Chemokinetic Motility Responses of the Cyanobacterium *Oscillatoria terebriformis*

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*Oscillatoria terebriformis*, a gliding, filamentous, thermophilic cyanobacterium, exhibited an inhibition of gliding motility upon exposure to fructose. The observed response was transient, and the duration of nonmotility was directly proportional to the concentration of fructose. Upon resumption of motility, the rate of motility was also inversely proportional to the concentration of fructose. Sulfide caused a similar response. The effect of sulfide was specific and not due to either anoxia or negative redox potential. Exposure to glucose, acetate, lactate, or mat interstitial water did not elicit any motility response.

Cyanobacteria exhibit complicated motility patterns in microbial mats (14), mudflats (13, 16), and other benthic environments. Daytime motility responses of filamentous cyanobacteria have been explained by photokinesis, phototaxis, and step-up and step-down photophobic reactions (6, 9). The light responses exhibited by cyanobacteria apparently are adaptations aimed at maintaining optimal light regimes for support of photosynthesis, as well as avoidance of burial by sedimentation (13). In addition to light responses, there have been three reports of cyanobacterial chemotaxis, or chemotaxis-related, behavior. Fechner (7) demonstrated a negative tactic response to acids by some members of the family Oscillatoriaceae. Malin and Walsby (12) reported a positive light-dependent chemotaxis to CO₂, HCO₃⁻, and O₂, again in an Oscillatoria sp. We (14) have recently reported a negative chemokinetic response to sulfide by *Oscillatoria terebriformis*.

Our results on *O. terebriformis* were part of an in-depth study (14, 15) concerning motility of this cyanobacterium in the natural environment during darkness, when chemotaxis would be expected to be important. Populations of *O. terebriformis* migrate during darkness to a position below the O₂/sulfide interface within a microbial mat to a microenvironment which is both anaerobic and highly reducing. In the laboratory, this species was shown to be capable of maintaining viability for periods up to 1 month by fermenting exogenous fructose to lactic acid, but only at a negative environmental redox potential. When respiring aerobically in the dark, *O. terebriformis* rapidly depleted intracellular stored glycogen and often lysed in 24 to 48 h. Therefore, the downward migration appears to be adaptive.

In this report, we present the results of laboratory experiments on chemokinetic responses of *O. terebriformis* to several organic compounds and interstitial mat water and additional results on the specificity of sulfide in eliciting the negative chemokinetic response.

An axenic clone of *O. terebriformis* (OH-80-0t-D) was isolated in 1980 from Hunter’s Hot Springs, Lakeview, Oreg. (15). This culture was maintained at 45°C on D medium, a mineral medium with 0.52 mM nitritotriacetic acid (a chelator) as its only organic constituent (5).

Instead of monitoring the behavior of individual tri-

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Clumping of *O. terebriformis* at 47°C in a glass petri dish. Time after dispersal: A, t = 0; B, 20 s; C, 40 s; D, 60 s; E, 90 s; F, 4 min. (Reprinted by permission of the author [3] and the *Journal of Phycolology*.)

tose. While the experiment shown was done in the light, a similar response occurred in darkness, although rates of withdrawal were slower.

When trichomes were redispersed in a fresh fructose solution (7 mM) after clumping in the presence of fructose, the duration of the lag (response A) decreased. Multiple exposures (up to four, including initial exposure) resulted in a final clumping rate comparable to an initial exposure of 1 mM fructose. Multiple exposures (up to four, including initial exposure) resulted in a final clumping rate comparable to an initial exposure of 1 mM fructose. Multiple exposures (up to four, including initial exposure) resulted in a final clumping rate comparable to an initial exposure of 1 mM fructose.

Clumping experiments were also done with glucose, acetate, and lactate (all at concentrations of 10, 15, and 30 mM), as well as interstitial water from the natural microbial mat from which *O. terebriformis* was isolated. None of these compounds had any effect on either the onset of clumping or the rate of clump edge retraction. The carbohydrates were selected because both glucose and fructose can serve as an extracellular carbon source to support fermentation in *O. terebriformis* (15) and because acetate and lactate are common organic compounds produced in hot spring mats (1).

In a previous report (14), we demonstrated a negative motility response by *O. terebriformis* to sulfide. Artificial gradients of sulfide were set up in vials. An overlay of dispersed *O. terebriformis* in soft (0.7%) agar was inoculated on top of a 0.7 mM sulfide plug (also soft agar). A discrete band of trichomes accumulated just below the boundary of the sulfide plug.

An additional series of experiments was done to determine whether the negative effect of sulfide on motility was, in fact, specific. It is possible that the observed accumulation of trichomes in the sulfide zone was due to the negative redox potential or to anoxia per se, both caused by sulfide. To test sulfide specificity, we compared clumping response in the presence of sulfide with clumping responses under conditions of anoxia (generated by a means other than the addition of sulfide) and the presence of an alternate strong reducing agent (sodium thioglycolate).
Sulfide alone (0.7 mM) inhibited the formation of clumps, but only for 5 min. Sulfide inhibition occurred in the dark in the presence or absence of DCMU (3-[3,4-dichlorophenyl]-1,1-dimethyl urea, an inhibitor of photosystem II; used at 5 μM). Under illumination, however, sulfide elicited the negative motility response only when DCMU was present; in the absence of DCMU, there was no inhibitory effect. Possibly the lack of inhibition by sulfide in the light without DCMU was due to partial oxidation of the sulfide by photosynthetically produced O₂.

Neither anoxia alone (flushed with N₂) nor lowering the environmental redox potential with sodium thioglycollate (4.4 mM) delayed the onset of clumping. These results indicate that the sulfide effect is specific.

Similar experiments were also done with the addition of 25 mM fructose. In all cases in which fructose was present, no clumps formed for at least 15 min.

Fructose and sulfide, when present together, acted synergistically (data not shown). With 0.7 mM sulfide and 7 mM fructose, clumping was inhibited for 1 h both in the light with DCMU and in the dark. This effect was much greater than the sum of the lag-inducing effects of each compound. Fructose (25 mM) stopped motility for 20 min. With the addition of 0.3 and 0.7 mM sulfide (no fructose), the effect was comparable to fructose at 3 and 5 mM, i.e., the onset of clumping was inhibited for 4 and 6 min, respectively.

Despite overall differences, there are two similarities between the negative chemokinesis of O. terebriformis and the common type of bacterial chemotaxis such as that seen in Escherichia coli. First, in both motility response types, the duration of the response is directly proportional to the concentration of substance which elicits the response (11; this study). Second, the ability to metabolize a substance is unrelated to the success of that substance in eliciting a motility response. Thus, in bacterial chemotaxis, both attractants and repellents can be metabolizable or nonmetabolizable substances (9). O. terebriformis responds to fructose but not glucose, each of which supports fermentation.

It has been suggested by Glagolev (8) that a simple, efficient, and probably primordial form of chemotaxis would be the halting of movement when favorable conditions are encountered. A substance which elicited stopping would be considered an attractant. For O. terebriformis, both fructose and sulfide, each of which is beneficial to the physiology of the organism in darkness, elicit such a response. Thus, negative chemokinesis is more similar to the primordial form of chemotaxis postulated by Glagolev than is the response of modern chemotactic bacteria, such as E. coli, to an attractant, in which individual cells continue to move forward (2, 11).

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**LITERATURE CITED**


