rates: the zero threshold for *Chromatium* and other genera was found at below 0.01 lx (230). It is possible that the photoreceptor pigments operate via a different mechanism because they can be substituted for by the addition of ferric ions in a nonpigmented *Rhodospirillum* sp. (115). Aerobically cultivated cells which do not develop measurable amounts of bacteriochlorophyll also show step-down photophobic responses (114).

When the organisms are cultivated anaerobically, they use the photosynthetic electron transport chain as a means for sensory transduction. The inhibitory effect of antimycin can be cancelled by adding phenazine methosulfate (116). The potassium ionophore valinomycin also inhibits photoorientation in the presence of potassium, while neither valinomycin nor potassium is effective when administered alone. The current interpretation of these observations is that potassium enters the cells passively through the ionophore and breaks down the membrane potential. This potential is believed to play an important role in the sensory transduction in these organisms, and a phobic response is mediated by a sudden change in the electrical potential when the photosynthetic electron transport is altered upon a change in the fluence rate (116).

The key question to be answered is whether or not a modulation of the electrical membrane potential is involved in the sensory transduction of phobic responses in purple bacteria. While the membrane potential of large eucaryotic cells can be monitored with microglass electrodes, such measurements of procaryotic cells pose serious technological problems (34). There are several indirect methods by which the potential can be determined. One is based on the passive distribution of lipophilic cations such as triphenylmethyl phosphonium, tetraphenyl phosphonium, and dibenzyl dimethyl ammonium, which easily penetrate the cell membrane and follow the existing potential gradient (43, 220). One disadvantage is that by diffusing along the gradient the existing potential is short-circuited. Another approach utilizes the change in the absorption or fluorescence of dyes incorporated in the cell membrane or inside or outside the cell as a function of the membrane potential (238, 267). Some of these substances need to be injected into the cells, which is impracticable in small cells; others such as ethylrhodamine (238) easily penetrate the membrane and serve as probes in the cytoplasmic compartment.

Armitage and Evans (13) have incorporated oxanols in *Rhodopseudomonas sphaeroides* to monitor membrane potential changes during chemotactic stimulation. Oxanol VI is a potential-sensitive dye which enters the cell as a permeant anion and has a fast response to potential changes. The difference between the absorption at 590 and 625 nm can be used to determine the bandshift. An alternative method is to measure the membrane potential-dependent electrochromic bandshift of native carotenoids by the absorption difference between 510 and 523 nm (12, 14).

By using these techniques, it was found that addition of both attractants and repellents caused an increase in the membrane potential; the authors attribute this effect to the binding of the substances to membrane receptor sites (12). Thus, the distinction between attractants and repellents is not based on a simple potential measurement of the cell. The electrical signal and the related bandshift are sensitive to carbonyl cyanide *m*-chlorophenylhydrazone (CCCP), which breaks down the membrane proton gradient (11). A similar change in potential was found in wild-type cells upon increasing the fluence rate (14). This increased light intensity caused a photokinetic effect and may simply reflect an increased photosynthetic activity and a higher energy supply for the motor apparatus in the form of an increased electrical membrane potential. Reaction center-less mutants did not show a light-dependent increase in velocity or a carotenoid bandshift, but they did show chemotactic responses. Similar chemotactically induced potential changes could not be detected in *E. coli*; only an energization of the membrane by, e.g., succinate caused an increased potential (13). CCCP at moderate concentrations did not impair motility in photosynthetically grown *R. sphaeroides* in light but did so in

darkness, indicating that the uncoupler was sufficient to collapse the respiratory PMF but not the photosynthetically produced PMF (16). The ATP concentration, however, controls the ability for chemotaxis. The situation is similar in *Pseudomonas aeruginosa*, in which the membrane potential was found to be necessary for motility. However, ATP was required for chemotaxis: addition of venturicidin to aerobically grown bacteria increased the membrane potential but decreased the ATP pool, resulting in motile but nonchemotactic bacteria (15).

Photophobic responses in *Rhodopseudomonas* spp. are also accompanied by sudden electrical potential changes: an increase in the light intensity caused an increase in the membrane potential. Since the membrane potential controls the direction of flagellar rotation, light influences the direction of movement of this organism (15).

Aerotaxis also depends on a change in PMF in *Rhodopseudomonas* spp. (17). There is a correlation between oxygen partial pressure and light-induced motility: in low intensity light the photoresponse was inhibited by oxygen, and under aerobic conditions high-intensity actinic light impaired aerotaxis. In summary, the results can be interpreted by the following model: motility depends on the existence of PMF. Chemotatic (attractant or repellent) or photic stimuli cause an increase in the PMF, reflecting, e.g., the binding to a membrane receptor. The specific response, reversal of movement or suppression of reversals, may be controlled by the interaction of specific MCPs sent out by the receptors.

CYANOBACTERIA

Cyanobacteria (or *Cyanophyceae* = blue-green algae) are gliding eubacteria. Most of the motile species form long nonpolar filaments with a typical procaryotic organization. The mechanism of photosynthesis strongly differs from that of other bacteria, since it has two photosystems arranged in sequence like those in photosynthetic eucaryotes, and oxygen is produced in a water-splitting reaction. The photosynthetic pigments are chlorophyll *a*, accessory carotenoids, and biliproteins (= phycobilins), which are arranged by phycobilisomes (85) on the surface of the thylakoids similar to the configuration found in red algae. Cyanobacteria (and red algae) also have the remarkable ability to adapt to the spectral quality of light by changing the pigment composition; this phenomenon has been called chromatic adaptation (78).

Mechanism of Gliding Movements

Since cyanobacteria lack flagella or other obvious motor organelles, the mechanism of the microscopically visible movement has puzzled researchers for a long time (55, 69, 113, 175, 280). The trichomes move along their long axis in a smooth gliding fashion and, when unstimulated, reverse the direction of movement at random intervals. Members of the *Oscillatoriaceae* rotate around their long axis during gliding, while the *Nostocaceae* do not. The direction and pitch of rotation are species specific (133). A large number of mechanisms have been proposed, but none has been proven yet (42, 56).

An early hypothesis proposed that gliding is mediated by secretion of slime (130, 231). In fact, most cyanobacteria do produce slime which is often organized into a slime sheath (215). The material seems to be produced by all cells of a filament, because when the trichome breaks out of its slime tube a newly formed thin sheath can be seen a few cells behind the tip. While a filament glides through this self-produced tube, new slime layers are added and the sheath grows in thickness. On the outside the slime becomes increasingly hydrated and is indistinguishable from the medium. The slime can be visualized by adding a suspension of dilute India ink (175) (Fig. 5). The sheath is discarded when the filament leaves it. It can be reutilized when the filament moves back or the trichome breaks out to form a new sheath. However, the filaments often use the same track over and over. When the filament glides out of the tube, the sheath collapses. The sheath is composed of individual strands which are twisted as the filament rotates during forward locomotion (Fig. 6). When forward movement of *Oscillatoria* is hindered by holding the filament in place by means of glass needles, the slime can be seen to be transported on the surface (130).

The slime could be secreted by either of two types of pores found in the cell wall (165, 235). Electron microscopic studies have revealed large pores of 30 to 60 nm in diameter in the cell walls of *Oscillatoria*; however, it was not clear from the electron micrographs if these are pores or merely depressions. Parallel to the cross walls, rings of smaller pores of <20 nm have been found in several cyanobacteria (67, 206). However, these structures are not visible in scanning electron microscopy of *Phormidium uncinatum* after cryofixation by liquid propane (Fig. 7) (267). During dehydration, the slime sheath is torn and forms a fibrillous layer on the filaments.

However, slime secretion does not seem to be the propelling mechanism. First, the amount of slime formed per second that would be necessary to push the filaments forward has been calculated to exceed the volume of the cells several times (129). Second, cyanobacteria have been observed to move through up to 5% agar at a considerable speed, and it is difficult to envision that the necessary power is produced by simple slime secretion. Third, the frequent directional changes (during the autonomous reversals or after photophobic stimulation) would require that either the extruding slime pores swing around by 180° during each reversal or two sets of pores exist which operate alternately. An additional difficulty is a feasible explanation for the rotation around the long axis that occurs during forward locomotion of the *Oscillatoriaceae* (69).

Several alternative models have been proposed to explain motility of gliding procaryotes. First, the filaments glide only when in contact with a surface (113); this requires an effective adhesion of the slime or the surface of the filaments or both. Hydrophobicity has been suggested to be the mechanism for adhesion in benthic cyanobacteria (75). The chemical composition of the membrane, cell wall, and the slime has been characterized only in a few of these organisms (35). It has been assumed that movement is powered by undulating membranes (60), but none have been observed on the surface of cyanobacteria. If they exist, they may be too small to be seen by light microscopy or they may be beyond the flicker frequency of the human eye. A mathematical model has been proposed to explain gliding movements by electrochemical forces (62, 242). However, no experimental evidence has yet been produced to support this hypothesis.

Jarosch proposed that gliding motility is effected by rotating protein fibrils in the outer cell wall layers (134). Rotation of the fibrils could produce tiny undulations or oscillations discussed above that propel the filament. In fact, shear-oriented microfibrils have been detected in the slime of two oscillatoriacean cyanobacteria (144). However, these fibrils may not be effective in propulsion. Other investigators have

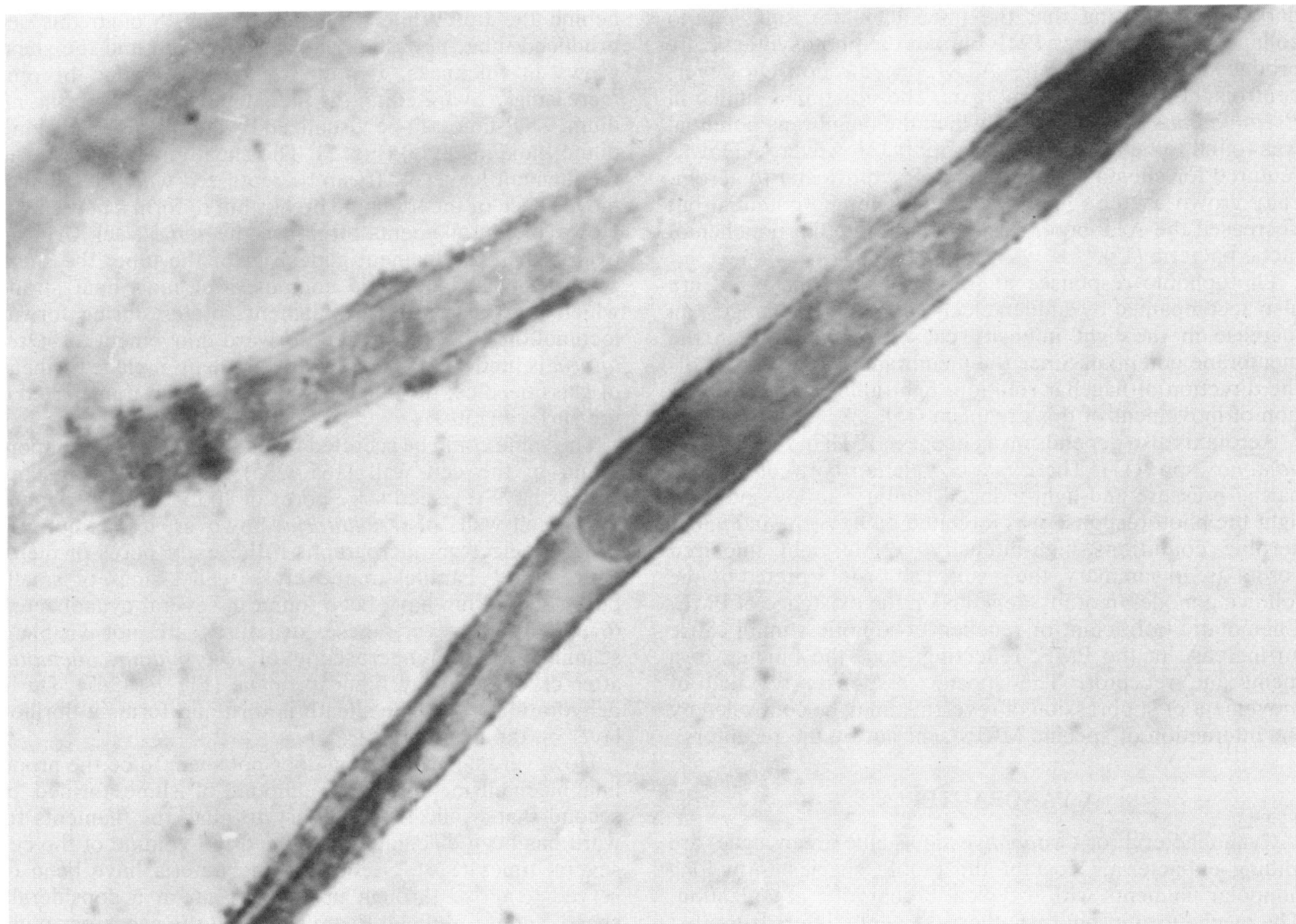

FIG. 5. *P. uncinatum* gliding in its slime sheath, visualized by India ink particles.

investigated the cell wall by means of electron microscopy and demonstrated microfibrils in the cell wall layers (135, 235). In *Anabaena* sp., 15-nm fibrils were found (D. C. Wildon, Ph.D. thesis, University of Sydney, Sydney, Australia, 1965), and similar structures were detected in *Oscillatoria* spp. (110). It is interesting to note that the fibrils were oriented at the same angle as the pitch of rotation. Therefore, it has been speculated that contraction of these fibrils is the basis for locomotion, which could be similar to an earthworm gliding through soil (112). The chemical nature of the microfibrils is unknown, but if they are involved in movement they seem to be different from those found in eucaryotes because motility in cyanobacteria is not affected by cytochalasin B (224). *p*-Chloromercuribenzoate, however, which blocks sulfhydryl groups, impairs motility in amoebae as well as in *Oscillatoria* spp. (2). Obviously, different organisms utilize different mechanisms for gliding motility. Other nonflagellated, motile bacteria such as *Flexibacter*, *Filibacter*, *Myxococcus*, and *Cytophaga* spp. may glide by mechanisms different from the one that drives cyanobacteria (39, 40, 140, 154, 285). Even unicellular cyanobacteria such as *Aphanothece* sp., which has been reported to be motile, may utilize a different mechanism of movement (241). In this organism a glycoprotein has been suggested to be involved in the gliding mechanism, but the motor apparatus has not been analyzed yet.

The gliding mechanism of *Cytophaga* spp. has been analyzed by Lapidus and Berg (147) by observing polystyrene latex particles which are attached to and transported by binding sites on the surface. The conclusion of this observation is that these binding sites are attached to the substratum and are transported within the fluid outer membrane along tracks fixed to the rigid peptidoglycan framework. This mechanism, however, cannot account for the movements in gliding cyanobacteria which are covered by a slime sheath.

Even though the cellular motor remains obscure in gliding cyanobacteria, there are indications of the mechanism by which the filaments are powered. Earlier reports assumed a direct powering by ATP (182). Recent investigations suggest the involvement of the PMF (83). There is an effective mechanism of energy transport along a filament (216): when a *Phormidium* trichome is kept in darkness and only a few cells are irradiated, the whole filament starts moving after a short delay (46). Another requirement for movement is Ca^{2+}, at least in some cyanobacteria (3), although *Phormidium* sp., e.g., moves even in distilled water.

It should be mentioned in passing that there is at least one report of a cyanobacterium capable of free swimming, but no indications as to the mechanism of movement or the motor apparatus are given (281).

Photokinesis

A dependence of the speed of movement on the fluence rate of the actinic light was observed long ago; the behavior

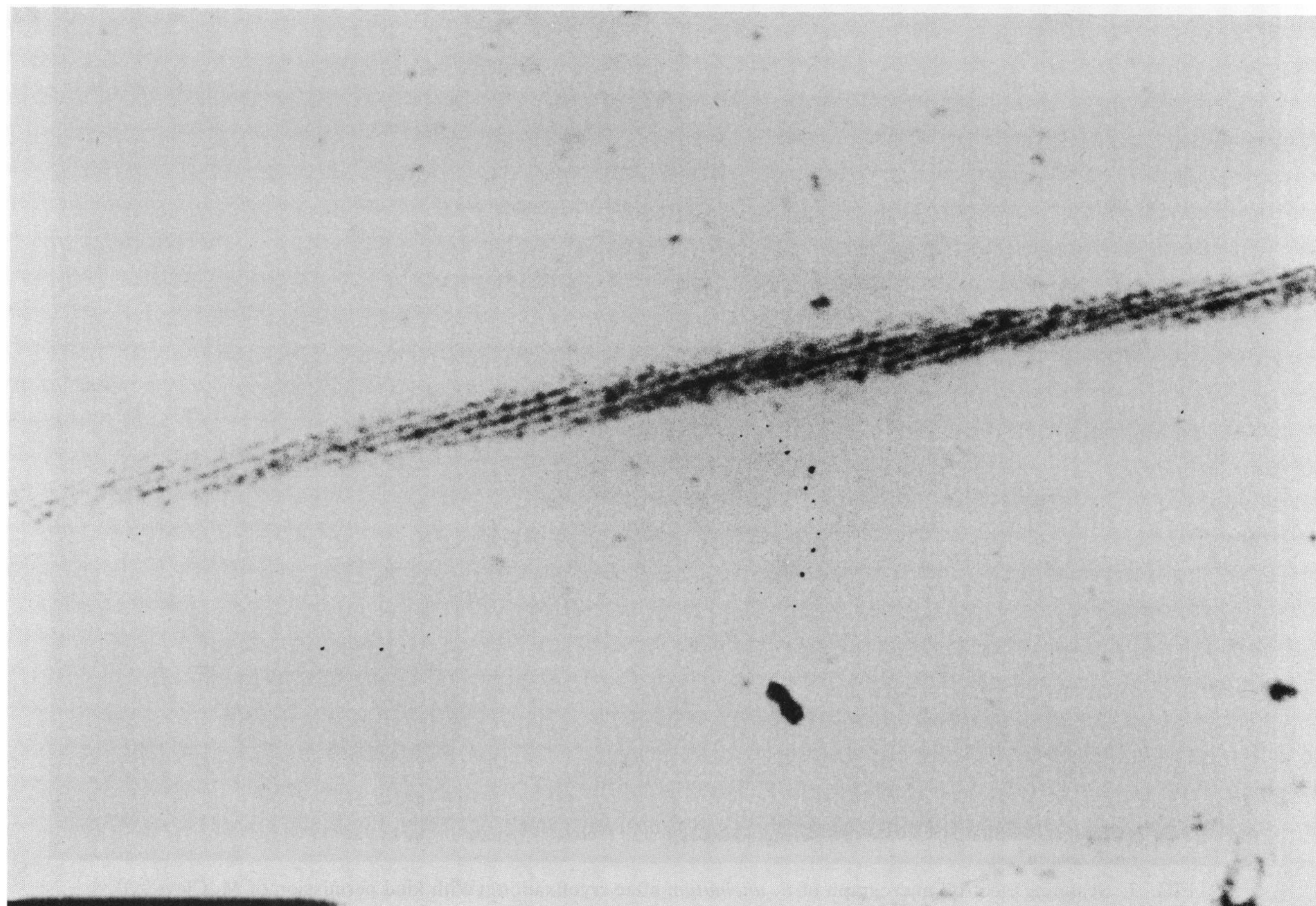

FIG. 6. Twisted and collapsed slime sheath of *P. uncinatum* after the filamentous organism has left it.

was studied and characterized by Nultsch in a *Phormidium* species (177). Two conceptually different techniques can be applied: the speed of movement or the percentage of motile filaments can be determined microscopically, or the spreading of a population from an inoculation point or line can be studied. The former technique requires a considerable amount of work since, due to the high biological noise, a large number of organisms need to be studied to obtain statistically significant data. Recently, video and computer techniques have been used to follow automatically the movement of individual organisms by means of image analysis (84, 95, 107, 150). Population techniques require that the experimenter make sure that only the desired response is measured, i.e., that no different photoresponses such as phototaxis or photophobic responses, or responses to other factors such as chemical or mechanical stimuli, are superimposed.

In white light *Phormidium* sp. shows a positive photokinesis up to irradiances of about 30,000 lx. Higher radiation results in negative photokinesis, perhaps due to damage of the organisms by the bright light. An increase in the speed of movement could be found over a threshold of 0.02 lx. The optimum was observed at about 2,000 lx (177). In *Anabaena* spp., the threshold was found to be 500 times higher; the optimum was near 1,000 lx, and up to 90,000 lx no negative photokinesis was observed (191).

The action spectrum of the photokinetic effect on *Phormidium autumnale* does not closely resemble the absorption spectrum of the organisms; the coincidence is restricted to the long- and short-wavelength range of the visible spectrum, while the green spectral region is underrepresented (177). The photokinetic action spectrum also does not resemble the action spectrum of photosynthetic CO_2 incorporation in this organism (193). In addition to chlorophyll *a*, *Phormidium* sp. possesses both carotenoids are phycobilins (C-phycoerythrin and C-phycocyanin plus small amounts of allophycocyanin) as accessory pigments. The action spectrum suggests that chlorophyll *a* is the main photoreceptor; the phycobilins are not involved. This interpretation is supported by the fact that the photokinetic action spectrum of the closely related *Phormidium ambiguum* resembles that of *Phormidium autumnale*, although it does not have any detectable amounts of phycoerythrin but a high content of C-phycocyanin.

It is obvious that some part of the photosynthetic machinery is involved in photokinesis, but it is also obvious that not all is involved. It could be speculated that only cyclic electron transport by photosystem I (PSI) is responsible. This interpretation is further supported by the fact that photokinesis in these organisms is only slightly impaired by DCMU, which inhibits the linear (but not the cyclic) electron transport chain between PSII and PSI just beyond the primary acceptor of PSII (182, 192). 2,5-dibromo-3-methyl-6-isopropylbenzoquinone (DBMIB), which prevents the reoxidation of plastoquinone, is also not strongly inhibitory of photokinesis in *Phormidium* spp. Similar results have

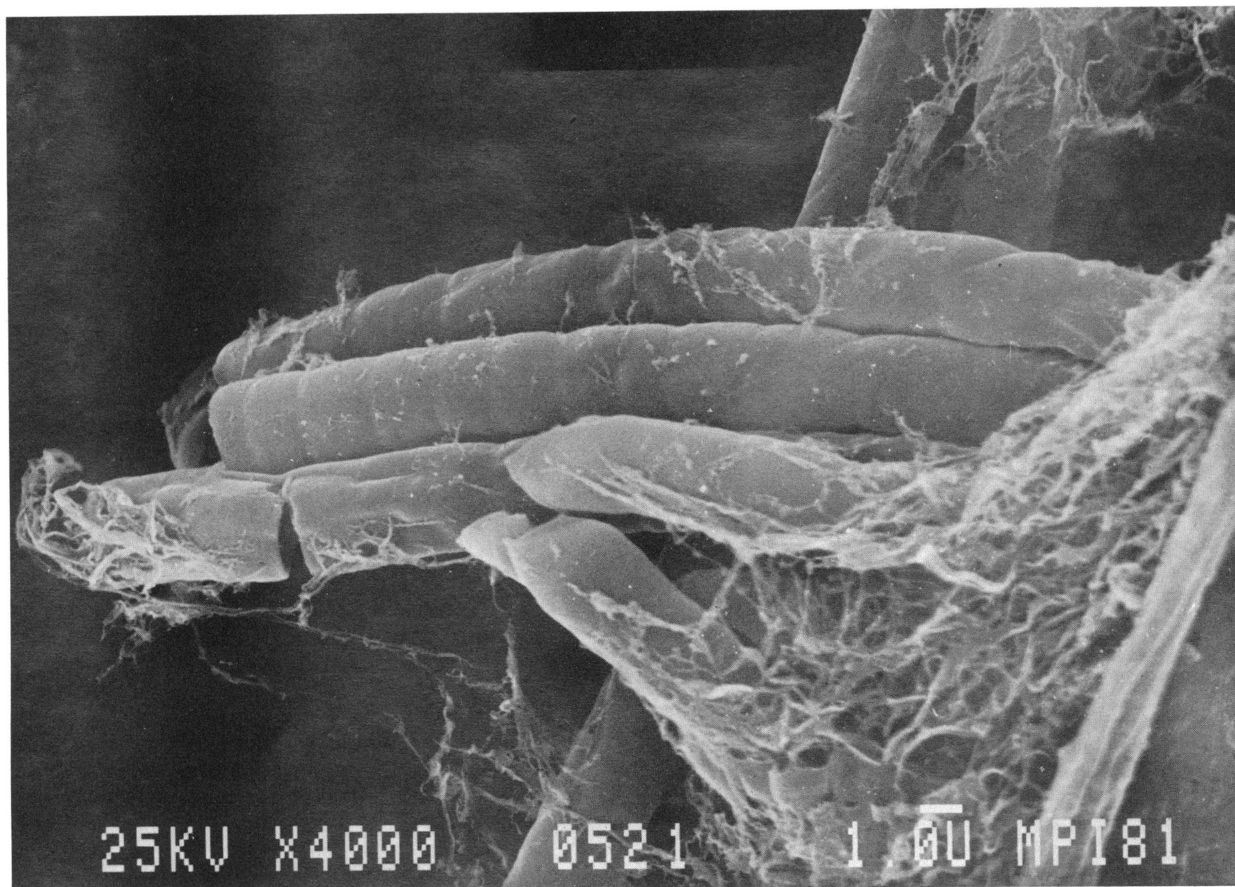

FIG. 7. Scanning electron micrograph of *P. uncinatum* after cryofixation. (With kind permission of M. Claviez.)

been obtained with other members of the *Oscillatoriaceae*, including *Oscillatoria*, *Pseudanabaena*, and *Spirulina* spp. (183).

Nultsch (181) tested the effect of a number of redox systems on photokinesis. Redox components capable of trapping electrons from the photosynthetic electron transport chain were most effective in inhibiting photokinesis. Methylviologen with a redox potential (E_0') of -0.44 V had a maximal effect; a second inhibitory maximum was found for phenazinemethosulfate ($E_0' = 0.064$ V). In darkness these redox systems also impair motility, probably by extracting electrons from the respiratory electron transport chain, provided their redox potential is more positive than that of oxidized nicotinamide adenine dinucleotide.

The results of the inhibitor and redox system experiments do not allow discrimination between a linkage of photokinesis to the electron transport chain and to photophosphorylation. In the case of *Phormidium* spp., cyclic phosphorylation could be involved. To test this hypothesis, uncouplers have been applied which leave electron transport uninhibited but impair ATP synthesis. CCCP strongly suppresses photokinesis at a concentration of $<10^{-5}$ M. However, uncouplers not only impair photophosphorylation but (likewise effectively) oxidative phosphorylation; as a result, the dark movement is also impaired. Other uncouplers such as sodium azide, imidazol, or dinitrophenol produced similar results (180), indicating that in fact photokinesis is the result of an increased energy supply to the motor apparatus. The modern interpretation would be based on the proton gradient produced in light: a higher PMF increases the speed of movement and the uncouplers such as CCCP diminish it (138). This interpretation is similar to that for photokinesis in flagellated procaryotes (see above).

A member of the *Nostocaceae*, *Anabaena variabilis*, shows different photokinetic behavior (191): the action spectrum revealed a strong activity of the biliprotein C-phycocyanin, while chlorophyll *a* was underrepresented if active at all. In the blue region of chlorophyll absorption no activity could be found. Such action spectra are difficult to interpret. It could be speculated that the light-harvesting pigments funnel their absorbed energy into a specialized chlorophyll reaction center which is present at a low concentration. *Nostoc*, another member of the *Nostocaceae*, showed similar behavior, so that in this family it is thought that the accessory pigments feed their energy into PSII (183).

This interpretation is further supported by the fact that DCMU and DBMIB strongly impair photokinesis in *Anabaena* spp. (191), indicating that PSII is involved in the response. Uncouplers were as effective as in the *Oscillatoriaceae*: at a concentration of 10^{-5} M, CCCP almost completely inhibited photokinesis. Atebrine also impairs photophosphorylation and thus photokinesis; the effect can be cancelled by the addition of flavin nucleotides (179).

In summary, photokinesis in cyanobacteria is an effect of the increased energy supply in light to the motor apparatus, probably in the form of PMF. Thus, photokinesis in cyanobacteria does not differ from that in purple bacteria (52, 270), and similar relationships have been found in red

algae (195) and desmids (98). The *Oscillatoriaceae* are distinguished from the *Nostocaceae* as the former use cyclic photophosphorylation while the latter utilize noncyclic or pseudocyclic phosphorylation as an energy source.

Phototactic Orientation

Probably cyanobacteria are the only procaryotes capable of a true phototactic orientation; above we define phototaxis as an oriented movement with respect to the light direction, which usually takes the form of a positive phototaxis (toward the light source) or negative phototaxis (away from the light source) (94, 256). Again, cyanobacteria can be divided into two classes which differ in their mechanisms of orientation, their action spectra, and their sensory transduction.

Oscillatoriaceae. *Phormidium* sp., a representative of the *Oscillatoriaceae*, orients in lateral light by a trial-and-error mechanism: the filaments reserve their direction of movement according to an endogenous rhythm. When an organism happens to move toward the light source (some angular deviation is allowed), the movement in this direction is prolonged by suppression of the autonomous reversals; when it moves away from the light source, the path is shortened and the organism soon reverses its direction of movement (119). It is not a trivial task for an organism to detect the light direction. It can be excluded that the filament detects differences in the irradiance between its front and rear ends because the behavior is also found in a parallel light beam. Several strategies for detecting light direction by motile microorganisms have been discussed; these include intracellular attenuation of the light beam by absorption or scattering, so that the front end of the cell receives more light than the rear end, which results in an intracellular light gradient. The alternative model is a focussing of the light beam when the intracellular refractive index is higher than the outside (106). Recently, Gabai (79) showed that in *Phormidium* sp. phototactic orientation is brought about by a "one instant" method: when he placed a light spot on the front cells and moved it with the gliding organism, autonomous reversals were repressed for more than 20 min while the normal rate of spontaneous reversals was once every 4 min. A light spot on the tail end induced a reversal within 1 to 2 min.

Phormidium sp. responds positive phototactically to white light above a threshold of about 5 lx. The optimum is found at about 200 lx, and beyond 10^4 lx the organisms stopped moving; there was no negative phototaxis (176). The action spectrum shows major peaks at around 400, 495, and 565 nm and a smaller maximum at 615 nm. The peaks correspond to absorption maxima of carotenoids and the phycobilins C-phycoerythrin and C-phycocyanin. The UV/blue-abosrbing pigment has not been identified. Chlorophyll does not seem to be involved (176). This is interesting because older reports indicated a strong activity in the red spectral region (57), and also *Cylindrospermum* sp. has been found to respond phototactically to red light (275); obviously, there are considerable differences in the sets of pigments involved in photoperception.

At least in *Phormidium* sp. the information pathway does not seem to involve the photosynthetic electron transport chain even though the accessory pigments seem to be the main photoreceptor pigments, because the classical inhibitors DCMU and DBMIB have no effect (185).

Nostocaceae. *Anabaena* sp., a member of the *Nostocaceae*, shows a totally different mechanism of phototactic orientation. In contrast to *Phormidium* sp., it is capable of true steering (196), which may or may not be correlated with the different mechanism of locomotion (*Phormidium* sp. rotates around its long axis, while *Anabaena* sp. does not). When subjected to a lateral light field, the tip of the filament turns into the direction of the light source at low fluence rates and away from it at high fluence rates. More often, the filaments glide in a U-shaped fashion and the leading curved portion turns with respect to the light source. Each cell seems to be capable of detecting the light direction. When a small rectangular light field is placed on the lateral half of a few central cells within the filament, this portion bulges out and starts moving toward the light source, forming a new leading "head" provided that the fluence rate is in the range causing positive phototaxis (199). At higher fluence rates (27 W m^{-2} = 5,100 lx), the organism moves away from the light spot. The interpretation of these observations is that the light direction is detected by an intracellular light gradient as in some eucaryotes such as *Dictyostelium* sp. (106).

The action spectra for positive and negative phototaxis in *Anabaena* sp. differ from each other and from that measured in *Phormidium* sp.: C-phycocyanin, which is the major accessory photosynthetic pigment in this organism, contributes to the action spectrum for positive phototaxis but so does chlorophyll *a*, which is responsible for the peaks near 440 and 670 nm. The action spectrum for negative phototaxis points to the same pigments, but in addition there are peaks at 550 and 730 nm which have been attributed to a type *b* phycochrome and a photoreversible pigment, respectively. As in the case of *Phormidium* sp., the photosynthetic electron transport chain does not seem to be involved in the sensory transduction of phototaxis in *Anabaena* sp. because neither DCMU nor DBMIB has any effect.

Recently, the switch controlling the sign reversal between positive and negative phototaxis has been studied in detail. NaN_3 has been found to impair negative but not positive phototaxis. When high fluence rates are applied, the negative response is reversed into a positive one in the presence of NaN_3. The photoreceptor system absorbing between 500 and 560 nm and above 700 nm is insensitive to azide. NaN_3 is known to exert a number of effects, including uncoupling and inhibition. In addition, it has been found to quench singlet oxygen ($^1O_2$) production. A further hint that the latter characteristic of NaN_3 may be responsible for the effect on phototaxis in *Anabaena* sp. comes from the observation that it effectively prevents photobleaching which occurs at high fluence rates (197). Other quenchers of singlet oxygen including 1,4-diazabicyclo(2.2.2)octane, L-histidine, and imidazole also impair negative phototaxis (234). These results led to a model (Fig. 8) recently proposed for the control of the reaction sense in phototaxis of *Anabaena* sp. (194). At high fluence rates (Fig. 8B) the photosynthetic apparatus produces high concentrations of $^1O_2$ as a by-product; at low fluence rates (Fig. 8A), the concentration may be low or even quenched by the carotenoids in the thylakoid membrane. The model proposes that a signal processor detects the internal light gradient by a one-instant mechanism and initiates a turn of the trichome if necessary. The signal processor is under control of a sign reversal generator, which in turn is influenced by the $^1O_2$ concentration. This model is further supported by the findings that solubilized β-carotene, canthaxanthin, and a C_{30} ester shift the transition point of phototaxis to higher fluence rates by about one order of magnitude. Similarly, the transition point is shifted to higher fluence rates when a stream of gas is passed over the filaments fast enough to remove $^1O_2$ from the surface of the organisms.

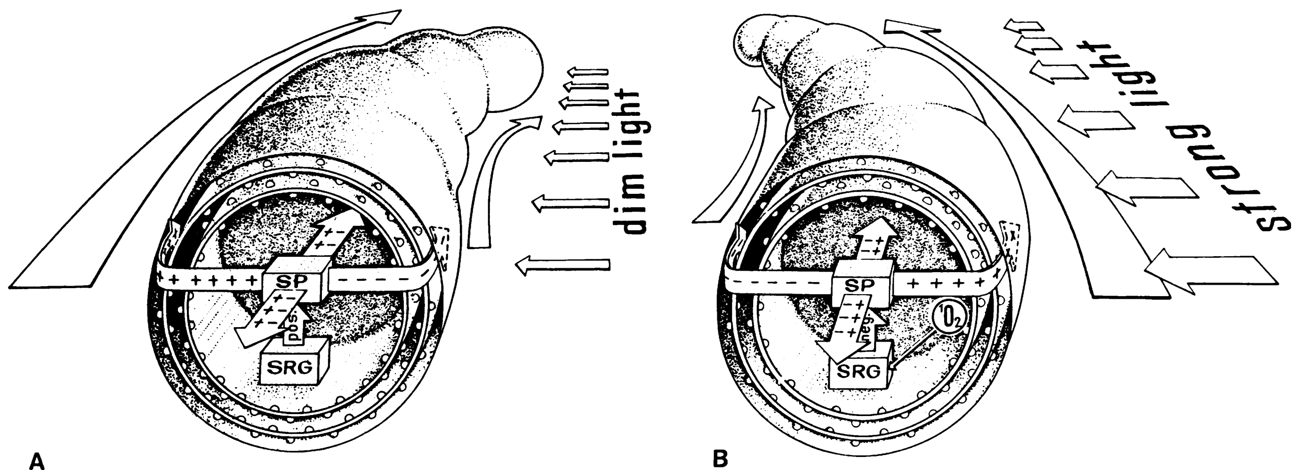

FIG. 8. Model of phototactic orientation of *A. variabilis* in lateral dim (A) and strong (B) light. SP, Signal processor; SRG, sign reversal generator. (Reprinted from Arch. Microbiol. **142**:180–184 [1985] [reference 194] with kind permission from Springer Verlag, Heidelberg.)

Photophobic Responses

When during microscopic observation the light intensity is suddenly decreased, in most organisms a photophobic reversal of movement can be observed. A similar response is seen when the fluence rate is decreased over the leading front of the filament; it is sufficient to darken only 10 to 25% of the filament length. A stimulation of the rear end does not induce a reversal. After cutting a long filament in smaller portions, each new trichome reacts independently, provided that it has a minimal length of about five cells (232). Photophobic reactions have been observed at least 100 years ago and studied intensely. Most of the older literature is summarized in several reviews (94, 185, 189).

Most of the recent work focused on *Phormidium* spp. The zero threshold in white light was found at about 0.03 lx, which is lower than moon light intensity. The optimum occurs at about 3,000 lx (178). When gliding from a bright to a less bright light field, some organisms detect differences in the fluence rate of as little as 4%, which equals the absorption of a single glass pane (187). When a suitable light field is projected into a dark suspension, the filaments accumulate in the light field since they are free to enter it during their random movements but are unable to leave it due to repetitive photophobic responses each time they hit the boundary of the light field (103).

The action spectrum clearly indicates the participation of all photosynthetic pigments (57) so that there is no doubt concerning the involvement of photosynthesis in the photoperception mechanism of phobic responses in *Phormidium* spp. It could be demonstrated by uncoupler studies, however, that the photophobic response is independent of photophosphorylation. Inhibitors of the photosynthetic electron transport chain strongly suppress phobic responses (87, 88), indicating that the coupling site is plastoquinone, a component of the electron transport chain linking PSII and PSI (28), which has also been demonstrated spectrophotometrically (109).

In cyanobacteria the thylakoids are scattered throughout the cytoplasm; they are not enclosed in plastids (162). When irradiated by light, there is a vectorial proton transport through the thylakoid membrane by plastoquinone which builds up a considerable pH and electrical gradient (210). Since some thylakoids are in contact with the cytoplasmic membrane, protons are extruded from the cells (72) and the gradient influences the transmembrane electrical potential (257). When a filament leaves a light field, this gradient decreases rapidly. Glagolev has proposed that cyanobacteria are capable of sensing changes in the μ_{H^+} gradient (82).

Light-induced potential changes can be measured by using very small intracellular glass electrodes (about 200 nm tip diameter); similar light-dependent electrical potential changes can be measured on the surface of the filaments (92). The action spectra of these potential changes coincide with that of photophobic responses. Inhibition of the potential changes by inhibitors of the photosynthetic electron transport chain or triphenylmethyl phosphonium simultaneously impair photophobic responses (93). Thus, it has been suggested that the first step in the sensory transduction chain is a light-dependent modulation of the proton gradient and the electrical membrane potential (169). This hypothesis is further supported by an experiment in which the primary photoperception is bypassed: when the organisms are subjected to a pH jump in darkness, they respond with a reversal of movement (similar to a phobic reversal) provided that the jump forces the pH from about 7.3 measured in the growth medium into the range of 4.9 to 5.7 (96). A jump of similar size in the alkaline region did not alter the direction of movement.

Since the zero threshold is low, it is unlikely that the measured changes of electrical potential really reflect the primary change in the proton gradient. Rather, we have to assume a considerable signal amplification. The most common mechanisms in biological systems for this purpose are enzymatic reactions (often as enzyme cascades) (260) or switching of voltge-dependent, cation-specific membrane channels (142). The sensory transduction chain of photophobic responses in *Phormidium* spp. utilizes the small electrical potential change caused by the breakdown of the proton gradient after a transition from light to dark to open calcium-specific ion channels in the cytoplasmic membrane, which allows a massive Ca^{2+} influx into the cells along a previously established Ca^{2+} gradient. There are several pieces of evidence that support this hypothesis. Calcium transport through channels can be impaired by specific blockers such as La^{3+}, ruthenium red, and organic calcium antagonists (71, 151). These drugs also inhibit phobic reactions (97). Ionophores are artificial ion channels which can

be incorporated into the cell membrane. Application of ionophores for monovalent ions did not inhibit phobic reactions, while A23187 (calcimycin) drastically impairs the responses (97, 167, 172). This ionophore forms a bypass for Ca^{2+} in parallel to the existing channels, and the Ca^{2+} gradient is decreased so that it is not available for a phobic response.

Several techniques have been used to monitor calcium concentrations in cells. The most direct method is the use of Ca^{2+}-sensitive microelectrodes (10), which, however, cannot be used in cyanobacteria because of their small cellular dimensions. Indirect optical methods utilize the absorption or fluorescence of a trapped dye in dependence of the Ca^{2+} concentration (213, 274) such as Arsenazo III (131), aequorin and related substances (53, 239, 240), Fura-2 (284), or quin 2 (282). A different technique monitors the distribution of $^{45}Ca^{2+}$. Indeed, $^{45}Ca^{2+}$ is taken up in massive amounts during a photophobic response and pumped out of the cell afterwards (108). Another, indirect proof of the involvement of Ca^{2+} fluxes in the sensory transduction chain of *Phormidium* spp. has been obtained by drastically reducing the concentration of free Ca^{2+} in the medium, which totally cancels photophobic responses, although the filaments remain motile (108). Readdition of Ca^{2+} fully restores the response. The existence of a Ca^{2+} gradient requires a Ca^{2+}-adenosine triphosphatase which constantly pumps Ca^{2+} out of the cells (207). Poly-L-lysine, an inhibitor of the Ca^{2+}-adenosine triphosphatase, effectively impairs phobic responses (Häder, in press). The possible occurrence and role of calmodulin in cyanobacterial photoresponses have not been clarified yet, while its involvement in flagellar reversal in eucaryotes has been demonstrated (141, 156). Thus, phobic behavior in cyanobacteria shows a closer resemblance to eucaryotes than to other bacteria.

In sensory responses of many plant and animal systems, biochemical control of calcium fluxes by inositol-1,4,5-trisphosphate and cyclic nucleotides has been shown (161,

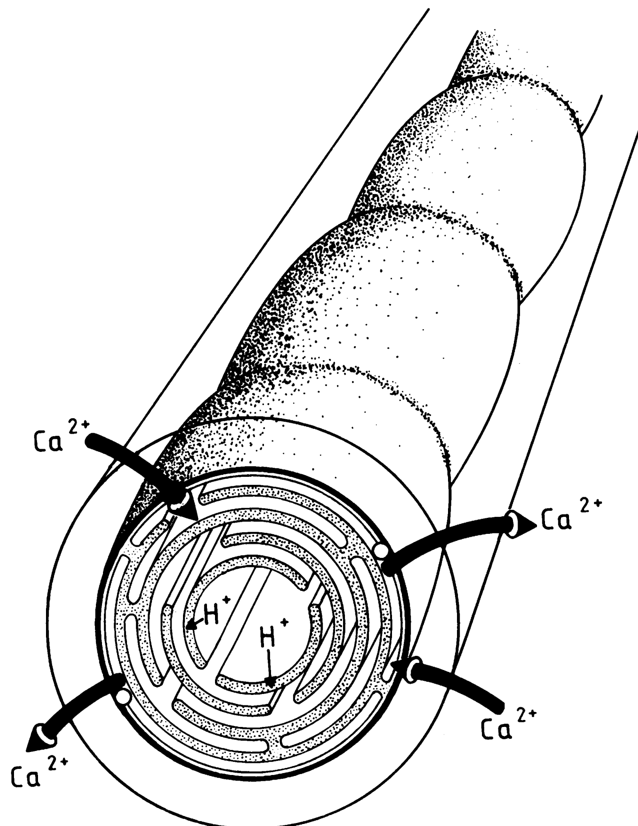

FIG. 9. Model of the sensory transduction chain responsible for photophobic responses in *Phormidium* spp. For details, see text.

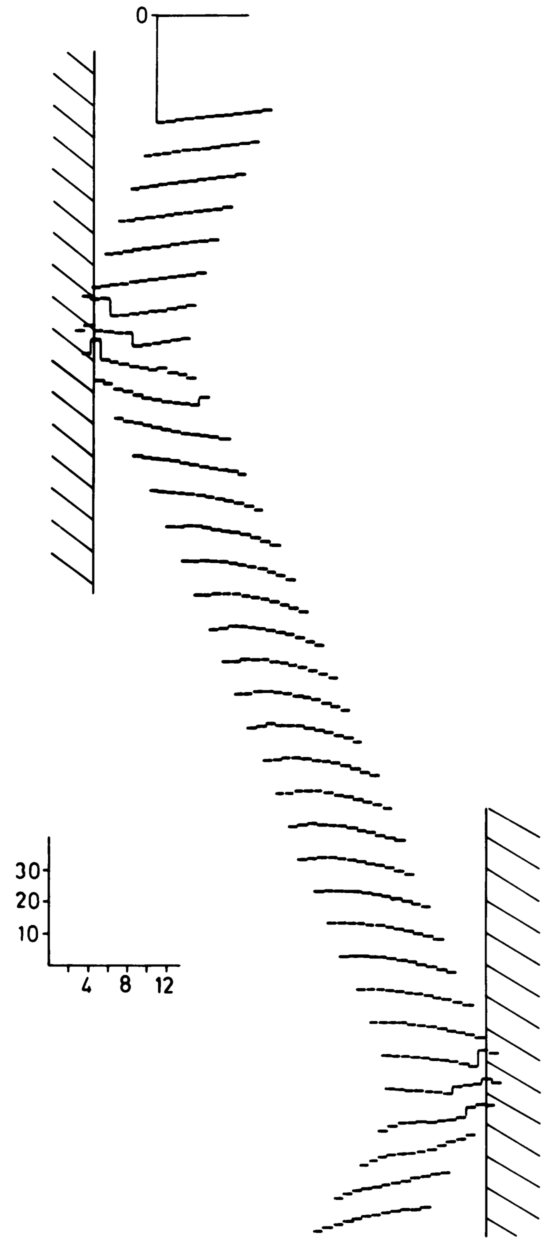

FIG. 10. Graphic representation of a mathematical model of photophobic responses in *Phormidium* spp. The steps on the ordinate indicate the electrical potential of each cell (negative with respect to the outside). The displacement on the abcissa reflects the movement of the filament. Each time frame is drawn with a vertical offset. When the trichome moves into the shaded areas (hatched), it reverses its direction of movement controlled by the electrical gradient between front and rear ends as symbolized by the (negative) electrical potential drawn as bars below the outside ground potential. (Reprinted from Math. Biosci. **58**:1–17 [1982] [reference 105] with kind permission from Elsevier Science Publishing Co., Inc., New York.)

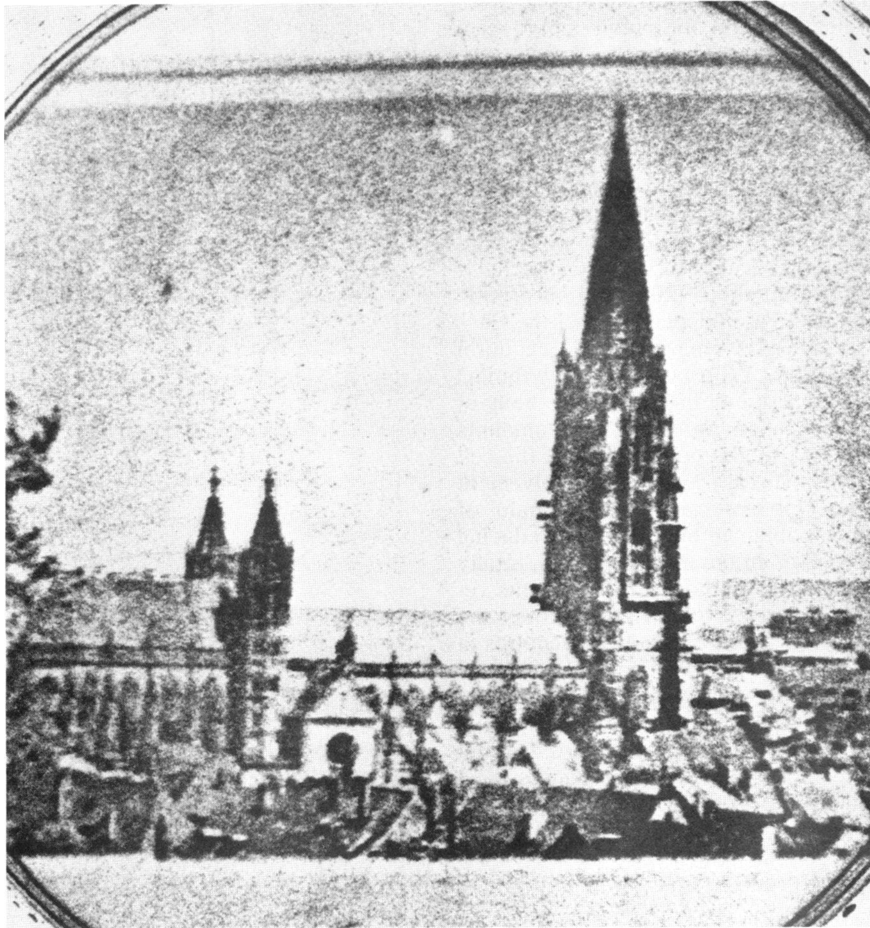

FIG. 11. Algograph produced by projecting a photographic negative of the Freiburg Münster onto a homogeneous suspension of *Phormidium* spp., which accumulate in areas of suitable fluence rates. (Reprinted from reference 99 with kind permission from Verlag Chemie, Weinheim.)

221). There are indications of the involvement of cyclic nucleotides in the sensory transduction of phobic responses in *Phormidium* spp., while the role of the inositol pathway has not been clarified yet (203).

Glagolev et al. have proposed a partially different mechanism for the sensory transduction. According to his model, the primary step is redox sensing: the organisms are suggested to detect the redox level of plastoquinone (80, 168). Support for this hypothesis is the fact that upon addition of DCMU a sudden reversal is induced, accompanied by an increase in the membrane potential due to the reoxidation of previously reduced plastoquinone. The redox level of plastoquinone can be influenced artificially by application of reduced or oxidized duroquinone. Addition of the drug in the reduced form suppressed reversals, and in the oxidized form it stimulated reversals.

In analogy to the chemotactic sensory transduction chain, the following step in phobic responses is supposed to be the methylation of a 40-kilodalton membrane protein which can be found in the methylated form after the addition of reductants or in white light and which can be demethylated by application of oxidants or uncouplers (80).

How is the reversal of movement connected with the Ca^{2+} influx into the cell? Or which parameter controls the direction of movement? The filaments are morphologically nonpolar; the leading end during locomotion is not different from the trailing end. However, when filaments were placed over external electrodes with a small gap between them, electrical potentials of about 10 mV could be measured between the front and rear ends (90, 91, 171). When a reversal of movement is induced experimentally, the electrical potential also reverses. Another support for the control of the direction of movement by electrical potentials is the inhibition of the photophobic response by means of externally applied electrical fields. A direct-current field applied to an organism moving more or less parallel to the electrical field lines suppresses the phobic response. Organisms moving perpendicular to the field lines are not affected (90). Potential differences are not static and are based on or result in electrical currents. Thus, one would expect to find a current between the two ends of the filament. However, Jaffe and Walsby (132) failed to detect such currents in the medium in the neighborhood of a trichome. A possible explanation is that the current loop uses the cell wall or slime sheath, or both, which may have a higher conductivity than the surrounding medium.

The experimental data obtained so far gave rise to a model (Fig. 9): in light the photosynthetic machinery builds up a proton gradient across the thylakoid membranes and the (negative) electrical potential increases. When the front cells move into a dark area, this proton gradient breaks down and the membrane depolarizes. This initial small potential

change causes voltage-dependent Ca^{2+} channels to open and allow a transient massive Ca^{2+} influx (99, 102a). The resulting large electrical potential change reverses the potential difference between the front and rear ends, which eventually reverses the direction of movement. The following steps in the transduction chain, the control and mechanism of the motor apparatus, still need to be revealed.

A mathematical model has been developed into which all known parameters have been incorporated (104, 105). The program calculates the potential of each cell in a trichome at predefined time intervals and calculates the kinetics of the light and dark effects. The speed and direction of movement of a trichome are defined by the overall potential difference between individual cells. Figure 10 shows a computer simulation of the movement of *Phormidium* spp. in a light field showing a phobic reversal each time a boundary is hit.

ECOLOGICAL SIGNIFICANCE OF PHOTOMOVEMENT

Each of the three photoresponses found in microorganisms can result in a net movement of a population. Positive photokinesis results in an accumulation of organisms in dark areas in the habitat, positive phototaxis causes organisms to move toward the light source, and step-up photophobic responses are a mechanism for photodispersal from light fields. Even small fluence rates such as moonlight have been found to affect vertical migration patterns of microorganisms (7). In addition, side effects need to be considered. For instance, due to their extreme light sensitivity, organisms can be attracted phototactically from the stray light scattered from debris or other organisms in an irradiated area (41).

Photomovement is used by many microorganisms for daily, tidal, or seasonal migration (173, 287). Of course, light plays a major role in photosynthetic organisms as an energy source, and growth and photosynthetic CO_2 fixation have been found to depend heavily on prevailing light conditions (209, 212). In addition, photomovement is used to construct and maintain a pattern of interwoven organisms in mat-forming filaments to minimize mutual shading. It is also an effective mechanism by which to escape sedimentation in turbid waters (208). The amazingly precise orientation with respect to the fluence rate can be demonstrated in *Phormidium* spp. by a simple experiment. When a photographic negative is projected onto a homogeneous suspension of filamentous organisms in an agar layer, they accumulate in areas of suitable fluence rates, avoiding too bright and too dark areas by step-up and step-down photophobic responses (Fig. 11).

Judging from the wide variety of photoreceptor pigments, procaryotic photomovement seems to have been an experimental stage in evolution. In eucaryotes a far smaller range of photoreceptor pigments is found (44). There are, however, examples of eucaryotic organisms that have adopted the photosensory mechanism of procaryotes by incorporating, e.g., cyanelles (symbiontic cyanobacterium-like inclusions) into their own cells (283). The colorless flagellate *Cyanophora paradoxa* contains cyanelles whose photoreceptor pigments are used by the host to sense light for photophobic and photokinetic responses (101).

Recently, a high sensitivity to solar UV radiation was found in cyanobacteria (100, 102). At ambient levels of UV-B (280- to 320-nm radiation), both motility and photoorientation are drastically impaired when the organisms are exposed to full sunlight. The stratospheric ozone layer which protects the surface of the earth from high UV-B doses undergoes seasonal fluctuations (29). In addition, gaseous pollutants such as chlorofluoromethanes have been found to accumulate in the stratosphere and partially break down the protective ozone layer (160). While most higher plants have been found to be resistant to substantial increases in the UV-B radiation resulting from the partial ozone layer reduction, motile microorganisms such as gliding cyanobacteria may be endangered since they are under UV-B stress even at currently measured doses.

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