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STUDY OF ELECTROGENIC ELECTRON TRANSFER STEPS IN CHROMATOPHORE MEMBRANE OF *CHROMATIUM VINOSUM* BY THE RESPONSE OF MEROCYANIN DYE

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Summary

1. Electrogenic steps in photosynthetic cyclic electron transport in chromatophore membrane of *Chromatium vinosum* were studied by measuring absorption changes of added merocyanin dye and of intrinsic carotenoid.

2. The change in dye absorbance was linear with the membrane potential change induced either by light excitation or by application of diffusion potential by adding valinomycin in the presence of K^+ concentration gradient.

3. It was estimated that chromatophore membrane became 40—60 mV and 110—170 mV inside positive upon single and multiple excitations with single-turnover flashes, respectively, from the responses of the dye and the carotenoid.

4. Electron transfers between cytochrome *c*-555 or *c*-552 and reaction center bacteriochlorophyll dimer ($BChl_2$) and between $BChl_2$ and the primary electron acceptor were concluded to be electrogenic from the redox titration of the dye response.

5. No dye response which corresponded to the change of redox level of cytochrome *b* was observed in the titration curve. Addition of antimycin A slightly decreased the dye response.

6. The dye response was decreased under phosphorylating conditions.

7. From the results obtained localization of the electron transfer components in chromatophore membrane is discussed.

Abbreviation: BChl, bacteriochlorophyll.

Introduction

The localization of electron transport components in the chromatophore membrane of photosynthetic bacteria has been studied towards understanding the mechanisms of coupling of electron transport and phosphorylation [1—3]. Extensive studies on the electrogenic steps in cyclic electron transport have been made, especially in chromatophore membranes of *Rhodopseudomonas sphaeroides*, in which large carotenoid band shift can be used as a measure of the intramembrane electrical field change [2—5]. In these membranes existence of three electrogenic electron transfer steps has been indicated from the kinetic analysis of the carotenoid band shift [5] as phases I, II and III, corresponding to the electron movements between the reaction-center bacteriochlorophyll dimer ($BChl_2$) to the electron acceptor (ubiquinone-iron complex, QFe), between cytochrome c_2 and $BChl_2$, and through cytochrome *b*. Localization of the electron transport components in the chromatophore membrane has been estimated by comparing the extents of membrane potential changes represented by these three phases [2—5]. On the other hand, in a sulfur bacterium, *Chromatium vinosum*, electrogenic electron transfer steps have not been clarified in detail. Different localizations of $BChl_2$ (very close to the outer surface) and of membrane bound cytochromes in the chromatophore membranes of this organism from those of non-sulfur bacteria can be estimated if we take small carotenoid bandshift around 500 nm or bandshift of bacteriochlorophyll around 800 nm studied by Case and Parson [6] to be indicators of membrane potential change [3]. Study of the heme-heme interaction by EPR measurements also suggested such situation [7]. As for the localization of cytochrome *c*-555 in the *Chromatium* membrane it was suggested that the cytochrome was situated on the inner surface of the chromatophore membrane from the response of its redox state to the membrane potential change [8]. Knaff and Carr [9] showed that the small carotenoid shift seen in *Chromatium* chromatophores quantitatively responded to the membrane potential change as in non-sulfur photosynthetic bacteria, and showed the electrogenic nature of the pyrophosphatase in the chromatophore membrane. However, our knowledge of the electron transport system and intramembrane localization of the electron transfer components in this organism is less than that of such components in non-sulfur bacteria [2, 3].

In the present study, quantitative analysis of the electrogenic steps in the cyclic electron transfer in the *C. vinosum* membranes was attempted by the measurements of the membrane potential change by the intrinsic carotenoid shift and the absorption change of an externally added merocyanin dye which is known to be a sensitive indicator of membrane potential change in various biological membranes [10, 11]. The dye used has a localized negative charge on one end and is not expected to affect the decay of membrane potential because of its low permeability through the membrane, which is a serious problem in some potential-indicating dyes such as oxonol [12].

Materials and Methods

Chromatium vinosum was grown photoautotrophically in the medium of Bose. Chromatophores were prepared as described previously [8] by disrupting cells in a French Pressure Cell in a medium containing 2 mM $MgCl_2$, 50 mM KCl and 50 mM Tris-HCl buffer (pH 7.8). Chromatophores obtained after centrifugation were dispersed in the above medium or in distilled water and stocked.

Bacteriochlorophyll concentration was determined in acetone/methanol (7:2, v/v) extracts using the absorption coefficient of 75 $mM^{-1} \cdot cm^{-1}$ at 772 nm [13].

Measurement of flash-induced absorption changes and the redox titration of the absorption change of merocyanin dye were performed as previously described [8] with a split-beam spectrophotometer (Union Giken) equipped with a microcomputer. A single-turnover excitation flash (20 μs duration) was obtained from a xenon flash lamp (Sugawara, s-3A) covered with a Wratten 88A filter and a red cut-off filter (Toshiba R-70). Redox potential of the medium was monitored by a Pt-Ag/AgCl electrode (Toa, Ps115C). Usually 4—30 signals obtained by repeated excitations at less than 0.1 Hz were averaged to increase the signal-to-noise ratio.

For the measurements of the diffusion-potential-induced absorption changes of merocyanin dye or carotenoid, a dual-wavelength spectrophotometer (Hitachi 356) was used. 5 μl ethanol solution of valinomycin was added by an air pippete to the reaction mixture, which was vigorously stirred by a magnetic stirrer. The time required to mix the solution fully was about 0.2 s.

Measurements were performed at room temperature.

Merocyanin dye (merocyanin 540), 5-[(3-γ-sulfopropyl-2(3H)-benzoxazolidene)-2-butenylidene]-1,3-dibutyl-2-thiobarbituric acid (NK 2272), was purchased from Japanese Research Institute for Photosensitizing Dyes.

Results

Absorption change of merocyanin dye in response to the membrane potential change

Fig. 1 shows the absorbance change of merocyanin dye observed at 570 nm upon flash excitation of chromatophores. After the excitation with a single-

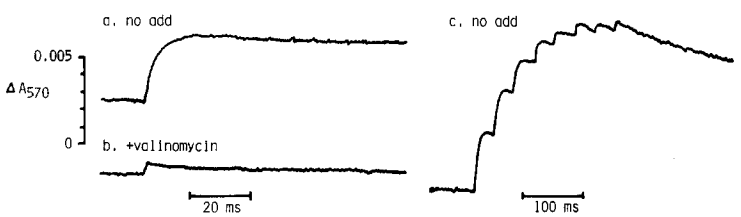


Fig. 1. Absorbance change of merocyanin dye upon excitation with single-turnover flashes. a, no addition; b, with 2 μM valinomycin; c, no addition, multiple excitations with eight successive flashes placed 33 ms apart. Reaction mixture contained 100 mM choline chloride, 100 mM KCl, 5 mM Tricine-HCl buffer (pH 7.0), chromatophores (10 μM bacteriochlorophyll), 1.8 μM tetramethyl-*p*-phenylenediamine, 1 mM ascorbate and 6 μM merocyanin dye.

turnover flash of saturating intensity, absorbance at 570 nm increased with a half-time of about 3 ms. The response rate was much faster than that with uncharged merocyanin or oxonol dye [11, 12]. The extent of the change depended on the concentrations of the dye, chromatophores and salts in the reaction medium. The response also depended on the temperature. The absorption increase was almost eliminated in the presence of K^+ and valinomycin (Fig. 1b), indicating that the absorption increase reflected the membrane potential change across chromatophore membranes. Upon excitation with multiple flashes (Fig. 1c) an about 3-times larger absorption increase was observed. The absorbance change almost saturated after four or five excitation flashes, as seen in the response of carotenoid bandshift in chromatophores of non-sulfur photosynthetic bacteria [2, 3, 5]. Within the concentration range of the dye used no acceleration of the decay of the absorbance change (usually with a half-time of 1—2 s) was observed. A preliminary measurement in *R. sphaeroides* chromatophores showed no change of the decay and extent of the carotenoid bandshift upon continuous illumination when the dye was added at concentrations of the same range. This was different from the result with the oxonol dye [12] which has a delocalized negative charge and accelerates the carotenoid decay by moving within the membrane electrophoretically. When a longer excitation was applied (approx. 30 s) a biphasic absorbance increase with a very slow phase of increase was observed (not shown) in the case of the merocyanin dye, which does not seem to reflect the membrane potential change. The spectrum of the flash-induced absorption change (at 10 ms after flash excitation) showed a maximum at about 570 nm with a minor peak at 520 nm after the absorbance change due to oxidation of cytochrome *c*-555 was corrected (Fig. 2).

The extent of the absorbance change of the dye depended on the intensity of excitation flash. In Fig. 3 the extent of the absorbance change of the dye at 570 nm seen after excitation at various intensities was plotted against the extent of the absorbance change at 422 nm, which indicated the extent of

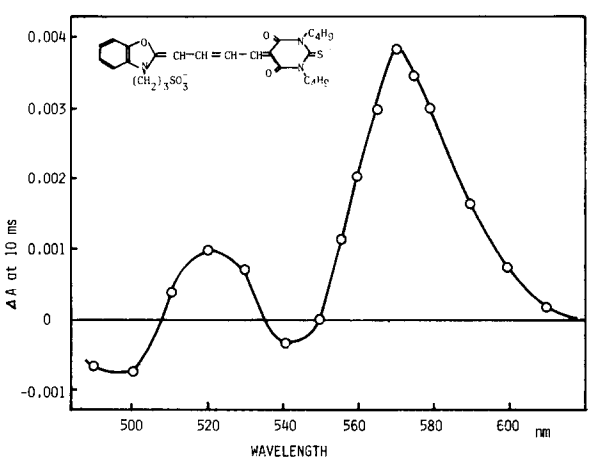


Fig. 2. Spectrum of flash-induced absorption change of the merocyanin dye. Absorption change of the merocyanin dye at 10 ms after the flash excitation was plotted after correcting the rapid absorption change due to cytochrome *c*-555. Experimental conditions were similar to those in Fig. 1 curve a.

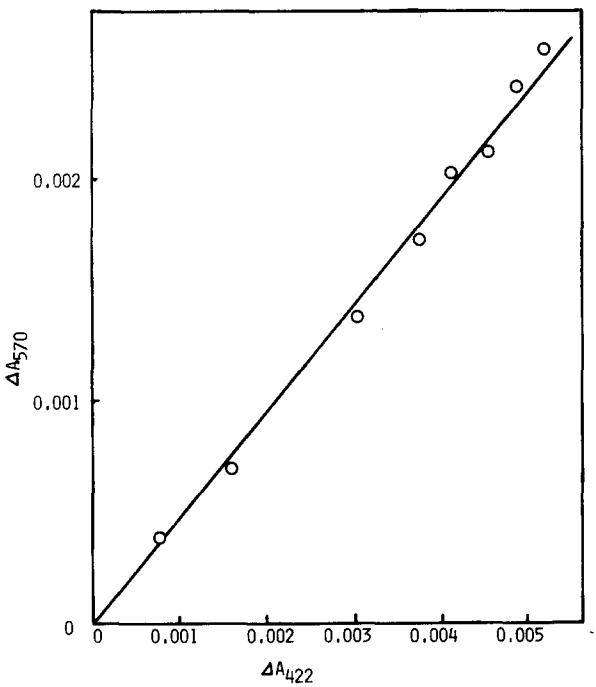


Fig. 3. Correlation between the absorbance change of the merocyanin dye (at 570 nm) and the oxidation of cytochrome *c*-555 (at 422 nm). Absorbance changes due to the response of the dye at 570 nm (at 20 ms after flash excitations) and to the oxidation of cytochrome *c*-555 at 422 nm (at the time of flash excitations) were measured at varied intensities of excitation flash and plotted. Reaction mixture contained 100 mM choline chloride, 5 mM Tris-HCl (pH 7.8), 1 mM ascorbate, chromatophores (10 μM bacteriochlorophyll) and 6 μM merocyanin dye.

photooxidized cytochrome *c*-555 and, therefore, the amount of photoreaction. The plot gave a straight line, indicating that the absorption change of the dye was linearly dependent on the amount of photoreaction and hence probably was proportional to the magnitude of the membrane potential change.

An absorbance change of the dye was also observed when the diffusion potential was applied to the membrane by adding valinomycin to the reaction mixture containing various concentrations of K^+. A careful examination of the time-course of the diffusion-potential-induced absorbance change was done by using the fast-mixing device, since it had been reported by Bashford et al. [12] that the calibration of the light-induced membrane potential change by diffusion potential was unreliable when an oxonol dye was used. A similar ambiguity seemed to exist in the case of uncharged merocyanin dye [11]. In the responses of the merocyanine dye to the addition of valinomycin in the presence of K^+, it was found that (1) the extent of the absorbance change upon the application of diffusion potential depended on the ionic conditions of the medium even when the same extent of membrane potential was expected; (2) the absorbance change upon valinomycin addition was biphasic; (3) the rates both of the first (completed within 1 s after the valinomycin addition) and the slow (several minutes to be completed) phase depended on the valinomycin concentration. The extent of the former was constant at a given K^+ concentration gradient across membranes when the valinomycin

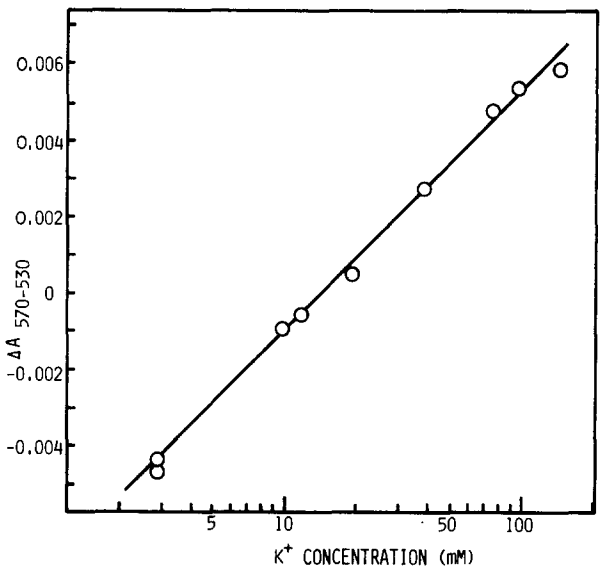


Fig. 4. Diffusion-potential-induced absorption change of the merocyanin dye. Difference absorbance of 570 nm minus 530 nm induced by adding 5 μl ethanol solution of valinomycin (final concentration of 0.8 μM) to the reaction mixture containing varied concentrations of K_2SO_4 and choline chloride (sum of concentrations of choline$^+$ and K^+ was kept at 300 mM in every case), 2 mM Tricine-NaOH buffer (pH 7.0), chromatophores (10 μM bacteriochlorophyll) and 6 μM merocyanin dye was measured. See the text for the details.

added was less than 1 μM, whilst that of the latter was not constant; (4) only the fast phase changed its direction from decrease to increase when K^+ concentration in the outer medium was varied from low to high (1 to 100 mM) (see Fig. 4); (5) absorbance increase was seen in the slow phase at any K^+ concentration in the outer medium; (6) both phases showed the same difference spectrum; (7) the extent of the fast phase related linearly to the logarithm of the K^+ concentration in the outer medium (Fig. 4) when a relatively low concentration of valinomycin was used. From these observations it was concluded that only the fast phase, which can be measured accurately without interference of the slow phase by using a low concentration of valinomycin, was linearly responding to the membrane potential change which can be calculated from the Goldman equation by neglecting permeabilities of ions other than K^+. Positive absorbance change of 0.006 $A_{570\text{-}530}$ corresponded to 60 mV inside-positive change of the membrane potential under the present experimental conditions (Fig. 4). By using this value, membrane potential changes caused by single and multiple flash excitations were estimated to be about 40 (at 10 ms after the flash excitation) and 110 mV inside-positive, respectively, under the typical experimental conditions as in Fig. 1. In this calculation a small flash-induced absorbance change at 530 nm was subtracted from the absorbance changes at 570 nm shown in Fig. 1.

Estimation of the light-induced change of the membrane potential was also attempted by measuring the absorption change of the endogenous carotenoid pigments [6, 9]. Fig. 5A shows time courses of difference absorbance (483—500 nm) upon flash excitation. Within a time shorter than the response time

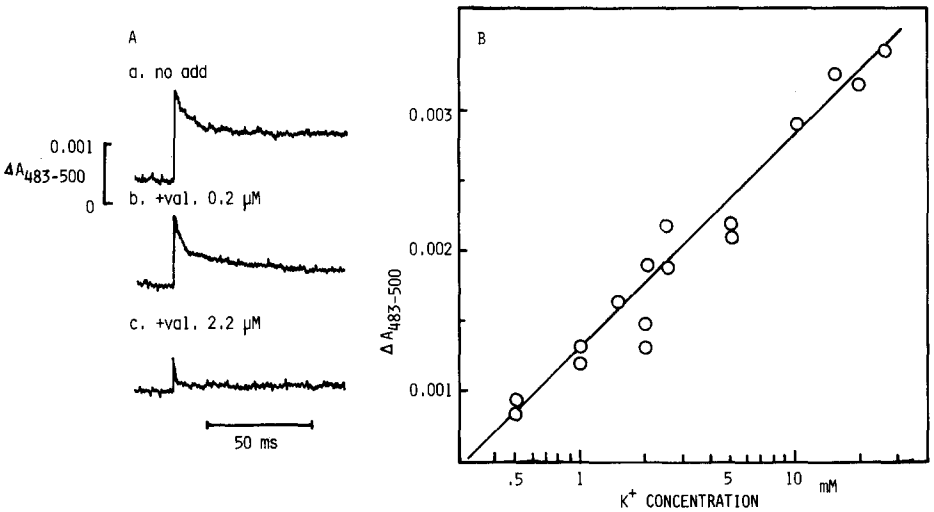


Fig. 5A. Flash-induced absorbance change of carotenoid in chromatophores of *C. vinosum*. Flash-induced absorbance changes at 483 and 500 nm were measured separately and the time courses of difference absorbance change were calculated. Reaction mixture contained 25 mM KCl, 100 mM choline chloride, chromatophores (10 μM bacteriochlorophyll), 2 mM Tricine-NaOH buffer (pH 7.0), 1 mM sodium ascorbate and 0.1 mM diaminodurene. B. Diffusion-potential-induced absorbance change of carotenoid. Change in difference absorbance induced by adding 0.8 μM valinomycin to the reaction mixture containing 2 mM Tricine-NaOH buffer (pH 7.0), chromatophores (10 μM bacteriochlorophyll) and varied concentrations of choline chloride and K_2SO_4 (sum of concentrations of K^+ and choline$^+$ was kept at 300 mM in every case), was plotted versus K^+ concentration in the outer medium.

of the measurement system, a rapid change occurred and a slower recovery followed. Addition of valinomycin in the presence of KCl made the decay faster as expected. The extent of the change in difference absorbance induced by diffusion potential of K^+ in the dark gave an almost straight line when plotted against logarithm of the K^+ concentration in the outer medium, as reported [9]. A positive change of 0.0016 $A_{483-500}$ was found to correspond to 60 mV inside-positive membrane potential change (Fig. 5B). By using this value and the results in Fig. 5A, about 60 mV and 40 mV inside-positive shifts of the membrane potential were estimated at immediately after and 10 ms after the excitation by the flash, respectively. The value at 10 ms was the same as that estimated from the response of the merocyanin dye. The concentration of K^+ in the outer medium, at which no absorption change was observed (about 0.2 mM), was lower in this case than that seen in the case of absorption change of merocyanin dye (about 15 mM) (Fig. 4). The discrepancy may have arisen from the different mechanisms for these phenomena in responding to membrane potential change.

It can be concluded that upon excitation with the flash a 40—60 mV inside-positive shift of the membrane potential occurs in the chromatophores of *C. vinosum*. 60 mV may be a little overestimated, since the rapidly decaying part of the carotenoid absorption change within first 10 ms after the flash may be attributed partially to the uncompensated absorption change due to other components.

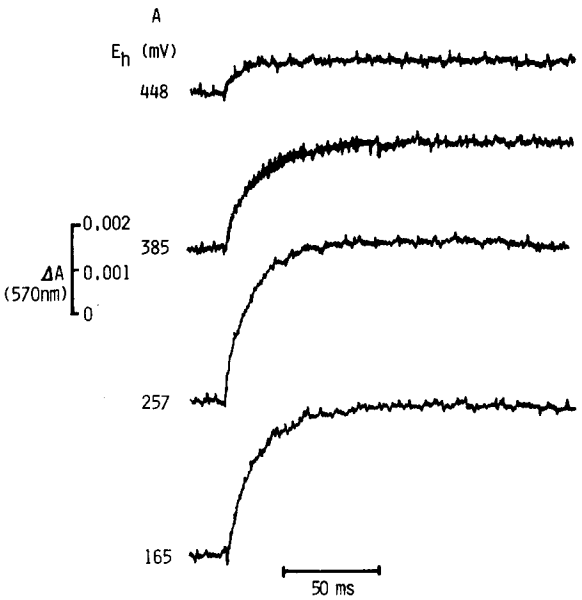
Redox titration of the response of merocyanin dye

The extent but not the half-times of rise and decay of the absorbance change of the merocyanin dye upon a flash excitation depended on the redox potential of the suspending medium (Fig. 6). At high redox potentials, at which most of the electron transfer components other than reaction center bacteriochlorophyll were oxidized, the extent was very small but not zero. With a decrease in the potential until 300 mV the response became much larger, with an apparent midpoint potential value of 360 mV, which was close to that of cytochrome *c*-555 [8, 14]. Between 300 mV and 120 mV almost the same extent of the absorption change was observed. Upon further decrease of the redox potential the extent decreased biphasically with apparent midpoint potential values of 44 mV and −210 mV. The former value seemed to correspond to the switching of the electron donor for $BChl_2$ from cytochrome *c*-555 to cytochrome *c*-552, which is known to be reduced in this redox range [14], and the latter value to the reduction of the primary acceptor which has a midpoint potential value of about −130 mV at this pH [14]. The value of −210 mV as above is a little ambiguous, since at redox potentials less than −200 mV the dye became unstable and prolonged preincubation could not be performed. The titration curve was almost the same as that of the bacteriochlorophyll bandshift (at potentials lower than 150 mV) or of the carotenoid bandshift (at potentials higher than 150 mV) reported [6] except that a small absorbance change was observed in the higher redox potential region where cytochrome *c*-555 was expected to be fully oxidized and no carotenoid bandshift was reported to occur upon flash excitation [6]. No indication for the participation of the *b*-type cytochrome, which seems to exist in this organism and to change its redox state at around −30 mV [15], was seen in the titration curve. This was somewhat different from the titration curve of the carotenoid bandshift in chromatophore membranes of non-sulfur bacteria [2—5] in which large increases of the extent took place with the reduction of cytochrome *b*, i.e., phase III of the carotenoid shift.

Effects of antimycin A and phosphorylating condition on the response of merocyanin dye

Fig. 7 shows the effect of antimycin A on the flash-induced absorption change of the merocyanin dye excited by two successive flashes. With 6 μM antimycin A, the dye responses after one and two flashes were 4 and 12% decreased, respectively. With a higher concentration (12 μM) the decreases were 17 and 37%, respectively. The decreases may be mainly due to the acceleration of dark decay. Addition of phenazine methosulfate slightly reduced the decreases, to 17 and 25%. With 12 μM antimycin A the extent of the absorbance change after eight successive flashes was 35% decreased and addition of phenazine methosulfate reduced the decrease to 12% (not shown). It seemed that antimycin A had little effect on the generation of membrane potential by a single turnover flash, although it accelerated the dark decay a little. The partial inhibition of cyclic electron transfer at a site, possibly taking place in the presence of antimycin A, may have been bypassed by phenazine methosulfate.

These results also suggest that the cyclic electron transport pathway of



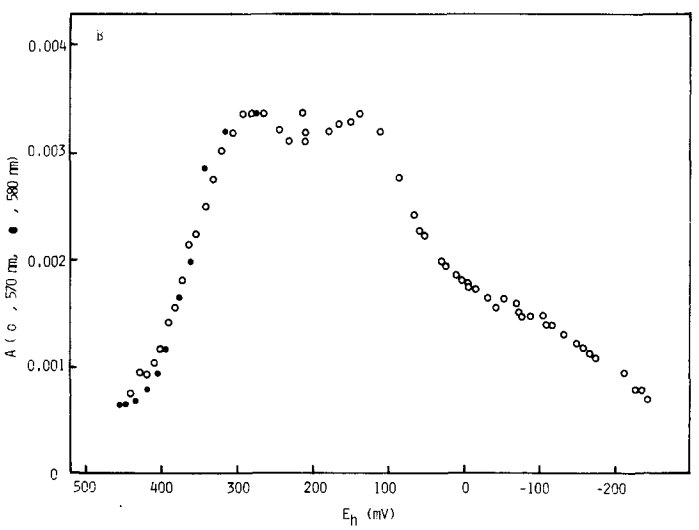


Fig. 6. A. Dependence of the flash-induced response of the merocyanin dye on the redox potential of the medium. Reaction mixture contained 5 mM $MgCl_2$, 50 mM KCl, 50 mM Tris-HCl buffer (pH 7.8), chromatophores (10 μM bacteriochlorophyll) and 6 μM merocyanin dye. As redox mediators, 10 μM phenazine methosulfate, 10 μM diaminodurene, 10 μM duroquinone, 10 μM indigosulfonate and varied concentrations of dithiothreitol and ferricyanide were used. B. Redox titration of the absorbance change of merocyanin. Extent of the absorbance change 100 ms after flash excitations were measured as in A and plotted versus redox potential of the medium. Open circles, oxidative titration at 570 nm (reaction mixture was brought to −240 mV by adding aliquots of dithiothreitol solution and then brought to higher redox potentials by mixing with air or by adding ferricyanide solution). Closed circles, reductive titration at 580 nm (reaction mixture was brought to 460 mV at first by adding ferricyanide and then brought to lower potentials by adding dithiothreitol solution).

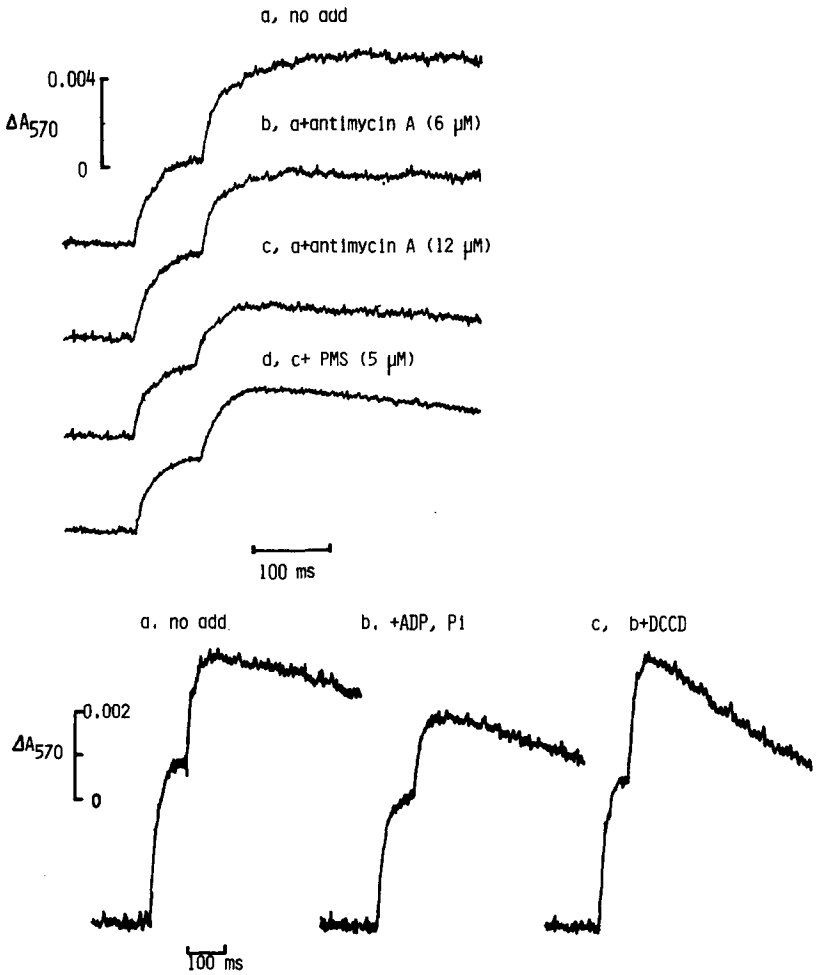


Fig. 7. Effects of antimycin A on the response of the merocyanin dye. Reaction mixture contained 5 mM $MgCl_2$, 50 mM KCl, 50 mM Tris-HCl buffer (pH 7.8), chromatophores (10 μM bacteriochlorophyll) and 6 μM merocyanin. E_h of the reaction mixture was adjusted to 230 ± 10 mV by adding aliquots of ascorbate or ferricyanide solution.

Fig. 8. Effect of phosphorylating conditions on the response of the merocyanin. a, no addition. b, with 6 mM ADP and 1.8 mM phosphate. c, b plus 16 μM dicyclohexylcarbodiimide (DCCD). Reaction mixture contained 5 mM $MgCl_2$, 50 mM Tris-HCl buffer (pH 7.8), chromatophores (10 μM bacteriochlorophyll), 6 μM merocyanin and 0.12 mM sodium ascorbate.

(isolated) *Chromatium* chromatophores is different from that of chromatophores of nonsulfur bacteria in which antimycin additions are known to eliminate the slow development of the carotenoid bandshift (phase III) due to electron transfer through cytochrome *b* after a single turnover flash [2—5].

In the presence of ADP and inorganic phosphate, i.e., under phosphorylating conditions, the flash-induced absorption change of the dye became smaller, especially after the second flash (Fig. 8). This decrease was not due to the acceleration of the dark decay, since the semilogarithmic plot of the absorption

change against dark time gave almost parallel lines (not shown). The decrease of the absorption change seemed to have occurred within a shorter time range than the response time of the dye to the membrane potential change. Addition of energy transfer inhibitor, dicyclohexylcarbodiimide, made the extent as large as that without ADP and phosphate (trace c). The reason for the slight acceleration of the dark decay in this case is not clear. These results seemed to be consistent with those seen in chromatophores of other bacteria [16] in which phosphorylating conditions accelerated the decay of carotenoid shift only within a short time range after the flash excitation and left the most part of the absorption change unchanged.

Discussion

The absorbance change of the merocyanin dye linearly responded to the changes of membrane potential either induced by the flash-induced electron transport or by an application of the diffusion potential of K^+ in the presence of valinomycin. The merocyanin used seems to be superior as a membrane potential probe to other types of dye such as oxonol or uncharged merocyanin dyes [11, 12] because of its faster response and smaller effect on the decay of membrane potential. The dye used in the present study has a negative charge and is expected to be located at the outer surface of the membrane [10]. The response of the merocyanin dye to the membrane potential change, as that of intrinsic carotenoid or bacteriochlorophyll, seems to indicate that the electric field produced by the electron movements inside the membrane rapidly delocalizes and is sensed by the dye at the surface.

It seems that the chromatophore membrane of *C. vinosum* experiences the inside-positive membrane potential changes of 40—60 mV upon flash excitation and 110—170 mV under the repetitive excitations as estimated in chromatophore membranes of non-sulfur bacteria [2—5] and that the flash-induced membrane potential is rapidly dissipated during the phosphorylation.

The redox titration curve of the flash-induced dye response is explained by the changes in the redox states of $BChl_2$, cytochromes *c*-555 and *c*-552, and X. However, little evidence for the operation of the electron transport through cytochrome *b* in producing membrane potential change was seen. This point was quite different from the response of the carotenoid shift observed in non-sulfur bacterial chromatophores [2—5]. That the addition of antimycin A only slightly inhibited the response of the dye also supports the above conclusion. The electron transport through cytochrome *b* may be very slow in the *C. vinosum* chromatophores or very different from those in other bacteria.

From the redox titration curve we can estimate that the inside-positive membrane potential changes of 9.2 mV (at E_h = 440 mV), 40 mV (at E_h = 120—300 mv) and 17 mV (at E_h = —100 mV) are induced by the electron movements of $BChl_2 \rightarrow$ I (bacteriopheophytin) $\rightarrow$ X, cytochrome *c*-555 $\rightarrow$ $BChl_2 \rightarrow$ I $\rightarrow$ X and cytochrome *c*-552 $\rightarrow$ $BChl_2 \rightarrow$ I $\rightarrow$ X, respectively. From these membrane potential values the relative arrangement of these components across the membrane can be estimated by assuming a chromatophore vesicle as a spherical condensor of about 200 Å radius and the effective thickness of approx. 30 Å for a low dielectric part of the membrane as done in other

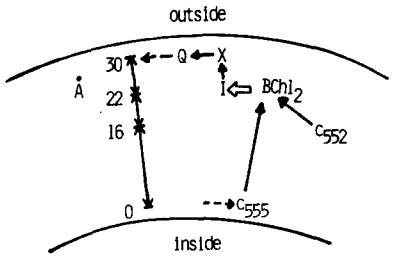


Fig. 9. Estimated localization of the electron transfer components in chromatophore membrane of *C. vinosum*. Inner radius of the chromatophore vesicle and effective membrane thickness are assumed to 200 Å and 30 Å, respectively.

chromatophore membranes [5] as shown in Fig. 9. The result is similar to the localization of these components estimated from the study of EPR [7]. A noteworthy feature of the topology of intramembraneous components shown in Fig. 9 is that $BChl_2$ is localized more closely to the outer surface of the chromatophore membrane than that in chromatophore membranes of non-sulfur bacteria [5]. This point may be worth studying to obtain more understanding of the mechanisms of the primary photoreactions in reaction centers.

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