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Role of Proton Motive Force in Phototactic and Aerotactic Responses of *Rhodopseudomonas sphaeroides*

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Rhodopseudomonas sphaeroides **grown under nonrigorous anaerobic conditions in the light developed components of a branched respiratory electron transfer chain, and a photosynthetic electron transfer chain. Both respiratory pathways were sensitive to rotenone and high concentrations of cyanide, but oxygen uptake was only partially inhibited by the addition of low concentrations of cyanide or antimycin A. When incubated anaerobically in the dark, *R. sphaeroides* responded positively to an oxygen gradient in the absence of rotenone. In the presence of rotenone, aerotaxis only occurred when the antimycin A-sensitive branch of the pathway was functioning, although both branches still reduced oxygen. Although there was electron movement along the respiratory chain, aerotaxis only occurred in response to a change in proton motive force. When incubated anaerobically in the light, the movement of *R. sphaeroides* up a light gradient depended on photosynthetic electron transport. When incubated aerobically, high-intensity actinic illumination inhibited oxygen uptake and aerotaxis. In a low-intensity light gradient the phototactic response was inhibited by oxygen. These results are discussed in relation to the interaction of the electron transfer chains and their roles in controlling tactic responses in *R. sphaeroides*.**

The photosynthetic purple nonsulphur bacterium *Rhodopseudomonas sphaeroides* can grow either in illuminated anaerobic environments by using photosynthetic electron transport to generate a proton motive force (pmf) or heterotrophically in dark aerobic environments by using respiratory electron transport. When grown in anaerobic conditions in the light, both *R. sphaeroides* and the closely related *Rhodopseudomonas capsulata* have been shown to develop components of both photosynthetic electron transport and an antimycin A-insensitive respiratory chain, the components of which apparently interact (4, 7, 11, 18, 20). When grown in the presence of oxygen, an antimycin A-sensitive respiratory pathway also was synthesized. In the case of *R. sphaeroides* one branch of the respiratory chain apparently terminates in an aa_3-type cytochrome (11, 18).

Movement towards either oxygen (aerotaxis) or light (phototaxis) by bacteria consists of two components. As the speed of swimming of flagellate bacteria is dependent on the pmf across the cytoplasmic membrane, the bacteria swim faster as the level of oxygen or light increases, until electron transport reaches the maximum rate of turnover (10). Respiratory bacteria therefore will swim faster when swimming into high-oxygen environments, and their velocity decreases as the pmf is reduced when moving down an oxygen gradient. The same applies for light in the case of photosynthetic bacteria. This velocity dependence on the concentration of the tactic effector results in an enhanced overall tactic response. This kinetic component of taxis is not a tactic response in the true sense. When responding to oxygen or light, bacteria also show a true tactic response, analogous to the chemotactic response, in controlling the frequency of tumbling, increasing the frequency when moving down the gradient and decreasing the frequency when moving up the gradient (13, 19). As has been done by other workers, in this paper we use the words phototaxis and aerotaxis to include both the kinetic and tactic components of the movement, that is the overall migrational response.

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Photosynthetically grown photosynthetic bacteria have been shown to be positively phototactic under anaerobic conditions. Phototaxis only occurred when the reaction center was functional, suggesting the involvement of electron transport in this process (1).

Similarly, *Salmonella typhimurium* has been shown to move towards oxygen only when the respiratory electron transport chain is functioning (14). These results suggest that both phototaxis and aerotaxis require either active electron transport or the resultant change in pmf to respond to light or oxygen. As *R. sphaeroides* in some circumstances develops both photosynthetic and respiratory electron transport components (18) but is only positively tactic to light-anaerobic or dark-aerobic environments, we have examined the interaction of these pathways, exploiting unique features of *R. sphaeroides* to investigate the role of electron transport in taxis. Although there is some evidence that active electron transport, rather than the binding of the terminal electron acceptor, causes the tactic signal, it has not been possible to distinguish between electron transport itself and the consequent redox state of intermediates, and the change in pmf as the primary tactic signal (19). *R. sphaeroides* possesses endogenous membrane-bound, potential-sensitive carotenoids which can be used to investigate changes in $\Delta\psi$ (membrane potential) in different conditions (8). Therefore, we were able to identify which sections of the various electron transport chains were coupled to changes in $\Delta\psi$ and thus compare the role of electron transport per se and changes in $\Delta\psi$ in phototactic and aerotactic signalling. We also were able to investigate the interaction of the photosynthetic and respiratory pathways and the effect on the overall tactic response.

We present results that show that *R. sphaeroides* grown in the light responded to either light or oxygen, the response depending on the pmf generated by electron transport, not on electron transport directly. We also have shown that the two pathways interact competitively, aerotaxis being inhibited by light and phototaxis being reduced by oxygen.

MATERIALS AND METHODS

Growth media and conditions. *R. sphaeroides* WS8 (wild-type strain, a gift from W. Sistrom) was grown as previously described (6) in 100-ml bottles at 25°C under continuous low illumination. Bacteria were harvested in early-exponential phase when maximally motile and suspended in 10 mM HEPES (*N*-2-hydroxyethylpiperazine-*N'*-2-ethanesulfonic acid) buffer (pH 7.0). The buffer was sparged for at least 1 h with either oxygen-free nitrogen or air before resuspending the bacteria, and the sparging was continued after resuspension for 20 min before beginning the experiment. Cell number, bacteriochlorophyll concentration, and optical density at 700 nm were measured in all experiments to try to ensure that the bacteria were comparable on different days. All experiments were carried out with 10^9 bacteria ml^{-1}.

All substrates or inhibitors were made as concentrated solutions in either buffer or ethanol and corrected for pH before use. Controls were solvent without substrate or inhibitor.

Measurement of oxygen uptake. The rate of oxygen uptake of a bacterial suspension was measured with a Clarke oxygen electrode. Measurements and additions could be made in the dark or under controlled, cooled illumination and under either a stream of nitrogen or air. As *R. sphaeroides* is a catalase producer, oxygen was added as small volumes of 1-volume hydrogen peroxide, to produce a 90% air-saturated O_2 concentration within 5 s of H_2O_2 addition. Controls showed a linear uptake of O_2 until less than 28 nmol. All experimental measurements were taken during this period.

Measurement of the membrane potential. At pH 7.0 the major component of the pmf has been shown to be the electrical potential. In *R. sphaeroides* this can be easily and rapidly measured by using the carotenoid band shift (5). The carotenoids are membrane-bound light-harvesting pigments which respond to a change in electrical potential across the cytoplasmic membrane by a shift in absorbance. The carotenoid band shift was measured on an Aminco dual-wavelength spectrophotometer by using the wavelength pair 510-523 nm, with actinic illumination by a variable light source through a 871-nm interference filter at a 90-degree angle to the stirred sample. Oxygenation was as in the oxygen electrode by the addition of hydrogen peroxide to the stirred cuvette. A stream of oxygen-free nitrogen was continually passed over the sample.

Measurement of phototaxis and aerotaxis. Phototaxis and aerotaxis were measured by using the taxis wells previously described (3). *R. sphaeroides* in either oxygenated or oxygen-free buffer (0.4 ml) were placed in the bottom chamber of taxis wells and covered with a 13-mm, 8.0-μm pore, polycarbonate unipore membrane (Nucleopore Corp.). The top well was filled with either oxygenated or oxygen-free buffer and sealed with Nescofilm (Nippon Shoji Kaisha Ltd.). The well was inverted to prevent any bubbles in the lower chamber from blocking the membrane. Wells for dark measurement were wrapped in aluminum foil before placing over light sources of variable intensity. The light intensities were measured with a solarimeter. The light intensity on both sides of the well was measured, and the carotenoid band shift was measured on the dual-wavelength spectrophotometer at the same light intensity. This gave a measure of the light gradient across the well and the intensity relative to that required for photosynthetic saturation. After 2 h of incubation, 0.1-ml samples were removed from the upper chamber, and the number of bacteria passing from the lower to the upper chamber was measured on a Coulter Counter (Coulter Electronics, Inc.). The number passing into the upper chamber was calculated as the percentage of bacteria added to the bottom of the well and compared with the number passing into control chambers. To take into account the different kinetic component in different conditions there were always light anaerobic, dark anaerobic, and dark aerobic controls.

Bacterial motility was checked microscopically at the beginning and end of each experiment. In all experiments described, motility at the end of the experiment was similar to that of control bacteria. Under conditions in which electron transport was totally inhibited, the pmf was maintained, probably as a result of ATPase activity.

RESULTS

Respiratory electron transport. Figure 1 shows the rate of oxygen uptake of a suspension of *R. sphaeroides* after the addition of a pulse of hydrogen peroxide. This oxygen uptake depended on endogenous electron donors. Uptake was inhibited by the addition of rotenone, indicating that the endogenous substrate donated electrons through NADH, but this inhibition could be overcome by the addition of sodium succinate. The addition of antimycin A (an inhibitor of the cytochrome bc_1 complex) only partially inhibited oxygen uptake with the endogenous donor or succinate. Oxygen uptake in the presence of both rotenone and antimycin A could be reinitiated by the addition of either ascorbate or succinate. If reinitiated by ascorbate, 0.1 mM cyanide inhibited uptake, but the same concentration of cyanide did not stop oxygen uptake initiated by succinate addition; 5 mM cyanide was required to stop oxygen uptake with either succinate or the endogenous donor. These results suggest that the electron transport chain is branched after the rotenone inhibitor site and that only one branch is antimycin A sensitive and also more sensitive to cyanide. One pathway therefore probably involved the cytochrome bc_1 complex. Since during aerobic dark growth *R. sphaeroides* contains an aa_3-type cytochrome, these results suggest that in early exponential growth in low light cells also may contain an aa_3-type cyanide-sensitive terminal oxidase. The other pathway appears to contain an alternative less-sensitive oxidase. The rather high cyanide levels required to completely inhibit oxygen uptake probably reflected the charge gradient in whole bacteria which resulted in a permeability barrier to the uptake of anions such as cyanide.

The ability of electron transport via these two pathways to generate an electrochemical proton gradient was examined by using the carotenoid band shift. When incubated anaerobically in the dark the potential fell to a low level (Fig. 2a and b), and the size of the residual potential being measured at the end of the experiment by the addition of an uncoupler (10 μM carbonyl cyanide *m*-chlorophenylhydrazone). The size of the anaerobic dark potential depended on the length of anaerobic dark incubation and was probably caused by either low-level respiration or ATPase activity. The addition of O_2 resulted in an increase in $\Delta\psi$ as measured by the band shift, which was lost on the addition of rotenone. This membrane potential could be regained by the addition of succinate alone but not by the addition of succinate in the presence of both rotenone and antimycin A. The addition of ascorbate in the presence of antimycin A resulted in the formation of $\Delta\psi$. Electron transport along the antimycin A-sensitive branch of the respiratory chain to the cyanide-

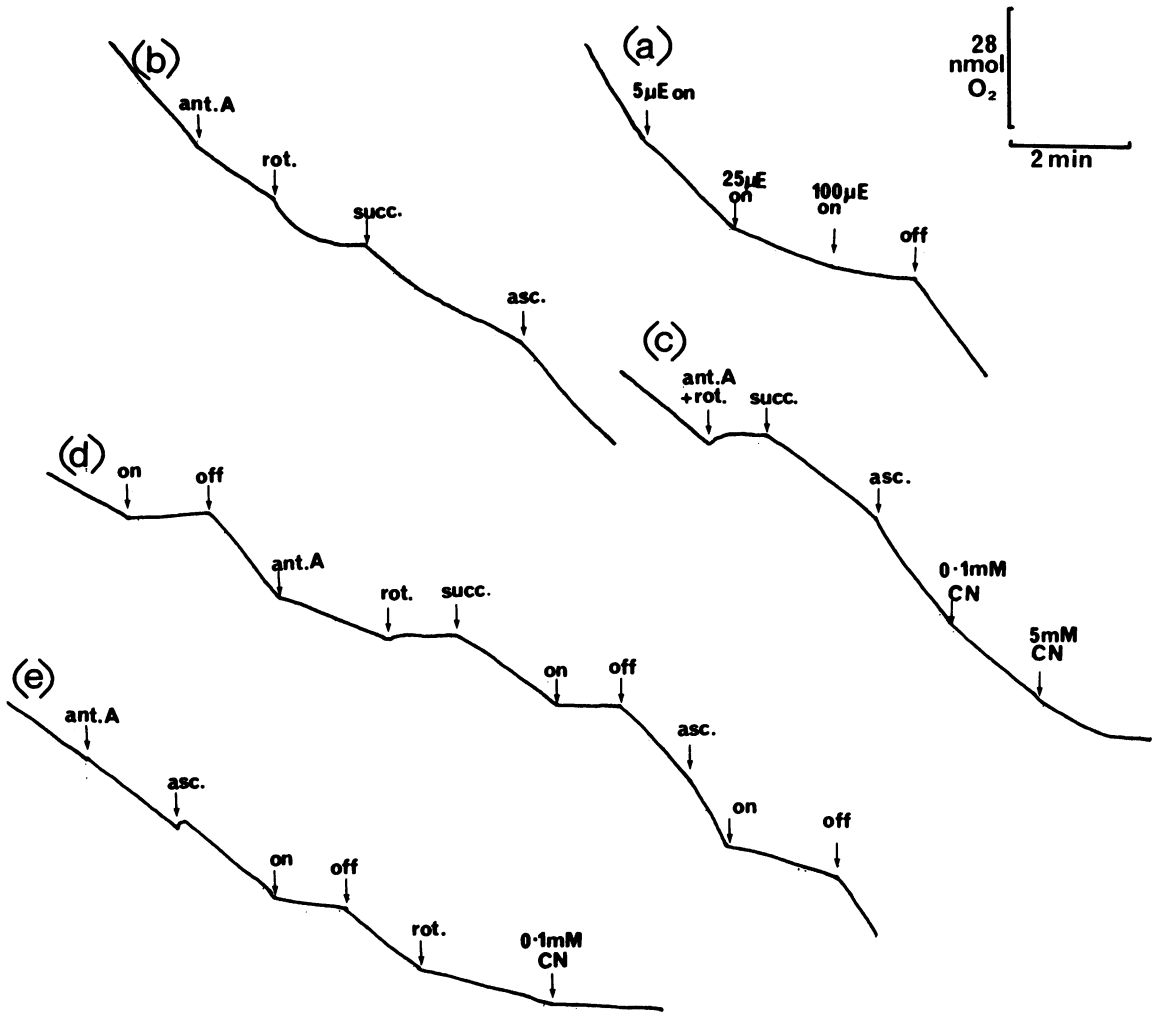

FIG. 1. Rates of respiration of intact cells of *R. sphaeroides* in the presence of inhibitors and electron donors. The bacteria were resuspended as described in the text and placed in an oxygen electrode reaction vessel. Respiration was initiated by the addition of 5 μl of 1 volume of H_2O_2. Under control conditions the respiration rate remained linear during the period of recording. A fresh suspension of bacteria was used for each recording. ant.A, 5 μM antimycin A; rot., 10 μM rotenone; succ., 1 mM sodium succinate; asc., 1 mM sodium ascorbate; CN, sodium cyanide. Unless otherwise indicated, on denotes saturating illumination. (a) Increasing inhibition of respiration with increasing illumination.

sensitive terminal oxidase was therefore coupled to an increase in pmf. There also was a reduction in $\Delta\psi$ when antimycin A was added to an endogenously respiring sample. These results show that electron transport after the site of rotenone inhibition via the antimycin A-insensitive branch of the respiratory chain was not coupled to an increase in $\Delta\psi$.

Photosynthetic electron transport. Figure 1 shows that, as previously reported (4), photosynthetic electron transport at saturating light intensities completely inhibited oxygen uptake. However, this could be partially overcome by the addition of ascorbate in the presence of antimycin A. Illumination by low light intensities (below 25 microeinsteins) only partially inhibited oxygen uptake.

The $\Delta\psi$ generated by saturating illumination of an oxygenated sample showed a 15% increase over the $\Delta\psi$ generated by the maximum rate of respiration alone (Fig. 2a). A slight fall in $\Delta\psi$ and gradual increase to the previous respiratory maximum could be seen when the light was switched off. The addition of antimycin A caused a fall in the photosynthetic $\Delta\psi$.

Measurement of taxis. (i) Aerotaxis. To investigate the role of the two branches of the respiratory chain in aerotaxis, the movement of the bacteria in response to oxygen gradients was measured in the presence and absence of the inhibitors used in the previous experiments.

Table 1 shows that when incubated in the dark there was a positive response to an oxygen gradient: an increased percentage of the bacteria added to the bottom well moving from an anaerobic to an aerobic buffer when compared with the number passing through the membrane in the absence of a major gradient.

Aerotaxis dependent on the endogenous donor was inhibited by rotenone but only to a small extent by antimycin A alone. In the presence of rotenone, succinate-dependent aerotaxis was inhibited by antimycin A. In the presence of rotenone and antimycin A, a normal aerotactic response was restored by the addition of ascorbate.

These experiments also were carried out with succinate and ascorbate on both sides of the membrane to ensure that the aerotactic response was not a negative response to weak acids. This proved not to be the case (Table 1).

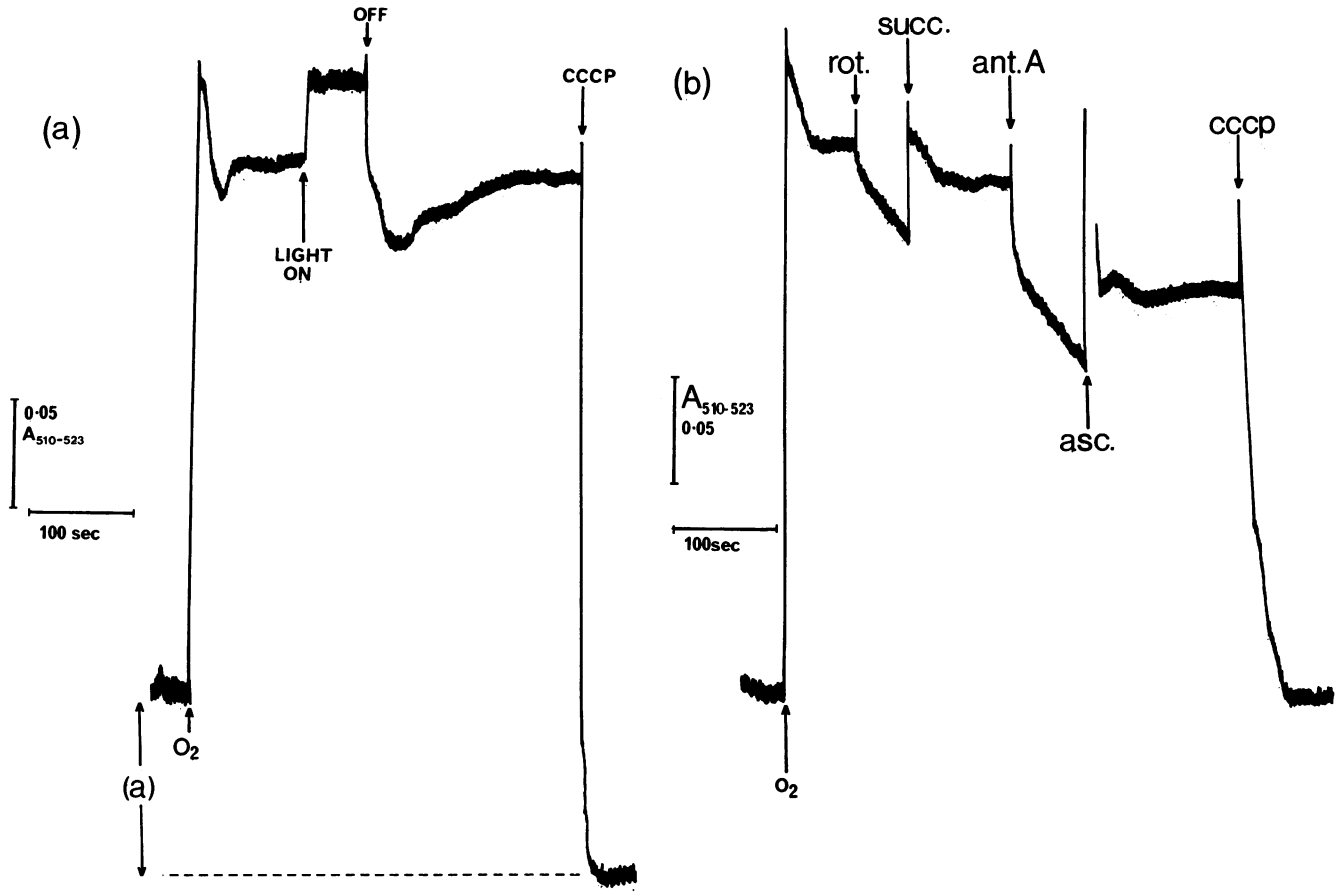

FIG. 2. Change in electrical potential of *R. sphaeroides* with increased respiration. The bacteria were incubated in the dark under a stream of nitrogen in the cuvette of a dual-wavelength spectrophotometer as described in the text. Respiration was initiated by the addition of 5 μl of H_2O_2. The change in $\Delta\psi$ was measured by the absorbance change ($A_{510-523}$) as arbitrary absorbance units. Carbonyl cyanide *m*-chlorophenylhydrazone (10^{-5} M) was added at the end of the experiment to measure the size of the base line; this varied according to the length of incubation and the growth state of the cells. (a) Increase in $\Delta\psi$ caused by photosynthetic electron transport with saturating actinic illumination; (b) change in $\Delta\psi$ with the addition of different electron transport inhibitors and electron donors. Conditions are as described in the legend to Fig. 1.

The general aerotactic response was inhibited by saturating illumination (Table 2).

(ii) Phototaxis. The phototactic response was very strong, saturating at ~5 microeinsteins when *R. sphaeroides* incubated in anaerobic buffer was moving into an upper illluminated chamber of anaerobic buffer (Table 2). The response was reduced by the aeration of the upper chamber or suspension of the bacteria in oxygenated buffer. In gradients of low light intensity oxygen therefore inhibited phototaxis, as at high light intensities photosynthesis inhibited aerotaxis. The phototactic response also could be inhibited by the addition of antimycin A. Photosynthetic electron transport could be shown to be inhibited by antimycin A by the loss of

TABLE 1. Aerotactic response of *R. sphaeroides*[a]

Bacterial suspension conditions				% of bacteria ± SD	
Rotenone	Antimycin A	Succinate	Ascorbate	Anaerobic buffer	Aerobic buffer
−	−	−	−	2.2 ± 0.9	6.1 ± 2
+	−	−	−	1.8 ± 0.6	3.0 ± 0.6
+	+	−	−	1.9 ± 0.6	2.3 ± 0.3
+	−	+	−	1.9 ± 0.7	5.9 ± 1.0
+	+	+	−	1.8 ± 0.5	2.3 ± 0.1
+	+	+	+	1.9 ± 0.5	6.0 ± 0.7
−	+	−	−	1.5 ± 0.5	4.8 ± 0.5
−	+	−	+	2.2 ± 0.9	8.2 ± 0.1

[a] The bacteria were incubated in the dark for 2 h in the presence of different inhibitors and substrates, as described in the text. Results are calculated as the percentage of bacteria (± standard deviation) added to the bottom well in anaerobic buffer (0.2 ml of 10^9 ml^{-1}) passing into the upper chamber which contained either oxygenated or oxygen-free buffer. The concentration of inhibitors and substrates was as described in the legend to Fig. 1.

TABLE 2. Inhibition of the tactic response by the presence of both oxygen and light

Buffer conditions		% of difference at following light intensity (microeinsteins)[a]			
Suspending	Attracting	50	5	0.5	0.1
Anaerobic[b]	Anaerobic	+18	+50	+10	−4
Anaerobic[c]	Aerobic	−1	−16	−17	−9

[a] The results are shown as the percentage of difference in bacteria passing into the upper well of the chemotactic vessel between those incubated in the dark and those in different intensities of illumination. At 50 microeinsteins, photosynthetic electron transport was saturated, but at 5 microeinsteins, there was a detectable light gradient.

[b] Phototactic response.

[c] Inhibition of the aerotactic-phototactic response by the same light intensities.

membrane potential in illuminated bacteria; the inhibition of phototaxis therefore was probably caused by the loss of membrane potential (unpublished data).

DISCUSSION

We have confirmed that when grown anaerobically in the light *R. sphaeroides* developed not only the components of photosynthetic electron transport but also those of respiratory electron transport. By using different combinations of inhibitors with known sites of action and different donor substrates we developed a model for electron transfer pathways in nonrigorously anaerobically light-grown *R. sphaeroides* (Fig. 3). Previous work has suggested that cytochrome aa_3 is formed by *R. sphaeroides* under conditions of chemotrophic growth (18). Figure 1 shows that at least during the early—exponential phase of phototrophic growth under nonrigorous conditions *R. sphaeroides* developed two terminal oxidases. The addition of antimycin A, an inhibitor of electron transport through cytochrome bc_1, only partially inhibited oxygen uptake (Fig. 1b), although control experiments on photosynthetic electron transport showed that it was fully inhibitory in whole cells. The addition of rotenone, an inhibitor of electron transport from NADH dehydrogenase to the quinone, did completely inhibit the residual oxygen uptake in the presence of antimycin A, showing an oxygen pathway before as well as after the antimycin A-sensitive site. Figure 1e shows that oxygen uptake in the presence of ascorbate and with electron transport inhibited by both rotenone and antimycin A could be inhibited by the addition of a low concentration of sodium cyanide, but 50 times that concentration was needed to inhibit oxygen uptake when succinate was present as well as ascorbate (Fig. 1c). The two oxidases therefore are probably not the same cytochrome at the end of different electron transfer branches. As the aa_3-type cytochrome is sensitive to low concentrations of sodium cyanide and also may be responsible for at least some proton pumping, we looked to determine whether there may be some coupling shown by this terminal oxidase. A change in $\Delta\psi$ is easily measured in phototrophically grown *R. sphaeroides* by the change in carotenoid absorption. Figure 2b shows the response of early exponential cells to electron transport inhibitors after $\Delta\psi$ had been induced in dark incubated cells by the addition of a pulse of H_2O_2 to initiate respiration. Rotenone caused a fall in $\Delta\psi$ which could be overcome by the addition of succinate. In the absence of antimycin A, succinate could donate electrons to either branch of the respiratory chain; however, the addition of antimycin A meant that oxygen reduction could only occur via the antimycin A-insensitive branch (Fig. 1b, c, and d). The $\Delta\psi$ fell although oxygen uptake continued in these conditions, the transport of electrons from succinate to the antimycin A-insensitive site did not result therefore in an increase in $\Delta\psi$. However, the subsequent addition of ascorbate to the sample did result in an increase in $\Delta\psi$, suggesting that electron transfer from ascorbate to the cyanide-sensitive site was in some way coupled.

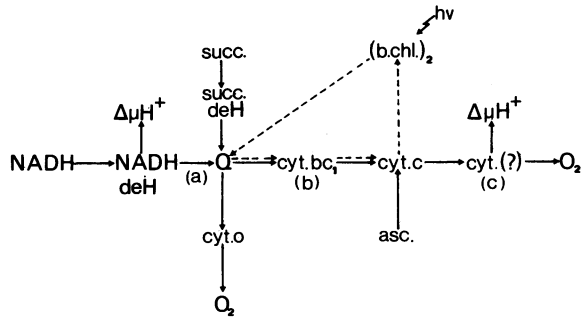

FIG. 3. Possible scheme for electron transport in *R. sphaeroides*. Sites of rotenone inhibition (a), antimycin A inhibition (b), and low-concentration cyanide inhibition. Symbols: →, respiratory electron transport; – – –, photosynthetic electron transport.

The increase in $\Delta\psi$ on ascorbate addition to respiring phototrophically grown cells was only seen in early-exponential cells. The increase was not observed either in respiring late-exponential cells or when ascorbate was added to nonrespiring bacteria in the dark. It was impossible to measure the effect of the loss of the ascorbate-induced $\Delta\psi$ potential in older bacteria on their aerotactic response, as motility also was reduced with increasing age.

Although the two terminal cytochromes were not characterized, the ability of *R. sphaeroides* to bind oxygen at two different sites, each of which could be independently inhibited and only one of which when stimulated resulted in a change in $\Delta\psi$, made it possible to examine the roles of electron transport and pmf in aerotaxis and phototaxis.

Motility is dependent on the pmf (12, 15) which has made it difficult to distinguish between the roles of: electron transport, oxygen binding to the terminal cytochrome, the change in pmf in aerotactic and phototactic signalling. Using the combination of inhibitors and substrates described here, we devised experiments in which oxygen binding and reduction by the terminal oxidase could continue in the presence or absence of a change in pmf. Aerotaxis only occurred in circumstances in which electron transport along the respiratory chain was coupled to an increase in $\Delta\psi$ Phototaxis also depended on an active electron transport chain.

Bacteria incubated in oxygen-free buffer moved into oxygen-free buffer in response to a light gradient. The maximum phototactic response occurred when the light intensity at the membrane was about 5 microeinsteins, although photosynthetic electron transport did not saturate until about 10 microeinsteins. The phototactic response therefore was greater with a reduced base-line pmf than at high light intensities when the background pmf was close to the maximum. As the pmf increased with increasing light the kinetic component of the phototactic response also would be expected to increase. If the number of bacteria passing through the membrane under anaerobic conditions in saturating light was compared with the number moving across the membrane in the dark highly aerated conditions, there were always more bacteria moving through the membrane under illuminated conditions. As there was no detectable gradient under either of these conditions the difference in the numbers was probably a measure of the difference in the maximum generated pmf by each electron transport chain, and thus the difference in maximum swimming velocity in each environment.

The respiratory and photosynthetic electron transport chains interacted, and this was reflected in the tactic response to mixed stimuli. Light intensities that have been shown to inhibit respiratory electron transport also caused the inhibition of the aerotactic response. Under these conditions the light intensity was above that detectable as a light gradient by the bacteria; the bacteria therefore showed increased motility but no gradient response.

At low light intensities, equivalent to those found in natural bodies of water, the interaction of the phototactic

and aerotactic responses was more interesting. In the presence of both an aerotactic and a phototactic gradient there was no tactic response. At low light intensities the rate of photosynthetic electron transport was similar to that of respiratory electron transport; the carotenoid band-shift was below maximum, and oxygen uptake was not completely inhibited by illuminating a respiring culture. However, the size of the $\Delta\psi$ generated by reduced photosynthetic electron transfer remained higher than that generated by a reduced rate of respiration. The bacteria moving up the phototactic light gradient would be confronted by an oxygen gradient, and some electrons would pass to the high-affinity terminal oxidase. The transfer of electrons away from the photosynthetic electron transfer pathway to the terminal oxidase would result in an overall reduction in pmf. This reduction in pmf would result in a negative tactic response.

The evidence presented here supports previous work on taxis in *Escherichia coli* and *S. typhimurium* terminal acceptors of electron transport, showing that active electron transport is involved, rather than the binding of the acceptor to the terminal cytochrome (14). It is not electron transport itself, however, that causes the tactic signal but instead it is the consequent increase in pmf. The primary signal involved in the chemotactic response is still unknown, but there is some evidence that there is a change in pmf on binding of the chemoeffector to the receptor in some bacterial species (2, 8, 9), although the evidence is conflicting and the time course of the chemotactic response suggests an additional requirement (16, 17). We currently are investigating the interaction of chemotaxis and the electron transport taxes to identify the mechanism of interaction.

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