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Oxygen as Attractant and Repellent in Bacterial Chemotaxis

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Studies of bacterial chemotaxis to oxygen (aerotaxis) over a broad range of oxygen concentrations showed that at high concentrations, oxygen was a repellent of *Salmonella typhimurium*, *Escherichia coli*, and some bacilli, whereas it is known that at lower concentrations (≤0.25 mM dissolved oxygen), oxygen is an attractant. In a temporal assay of aerotaxis, *S. typhimurium* in medium equilibrated with air (0.25 mM dissolved oxygen) and then exposed to pure oxygen (1.2 mM) tumbled continuously for approximately 20 s. The oxygen concentration that elicited a half-maximal negative (repellent) response was 1.0 mM for both *S. typhimurium* and *E. coli*. The receptor for the negative chemoresponse to high concentrations of oxygen is apparently different from the receptor for the positive chemoresponse to low concentrations of oxygen, since the oxygen concentration that elicits a half-maximal positive (attractant) response in *S. typhimurium* and *E. coli* is reported to be 0.7 μM. Adaptation to high concentrations of oxygen, like adaptation to low concentrations of oxygen, was independent of methylation of a transducer protein. Only the response to low oxygen concentrations, however, was altered by interaction with the amidated Tsr transducer in *cheB* mutants.

Aerotaxis is a migrational response of microorganisms to a gradient of oxygen. Early studies of aerotaxis were made by generating an oxygen gradient in situ and observing the migration of a population of bacteria. Beijerinck placed 1 drop of a bacterial culture beneath a cover slip, and the bacteria consumed the oxygen in the medium and then migrated in response to oxygen diffusing in from the edges of the cover slip (3). Obligate aerobes formed a band at the edge of the cover slip, microaerophilic spirilla formed a band that was some distance in from the edge, and anaerobes collected in the center of the cover slip. Engelmann placed bacteria in a vessel with illuminated algae (6). The bacteria accumulated near the algal chloroplasts, where oxygen was formed. Spirilla were characterized by a cell-free zone between them and the oxygen source. If the illumination was sufficiently intense, the cells were repelled entirely.

Expanding on the early studies of aerotaxis, Baracchini and Sherris screened 24 motile species of bacteria for aerotaxis by using the algal assay and a capillary assay (2). In the capillary assay a pellet of bacteria was placed at one end of a liquid-filled tube, and the end was sealed. In response to the oxygen gradient generated by respiration, a band of bacteria migrated along the length of the capillary. Positive aerotaxis, i.e., an attraction to oxygen, was demonstrated in 20 species, including *Escherichia coli*, *Salmonella typhi*, and *S. paratyphi* B. Three motile clostridia were repelled by oxygen. Adler investigated aerotaxis of *E. coli* in a defined medium and, for the first time, used measurements of oxygen concentrations to establish that oxygen was a primary attractant for the bacteria (1).

The observed behavior of bacteria suggests that oxygen can function as both an attractant and a repellent, even in a single organism. The net result is the accumulation of motile bacteria at a preferred concentration of oxygen. For a given species the preferred concentration of oxygen is appropriate for the metabolic characteristics of the species. The dual role of oxygen in aerotaxis is not surprising in view of current knowledge of the metabolic consequences of oxygen in cells. Oxygen permits highly efficient aerobic metabolism but is also toxic to cells. The superoxide radical generated during respiration and, particularly, its protonated form, $HO_2\cdot$, is harmful to cells and gives rise to other toxic species, such as the hydroxyl radical, OH· (7). Aerotaxis appears to enable the bacteria to accumulate at concentrations of oxygen that are optimal for respiration while avoiding the harmful side effects of unnecessarily high concentrations of oxygen.

An ongoing study in this laboratory seeks to elucidate the molecular mechanism of sensory transduction in bacterial aerotaxis. Previous studies have been concerned with positive aerotaxis in *S. typhimurium* and *E. coli* (12, 14, 16, 23). Aerotaxis was quantitated in a temporal assay in which 1 drop of a bacterial culture was placed in a gas flow chamber on the stage of a dark-field microscope (14). The concentration of dissolved oxygen was controlled by choosing the oxygen content of the gas ventilating the chamber. At a constant oxygen concentration, the bacteria had a random-walk motility and changed direction by tumbling briefly about once each second. When the concentration of oxygen was increased from 0 to 0.25 mM (air-saturated medium), *S. typhimurium* responded by suppressing tumbling and swimming smoothly for 10 to 15 s (14, 23). This is a typical response of *S. typhimurium* to a temporal gradient of an attractant (15).

In *E. coli* and *S. typhimurium*, the $K_{0.5}$ for aerotaxis, i.e., the concentration of oxygen eliciting a half-maximal response, is approximately 0.7 μM, and cytochrome *o* has been identified as the primary receptor for the aerotactic response (12; D. J. Laszlo, Ph.D. dissertation, Loma Linda University, Loma Linda, Calif., 1981). In chemotaxis, adaptation to most chemicals is dependent on methylation of a transducer protein (11, 24). Adaptation to oxygen (air) was shown to be independent of transducer methylation (16), although an interaction between aerotaxis and one of the methyl-accepting transducer proteins was reported recently (5). Aerotaxis is mediated by the proton motive force (23),

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and a protometer which detects the level of proton motive force has been proposed as the ultimate sensor (25, 26).

In this paper a negative (repellent) aerotactic response to high concentrations of oxygen was demonstrated for the first time in a temporal assay of *S. typhimurium* and *E. coli*. The response was characterized, and the $K_{0.5}$ for the repellent oxygen receptor was determined.

(A preliminary account of these investigations has been presented at the 74th Annual Meeting of the American Society of Biological Chemists, June 1983, San Francisco, Calif. [B. L. Taylor, J.-I. Shioi, B. R. McCorkle, and M. Niwano, Fed. Proc. 42:2136, 1983].)

MATERIALS AND METHODS

Bacterial cells and growth. *S. typhimurium* ST1 (*che*$^+$), ST120 (*flaQ*), and ST134 (*flaAII.2*) (15, 19, 31) and *E. coli* RP437 (*che*$^+$), RP1119 [Δ(*tar-cheB*)*2234 tsr-14*], RP2896 [Δ(*tar-cheB*)*2234*] (18), and RP4790 (*tsr-14*) (17) were grown on synthetic medium (Vogel-Bonner medium E [28]) supplemented with nutritional requirements and 0.7% glucose or 1% glycerol for *S. typhimurium* or *E. coli*, respectively. *Bacillus subtilis* BC26 (22), *B. cereus* M1 (13), and *B. alcalophilus* YN1 (8) were grown in accordance with published procedures. Mid-exponential-phase cultures were used for the taxis assays unless stated otherwise. For quantitative experiments, cells were washed and suspended in chemotaxis medium consisting of 10 mM phosphate buffer (pH 7.5), 0.1 mM EDTA, and 0.7% glucose.

Spatial assay. One drop of bacteria suspended in growth medium (1.1×10^9 cells per ml) was placed between a glass microscope slide and a cover slip, one side of which rested on a piece of a cover slip (0.17 mm thick). The glass slide was transferred to a microchamber, which was ventilated with humidified pure oxygen or nitrogen gas. Air was introduced by stopping the gas flow (14). A band of migrating bacteria was observed and photographed (TriX Pan film; Eastman Kodak Co.) through a microscope with dark-field illumination. The film was analyzed by the scanning densitometer accessory for a Beckman DU-8 spectrophotometer. Chromatography-grade nitrogen (99.9998%) and oxygen (99.15%) were obtained from Big Three Industries.

Temporal assay. Four microliters of bacteria suspended in chemotaxis medium (5×10^7 cells per ml) was placed on a glass microscope slide without a cover slip. The slide was inserted into a microchamber, which was connected to a gas proportioner that mixed oxygen and nitrogen at a selected ratio (14). The chamber was ventilated with the initial gas mixture for 3 min before a second gas was admitted, and any transient tactic response was observed under a microscope. For quantitative analysis of the time course of a response, a sequence of 1-s photographic exposures was made while using a continuous light source. The tracks of swimming cells were analyzed to determine the fraction of cells that were tumbling in each exposure (21). For routine determination of the oxygen response time, the behavioral response of the cells to high oxygen concentrations was video recorded through the microscope (23). The time required for one-half of the cell population to resume prestimulus random motility was estimated. To determine the $K_{0.5}$, we performed five assays of the response time for each oxygen concentration. A sequence recorded for each assay was replayed five times, and the resulting response times were averaged. The experiment was repeated on a subsequent day. The $K_{0.5}$ was obtained from a linear regression analysis of the double-reciprocal plot of the combined data from the two experiments. A Beckman E2 oxygen analyzer was used to calibrate the proportioner. It was assumed that the solubility of oxygen in the chemotaxis medium was equivalent to the solubility of oxygen in a 12.5 mM NaCl solution (29). The oxygen concentrations dissolved at 23.5°C in chemotaxis medium, equilibrated with humidified oxygen and air, were calculated to be 1.2 and 0.25 mM, respectively, when corrected for temperature, water vapor pressure (22 mm Hg [ca. 2.93 kPa] at 23.5°C), and mean barometric pressure (730 mm Hg [ca. 97.3 kPa]).

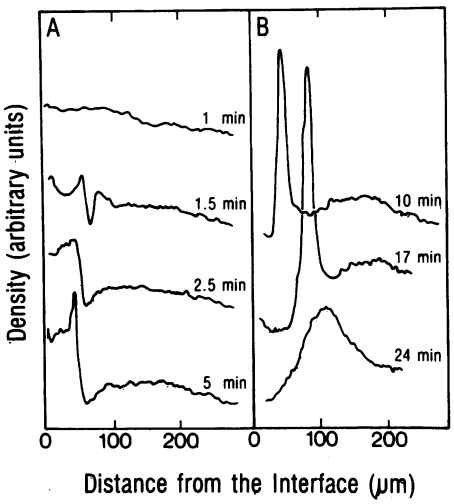

FIG. 1. Chemotaxis of *S. typhimurium* ST1 in a spatial gradient of oxygen. The bacteria were grown to the late-log phase (approximately 5×10^8 cells per ml) in Vogel-Bonner medium E containing glucose. The cell suspension was concentrated to 1.1×10^9 cells per ml by centrifugation. One drop of the bacterial suspension was placed between a microscope slide and cover slip, and the slide was transferred to a microchamber on a microscope stage (see Materials and Methods). Photographs of the dark-field images were taken at the indicated times after the cell suspension was placed between the glasses. Pure oxygen was introduced into the microchamber at 10 min and then replaced with nitrogen at 17 min. The negative film was scanned by a densitometer. The ordinate is the density of the image on the photographic film expressed in arbitrary units and is proportional to the cell density. (A) Time-dependent profile of the aerotactic band adjacent to the air-medium interface. (B) Bacterial distribution after gas changes. Top, air for 10 min; middle, 7 min after the change from air to oxygen; bottom, 7 min after the change from oxygen to nitrogen.

RESULTS

Accumulation in a spatial gradient. In a dense suspension (1.1×10^9 cells per ml) of *S. typhimurium* ST1 placed beneath a cover slip (see Materials and Methods), an oxygen gradient was generated by the oxygen consumption by the bacteria and oxygen diffusing from the interface of the suspension and the surrounding air. Under the conditions used, an aerotactic band of accumulated bacteria was first recognized between 1.2 and 1.5 min after the start of the experiment at approximately 110 μm from the interface (the resolution of the photofilm and the densitometer was not high enough to visualize this premature phase of the band emergence). The band became more dense and moved toward the interface (Fig. 1A). By 2.5 min the band had broadened into a 60 μm-wide zone of accumulated bacteria adjacent to the interface. A peak in cell density developed at approximately 50 μm from the interface where it remained

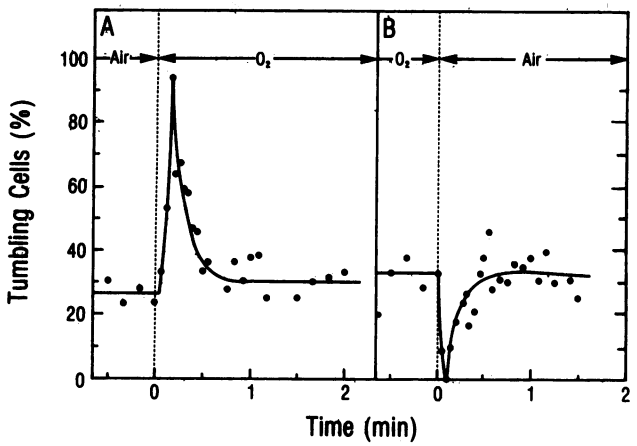

FIG. 2. Behavioral response to pure oxygen in *S. typhimurium* ST1. The bacteria were grown to the mid-log phase in Vogel-Bonner medium E containing glucose, washed, and suspended in chemotaxis buffer (see Materials and Methods). The percentages of cells that tumbled at the times indicated were determined photographically (see Materials and Methods). (A) The cell suspension was preincubated in air and then exposed to pure oxygen. (B) After adaptation to oxygen for 3 min, the cell suspension was reexposed to air.

and increased while cell-free zones developed at the interface and interior to the aerotactic band.

When air was replaced with pure oxygen, the sharply defined aerotactic band retreated over several minutes to a position 80 to 90 μm from the interface (Fig. 1B). It remained there for more than 20 min. The individual bacteria in the prominent band swam most actively, i.e., at maximum speed with occasional vigorous tumbles (compare with reference 1). The bacteria in the diffuse zone between the band and the interface swam at moderate speed, and the bacteria interior to the band were very sluggish in their movements. The aerotactic band dispersed when oxygen was replaced with nitrogen (Fig. 1B). Readmission of air resulted in reformation of a sharp band 50 μm from the interface (data not shown). *E. coli* RP437 (*che*$^+$) showed essentially the same phenomena.

The band formation and migration observed in these experiments are similar to those reported previously in *Pseudomonas viscosa* (20) and are analogous to band migration in spirilla and other microaerophilic species (3, 4, 6), but this is the first report of such responses in the facultative anaerobes *E. coli* and *S. typhimurium*. As discussed in the Introduction, these phenomena can be explained on the basis of a dual role for oxygen as both repellent and attractant. Because other explanations can be devised, direct evidence for a repellent action of high concentrations of oxygen was sought with a temporal assay.

Temporal response to pure oxygen. One drop of a culture of *S. typhimurium* ST1 was placed in a microchamber (see Materials and Methods), and the gas ventilating the chamber was changed from air to pure oxygen, corresponding to a change in the concentration of dissolved oxygen from 0.25 to 1.2 mM. The bacteria responded with increased tumbling, as they would for a repellent (Fig. 2A). The increased tumbling frequency continued for 20 to 30 s and then returned to a normal swimming pattern with occasional tumbling. When air was reintroduced after the bacteria had adapted to pure oxygen, the occasional tumbling of the cells was temporarily suppressed (Fig. 2B). This smooth-swimming response also lasted for 20 to 30 s.

In a similar experiment, 21% oxygen in nitrogen was substituted for air, and the same pattern of responses was observed. This result established that *S. typhimurium* was not responding to the loss of carbon dioxide when air was replaced with pure oxygen but was repelled by the higher concentration of oxygen. The smooth-swimming (attractant) response when pure oxygen was replaced with air is evidence that *S. typhimurium* is able to adapt to high concentrations of oxygen. Unlike the positive aerotactic response to low concentrations of oxygen (14), the response to high concentrations of oxygen was not accompanied by any significant change in swimming speed (data not shown).

Repellent action of oxygen in *Bacillus* spp. The temporal assay was used to study the repellent action of pure oxygen in *B. subtilis*, *B. cereus*, and *B. alcalophilus*, all of which show positive aerotaxis to air. *B. cereus* and *B. alcalophilus* showed a negative aerotaxis to high concentrations of oxygen, but *B. subtilis* did not (data not shown).

Repellent action of oxygen in *che* and related mutants. The *flaQ* and *flaAII.2* gene products in *S. typhimurium* are associated with the switch on the flagellar motors (31). *S. typhimurium* ST120 (*flaQ*) and ST134 (*flaAII.2*) are known to show an inverse chemotactic response (10, 19). These mutants also showed an inverse response to pure oxygen, i.e., a positive aerotaxis to pure oxygen (Table 1). The results are consistent with the idea that the information which flows from pure oxygen and other chemoeffectors converges at or before the flagellar motors.

In *tsr* (RP4790) and *tar* (RP437*tar*) mutants of *E. coli*, which have defects in the serine transducer and the aspartate transducer for chemotaxis, respectively, pure oxygen initiated a repellent response (data not shown). This result suggested that the response to pure oxygen is not transduced by the *tsr* or *tar* gene product and that adaptation to high concentrations of oxygen might be independent of methylation of the transducer protein, as is the case for attraction to low concentrations of oxygen (16, 25). Adaptation to most chemicals is dependent on the methylation of methyl-accepting transducer proteins (24). *E. coli* RP1119 has a deletion through the *cheR* and *cheB* genes, which code for the methytransferase and the methylesterase that are required for methylation-dependent adaptation, and defects in

TABLE 1. Tactic responses to pure oxygen in various chemotactic mutants

Bacterial strain	Relevant mutation	Response time (s) for indicated change[a]	
		Air to O_2[b]	O_2 to air[c]
S. typhimurium			
ST1		23 ± 3 (9/9)	17 ± 3 (9/9)
ST120	*flaQ (cheC)*	Inverse	Inverse
ST134	*flaAII.2 (cheV)*	Inverse	Inverse
E. coli			
RP437		16 ± 3 (13/16)	14 ± 2 (11/16)
RP1119	*tsr* Δ(*tar-tap-cheRB*)	16 ± 3 (9/13)	14 ± 2 (10/13)
RP2896	Δ(*tar-tap-cheRB*)	18 ± 4 (16/19)	13 ± 2 (9/19)

[a] The results are expressed as the mean ± standard deviation. Numbers in parentheses represent number of assays in which responses were visible/total number of assays.

[b] A tumbling response, except where "inverse" denotes a smooth-swimming response.

[c] A smooth-swimming response, except where "inverse" denotes a tumbling response.

the *tsr*, *tar*, and *tap* genes, which code for methyl-accepting transducer proteins. The response of methylation-deficient RP1119 to pure oxygen was similar to the response of the wild type (Table 1), establishing that adaptation to high oxygen concentrations was independent of methylation.

Recently, an inverse response to low concentrations of oxygen in an *E. coli cheB* mutant but not in a *cheB tsr* double mutant was reported (5). Since the newly synthesized Tsr protein undergoes covalent modification by the CheB protein, it was postulated that an unmodified Tsr protein interfered with the aerotactic response, even though the Tsr protein is not required for aerotaxis. The effect of a *cheB* mutation on the aerotactic response to high concentrations of oxygen was investigated with *E. coli* RP2896 [Δ(*tar-tap-cheRB*)]. Normally, a *cheB* mutant is constantly tumbling, but RP2896 has a random motility pattern, and previous studies have shown that *tar*, *tap*, and *cheR* mutations do not interfere with the inverse response of *cheB* mutants to low concentrations of oxygen (5). *E. coli* RP2896 showed a negative tactic response to high concentrations of oxygen, although the smooth response to a decrease in oxygen from 1.2 to 0.25 mM was relatively weak and not always visible (Table 1). That is, the unmodified Tsr protein did not appear to substantially interfere with the negative aerotactic response to high concentrations of oxygen. The results suggested a difference in the mechanism of aerotactic responses to low and high concentrations of oxygen.

Comparison of aerotactic responses to various concentrations of oxygen. The $K_{0.5}$ for the positive response to low concentrations of oxygen is known to be 0.7 μM for *S. typhimurium* (12) and 0.8 μM for *E. coli* (Laszlo, Ph.D. dissertation). It was postulated that the most favorable concentration of oxygen for *S. typhimurium* and *E. coli* might be in the range of 6 to 10 μM, at which the oxygen receptor (cytochrome *o*) is almost saturated. Changing the oxygen concentration from that range to a higher or lower concentration might elicit a tumbling response in the bacteria, and changing from a higher or lower concentration to the favorable concentration might suppress tumbling. To explore this possibility, we investigated the aerotactic responses to changes in oxygen concentration from 0 to 6 μM and from 6 to 250 μM. In the lower range (0 to 6 μM), *S. typhimurium* ST1 showed strong positive aerotaxis, as expected, that is, a brief tumbling response to a decrease in oxygen concentration and a brief smooth-swimming response to an increase in oxygen concentration. Surprisingly, when there was a step increase in oxygen from 6 to 250 μM, the bacteria showed a weak but detectable positive aerotactic response to oxygen. Apparently, the receptor for positive aerotaxis was not fully saturated by 6 μM oxygen, but the absence of a negative response to 250 μM oxygen suggested that the dissociation constant of the negative aerotaxis receptor for high concentrations of oxygen was much greater than 250 μM.

$K_{0.5}$ for the negative response to high concentrations of oxygen. The $K_{0.5}$ for the repellent response would be a good approximation of the dissociation constant of the receptor for negative aerotaxis. The temporal assay was used to determine the $K_{0.5}$ for *S. typhimurium* ST1 and *E. coli* RP437. The oxygen concentration of the ventilating gas in the microchamber was changed from 15% oxygen (equivalent to 0.18 mM dissolved oxygen) to a selected higher oxygen concentration. Since the $K_{0.5}$ for positive aerotaxis is approximately 0.7 μM, 0.18 mM oxygen in the medium essentially saturates cytochrome *o*, the receptor for the attractant response to oxygen (12), and that response system would not contribute to or interfere with the response to much higher concentrations of oxygen. The dose-response plots for negative response of cells preadapted to 0.18 mM oxygen showed significant changes in response times when the oxygen concentrations to which the cells were exposed were varied between 0.42 and 1.2 mM (pure oxygen). This result suggested that the receptor was not saturated by even 1.2 mM oxygen. Double-reciprocal plots of the dose-response data gave a value of 1.0 mM for the $K_{0.5}$ for negative aerotaxis in *S. typhimurium* ST1 and *E. coli* RP437 (Fig. 3). Dose-response relationships for the smooth-swimming response to a decrease in oxygen concentration from higher concentrations to 0.18 mM were also studied in both *S. typhimurium* and *E. coli*. The $K_{0.5}$ for negative aerotaxis obtained from double-reciprocal plots of data for both species was 1.0 mM, the same as the value obtained with increasing oxygen concentrations.

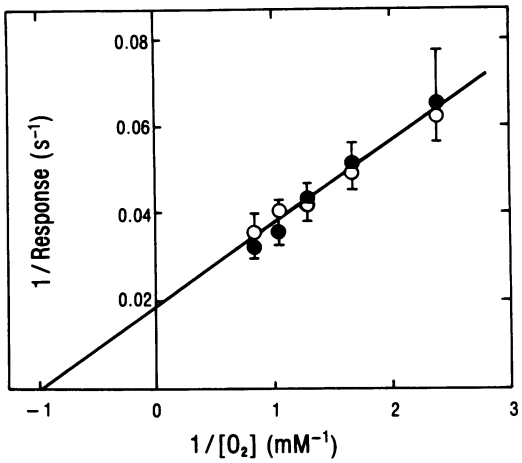

FIG. 3. Double-reciprocal plot of the dependence of the negative tactic response in *S. typhimurium* ST1 and *E. coli* RP437 on the concentration of oxygen. The bacteria were prepared as described in the legend to Fig. 2. Cells were preadapted to humidified 15% oxygen in nitrogen (0.18 mM dissolved oxygen at a barometric pressure of 730 mm Hg and 23.5°C) and then exposed to the indicated concentrations of oxygen. Symbols: ○, *S. typhimurium* ST1; ●, *E. coli* RP437.

DISCUSSION

The results show for the first time that *E. coli* and *S. typhimurium* collect at a certain distance from the source of oxygen. This result had been previously observed in spirilla and other unclassified species (3, 6) and in *P. viscosa* (2). In proposing an explanation for this phenomenon, Jennings (9) wrote in 1906: " . . . Thus any given species is adapted to a certain concentration of oxygen, which may be called its optimum. Passage from the optimum in either direction—toward more oxygen or less oxygen—causes the reversal of movement, so that the bacteria remain in the optimum." The findings in this study are consistent with bacterial migration to an optimal concentration.

Previous investigations of *E. coli* and *Salmonella* spp. failed to demonstrate a repellent action of oxygen in these species (2, 14). Microscopic observations, rather than the macroscopic observations used by Baracchini and Sherris (2), and the development of a temporal assay were successful in revealing oxygen as a repellent in these species in addition to being an attractant. This finding is important

because sensory transduction in both chemotaxis and positive aerotaxis is best understood in *E. coli* and *S. typhimurium*, in which the genetics of sensory transduction are well defined. It will now be possible to study the mechanism of repulsion by high concentrations of oxygen in the same species.

The responses of *E. coli* and *S. typhimurium* when the gas with which the medium was equilibrated was changed from air to pure oxygen were similar to the responses to other repellents. The bacteria tumbled continuously for approximately 20 s and then adapted. When oxygen was replaced with air, the cells suppressed tumbling for 20 s. The similar duration of the responses to increases and decreases in oxygen concentrations was unexpected. Usually, repellent responses are much shorter than are attractant responses (27).

Cytochrome *o*, the oxygen receptor for positive aerotaxis, is clearly not the oxygen receptor for negative aerotaxis. The $K_{0.5}$ for negative aerotaxis was 1 mM (Fig. 3), whereas the $K_{0.5}$ for positive aerotaxis was approximately 0.7 μM (12). It follows that negative aerotaxis could not be mediated by changes in electron flux through the respiratory chain. Under the conditions used in the temporal assay for negative aerotaxis, the initial concentration of oxygen fully saturated the electron transport system. This was confirmed by direct measurement of oxygen uptake in *S. typhimurium* exposed to air and to oxygen (K. Kamiya and J. Shioi, unpublished data). The identity of the receptor for negative aerotaxis has not been established. It is important to note that it might not necessarily be a receptor for oxygen per se. The receptor might detect reactive by-products of high oxygen concentrations such as the superoxide anion, the hydroxyl radical, or hydrogen peroxide. This would directly relate the behavioral response to the concentration of reactants that endanger the cell.

Positive aerotaxis is mediated by changes in respiration and the proton motive force rather than by a direct interaction of oxygen with the aerotaxis transducer protein (25). However, it is highly improbable that the proton motive force changes significantly in negative aerotaxis. The observed $K_{0.5}$ of 1 mM for negative aerotaxis in *E. coli* and *S. typhimurium* indicates that only hyperbaric oxygen concentrations repel these facultative aerobes. This probably explains why negative aerotaxis has not been reported previously in these species. Microaerophilic species, such as spirilla, are evidently repelled by much lower concentrations of oxygen (3, 30). Like previous investigators, we did not observe any negative aerotaxis in the obligate aerobe *B. subtilis*. Anaerobiosis might be a greater threat to *B. subtilis* than is hyperbaric oxygen.

The observation of normal, negative aerotaxis in *tar*, *tsr*, and *cheRB* mutants established that the mechanism of adaptation is independent of transducer methylation in negative aerotaxis. However, the methylation-independent pathways of negative and positive aerotaxis must converge with the methylation-dependent chemotactic pathway at or before the switch on the flagellar motors. The point of convergence of the pathways is currently being investigated. It is interesting that both aerotaxis pathways involve methylation-independent adaptation, but only positive aerotaxis is reversed by the amidated Tsr protein in a *cheB* mutant (5).

Although it has been known for a long time that many species of motile bacteria move to an optimal concentration of oxygen, it has not been clear whether this involved a single sensory system. This investigation has established, at least for *E. coli* and *S. typhimurium*, that there are two sensory systems controlling the behavioral response to oxygen: one system responding to low concentrations of oxygen as to an attractant and one system responding to high concentrations of oxygen as to a repellent. Thus, oxygen is unusual among sensory stimuli in that it serves as both an attractant and a repellent for the same organism.

ACKNOWLEDGMENTS

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