Biochimica et Biophysica Acta, 545 (1979) 223—235

BBA 47615

ELECTROGENIC EVENTS IN THE UBIQUINONE-CYTOCHROME b/c_2 OXIDOREDUCTASE OF *RHODOPSEUDOMONAS SPHAEROIDES*

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Key words: Cytochrome c_2; Carotenoid bandshift; Second-order process; Ubiquinone-cytochrome b/c_2 oxidoreductase; Bacterial photosynthesis; (Rhodopseudomonas sphaeroides)

Summary

The reductant of ferricytochrome c_2 in *Rhodopseudomonas sphaeroides* is a component, Z, which has an equilibrium oxidation-reduction reaction involving two electrons and two protons with a midpoint potential of 155 mV at pH 7. Under energy coupled conditions, the reduction of ferricytochrome c_2 by ZH_2 is obligatorily coupled to an apparently electrogenic reaction which is monitored by a red shift of the endogeneous carotenoids. Both ferricytochrome c_2 reduction and the associated carotenoid bandshift are similarly affected by the concentrations of ZH_2 and ferricytochrome c_2, pH, temperature the inhibitors diphenylamine and antimycin, and the presence of ubiquinone. The second-order rate constant for ferricytochrome c_2 reduction at pH 7.0 and at 24°C was $2 \cdot 10^9$ $M^{-1} \cdot s^{-1}$, but this varied with pH, being $5.1 \cdot 10^8$ $M^{-1} \cdot s^{-1}$ at pH 5.2 and $4.3 \cdot 10^9$ $M^{-1} \cdot s^{-1}$ at pH 9.3. At pH 7 the reaction had an activation energy of 10.3 kcal/mol.

Introduction

The cyclic photosynthetic electron transport system of *Rhodopseudomonas sphaeroides*, which includes *b* and *c*-type cytochromes and ubiquinone-10, closely resembles the ubiquinone-cytochrome *b/c* oxidoreductase system of mitochondria [1]. However, while the mitochondrial system transfers electrons from substrate dehydrogenases to cytochrome oxidase, the bacterial pathway is driven by the photochemical reaction center (see ref. 2). Within 1 ms of a single-turnover flash of light, the ubiquinone-cytochrome b/c_2 oxidoreductase of *Rps. sphaeroides* is presented with a single reducing equivalent (probably a protonated ubisemiquinone at neutral pH, see ref. 3) and a single oxidizing equivalent, ferricytochrome c_2 [4]. The ubiquinone cytochrome b/c_2 oxidoreductase subsequently catalyzes the reduction of the ferricytochrome c_2 and the oxidation of the ubisemiquinone. The direct reductant of the ferri-

cytochrome, which in the absence of unambiguous identification has been called Z [5], requires two electrons and two protons for its equilibrium reduction from pH 5 to 11 [16] and has an oxidation-reduction midpoint potential of 155 mV at pH 7.0 [1,6,7]. Somewhat surprisingly, the reduction of ferricytochrome c_2 by ZH_2 has second order characteristics [1,7,8] although there is only approximately a single Z moiety per reaction center in the chromatophore membrane [1,6]. Recent extraction and reconstitution experiments indicate that Z is a ubiquinone [9].

Many species of photosynthetic bacteria, including *Rps. sphaeroides*, possess carotenoid pigments whose spectra shift to the red in response to 'energy-linked' events (see refs. 10—12 for recent work on this topic). While there is considerable controversy over the mechanisms of the carotenoid bandshift [10—12], there is general agreement that the carotenoids respond to some form of transmembrane potential. Indeed, using valinomycin/KCl pulses, Jackson and Crofts [13] have demonstrated that the magnitude of the bandshift is linearly proportional to the transmembrane electrical gradient. A single turnover of the reaction center can elicit three distinct phases of carotenoid bandshift [14], all of which are promptly collapsed by the addition of uncoupler or valinomycin. Phase I is associated with charge transfer within the reaction center, and phase II accompanies the reduction of the photo-oxidized reaction center bacteriochlorophyll dimer by ferrecytochrome c_2 [3,14]. The third phase, which is the only phase inhibited by antimycin, seems to be linked to events within the ubiquinone-cytochrome b/c_2 oxidoreductase [5—7,14], although the nature of the coupling is unclear.

In this paper we examine the third phase of the carotenoid bandshift in more detail, and compare its kinetic and thermodynamic behavior with the reduction of ferricytochrome c_2. Our results confirm earlier suggestions [5—7,14] that phase III of the bandshift is obligatorily coupled to ferricytochrome c_2 reduction, and reinforce our earlier conclusion that the reduction of ferricytochrome c_2 is a second order process where the ratio of reductant to oxidant is close to unity.

Materials and Methods

Rhodopseudomonas sphaeroides Ga was grown photosynthetically with succinate as the sole carbon source, and chromatophores were prepared as described previously [4]. Oxidation-reduction potentiometry and the analysis of rapid, flash-induced absorbance changes in a dual wavelength spectrophotometer, together with a critical assessment of experimental procedures, have been described earlier [1,4,6]. Previously, the carotenoid bandshift and the reduction of ferricytochrome c_2 were monitored by determining the reaction amplitudes at fixed times after a single turnover flash [6,7]; subsequently both the initial rate and the halftime of each reaction were also measured [1,7]. Fig. 1 shows typical data obtained in the experiments reported here, and illustrates how we have determined both the initial rates and amplitudes of cytochrome c_2 reduction and of the third phase of the carotenoid bandshift. In all cases the amplitude of cytochrome c_2 reduction was taken to be equal to that of its oxidation by the reaction center. Under the conditions of the experiments reported here 77 ± 7% (n = 50) of the flash-oxidized cytochrome was

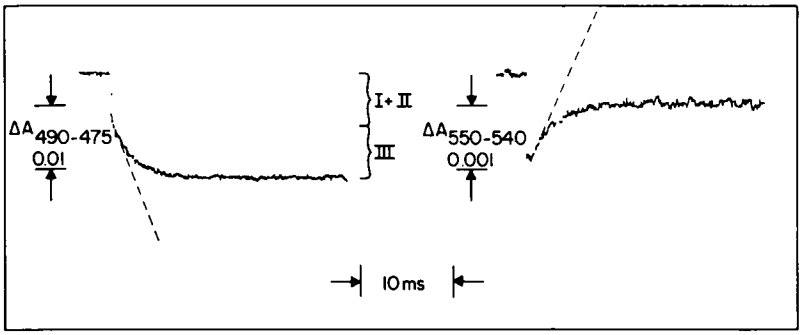

Fig. 1. The kinetics of carotenoid bandshift phase III and ferricytochrome c_2 reduction. Chromatophores (137 nm reaction centers) were suspended in 20 mM *N*-morpholinopropane sulfonate, 100 mM KCl, 1 mM $MgCl_2$ with 10 μM each of *N*-methylphenazonium methosulfate, *N*-ethylphenazonium ethosulfate, pyocyanine, 2-hydroxy-1,4-naphthaquinone and 2,3,5,6-tetramethylphenylenediamine as redox mediators. The pH was 6.0, the temperature 21°C and the ambient redox potential 90 mV. The traces reflect the average of 8 flashes for the carotenoid response and of 32 for the cytochrome reactions, the flashes being separated by 40 s. The dashed lines represent the method we have used to determine the initial rates of the reactions.

reduced on a millisecond time scale when Z was fully reduced before activation. Events within the reaction center do not make any significant contribution to the changes measured at 550—540 nm which can be entirely ascribed to cytochrome c_2 [4].

Ubiquinone was extracted from chromatophores by isooctane extraction after lyophilization at —40°C [15]. The chromatophores had first been washed in a medium of low ionic strength, where the usual 100 mM KCl [4] had been replaced by 1 mM KCl. Reconstitution was carried out by the addition of pure ubiquinone-10 (Sigma) in isooctane to the lyophilized pellet, and the isooctane was evaporated in vacuo.

Results

Fig. 2 illustrates an oxidation-reduction titration of phase III of the carotenoid shift, where the ratio of the initial rate and the extent of the reaction is plotted against the ambient potential. The ratio (initial rate/extent) has the dimensions of a first order rate constant and is subsequently referred to as k'_{app}. Presentation of the data in terms of k'_{app} allows a direct comparison of experiments performed on different chromatophore preparations on the same scale. The titration presented in Fig. 2 complements those reported previously [6], where the extent of phase III was plotted as a function of E_h. The latter approach yielded symmetrical, $n = 2$ Nernst curves, attributed to the Z/ZH_2 couple, with a midpoint potential of approximately 155 mV at pH 7. Fig. 2 demonstrates that k'_{app} (initial rate/extent) for phase III follows an identical oxidation-reduction titration.

The reduction kinetics of cytochrome c_2 in uncoupled chromatophores showed second-order characteristics and the halftime of the reaction varied with the concentration of the reactants, which allowed a determination of the ratio of reactants within the chromatophore membrane [1]. Fig. 3 presents a similar series of experiments with coupled chromatophores, while Fig. 4

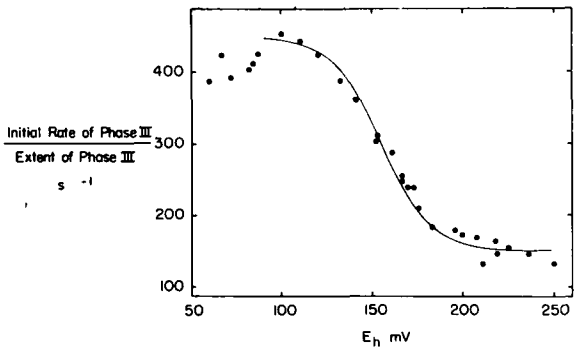

Fig. 2. Characteristics of carotenoid bandshift phase III. Chromatophores (143 nM reaction centers) were suspended in a medium similar to that used for Fig. 1 except that the redox mediators were present at only 7 μM. The pH was 6.9 and the temperature 28°C.

illustrates the behavior of the third phase of the carotenoid bandshift under similar conditions. In these experiments the concentration of ZH_2 was held constant by maintaining the redox potential at the stated $E_h \pm 5$ mV while the concentration of ferricytochrome c_2 was varied by attenuating the actinic flash [1]. At each potential the initial rates of the reactions (open symbols and right hand ordinate) were proportional to the extent of the reaction. In contrast, the halftimes of the reactions (solid symbols, left ordinate) exhibited a complex behavior, similar to that seen for the reduction of ferricytochrome c_2 in the uncoupled state [1]. At ambient potentials below 100 mV, where all the Z is in

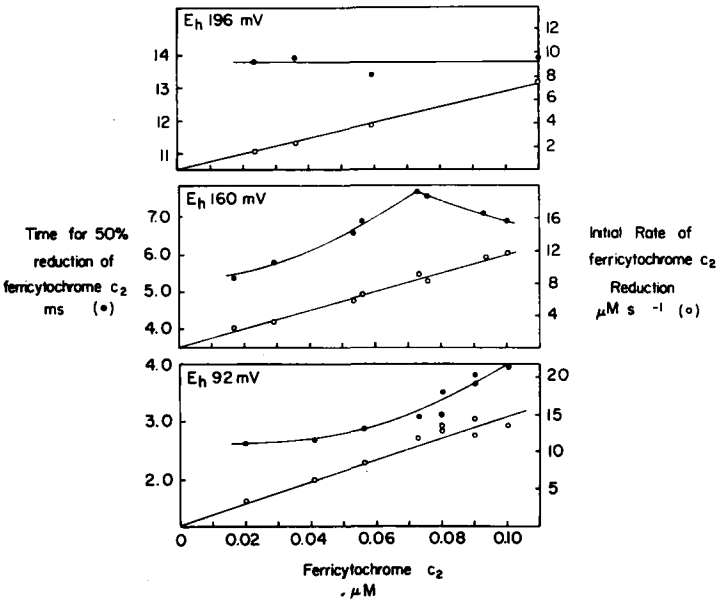

Fig. 3. Characteristics of ferricytochrome c_2 reduction. Chromatophores (159 nM reaction centers) were suspended in a medium similar to that for Fig. 2. The pH was 6.9 and the temperature 24°C. The extent of the reaction was varied by attenuating the actinic flash using neutral density filters (Wratten 96ND).

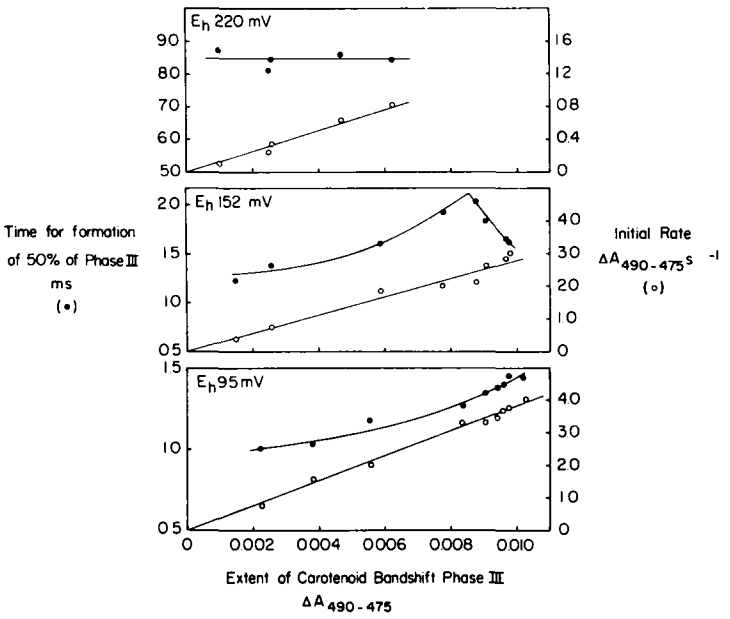

Fig. 4. Characteristics of carotenoid bandshift phase III. Chromatophores (143 nM reaction centers) were suspended in a medium similar to that used for Fig. 2. The pH was 6.9 and the temperature 28°C. The extent of the reaction was varied by attenuating the actinic flash (Fig. 3). At 220 mV there is little carotenoid phase III (see ref. 6), even with saturating flashes.

the reduced form, the limiting halftimes of the reactions vary by a factor close to the natural logarithm of 2, and there is no maximum in the halftime plot. At potentials near the midpoint potential of the Z/ZH_2 couple, the plots of reaction halftime versus ferricytochrome c_2 concentration contain a maximum (see ref. 1). The second-order rate law predicts that the reaction halftime is maximal when the concentrations of the reactants, in this case ZH_2 and ferricytochrome c_2, are equal (see ref. 1 and Appendix). Thus in the experiments shown in Fig. 3, there was 72 nM ZH_2 at 160 mV. Using the E_m of the Z/ZH_2 couple determined previously [6] this extrapolates to a total $Z + ZH_2$ concentration of 144 nM, which is equivalent to 0.9 Z per reaction center. This value is not significantly different from the average of 15 determinations in the uncoupled state, which yielded a total Z to reaction center ratio of 0.8 ± 0.1 [1]. The determination of the concentration of ZH_2 at 160 mV also allows a calculation of the apparent second-order rate constant for the reaction of $1.8 \cdot 10^9\ M^{-1} \cdot s^{-1}$, and similar values, 1.7 and $1.5 \cdot 10^9\ M^{-1} \cdot s^{-1}$, can be obtained from the initial rates (k_2 = initial rate/$[c_2^+]_i \cdot [ZH_2]_i$, where subscript i indicates the initial concentration of the reactant). When *Rps. sphaeroides* chromatophores are uncoupled, the apparent second order rate constant for the reduction of ferricytochrome c_2 has a value of $3.0 \pm 1.8 \cdot 10^9\ M^{-1} \cdot s^{-1}$ [1], indicating that uncoupling agents have no significant effect on the second-order reaction during the first turnover.

The data for the carotenoid bandshift, shown in Fig. 4, are more difficult to evaluate because the bandshift is an indirect measure of the reaction, and has no 'molar extinction coefficient'. Nevertheless, Fig. 4 is qualitatively very

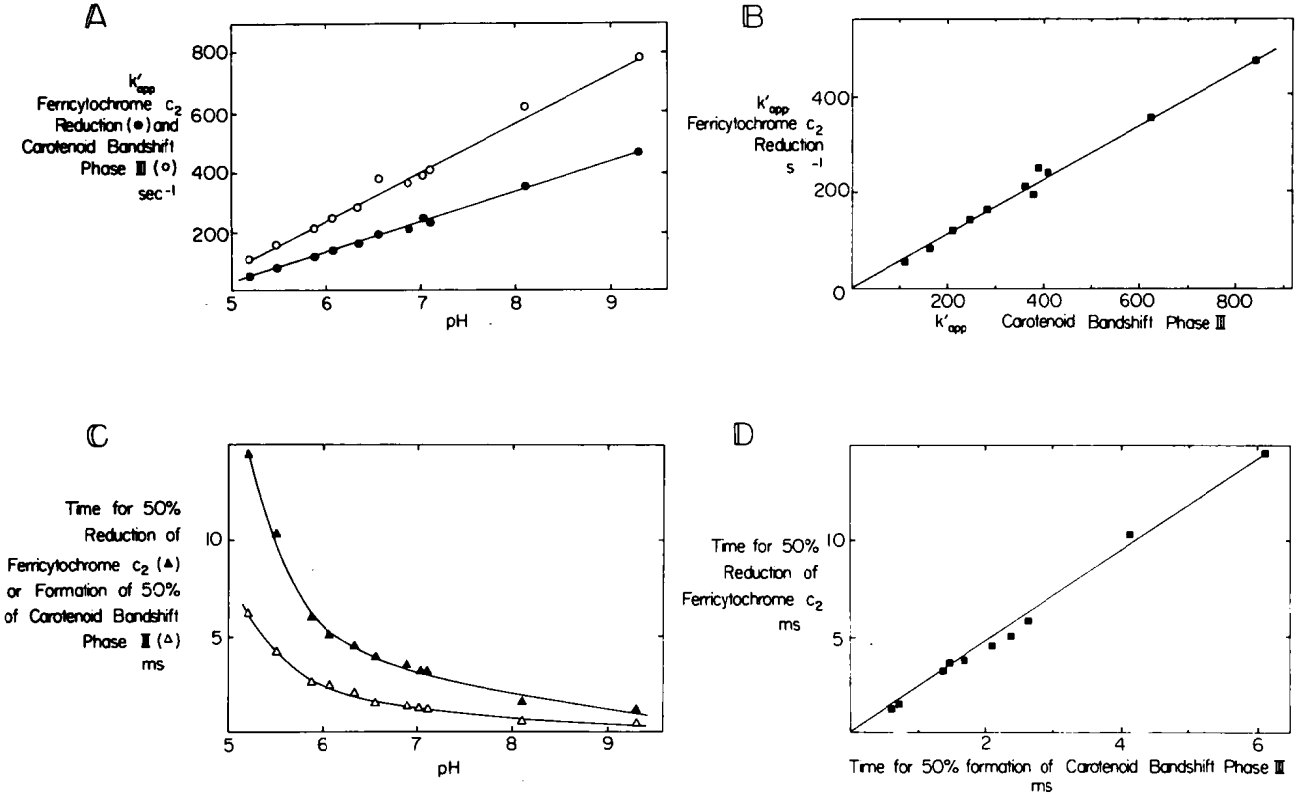

Fig. 5. The effect of pH on electron flow through the ubiquinone-cytochrome b/c_2 oxidoreductase. Chromatophores (137 nM reaction centers) were initially suspended in a medium similar to that of Fig. 1, and the pH was then adjusted with small volumes of 1 M Tris base, alkaline glycine, or 2 *N*-morpholinoethane sulfonic acid. The temperature was 21°C, and the E_h was adjusted to (510—60 pH) ± 10 mV.

similar to Fig. 3, although the halftimes of phase III are significantly less than the halftimes of ferricytochrome c_2 reduction under similar conditions. The lower halftimes found for phase III of the carotenoid bandshift suggest that the apparent second-order rate constant for this reaction exceeds that for ferricytochrome c_2 reduction by a small, but significant factor (2—4-fold). However, the difference in rate observed for the two reactions may reflect systematic factors in the measurements of the reactions (see below).

The effect of pH on the reduction of ferricytochrome c_2 and the third phase of the carotenoid bandshift is shown in Fig. 5. The chromatophores were poised at an ambient potential sufficient to reduce Z fully (see ref. 6) and the k'_{app} and the halftime of the reduction of ferricytochrome c_2 and the third phase of the carotenoid bandshift were determined. The rates of both processes

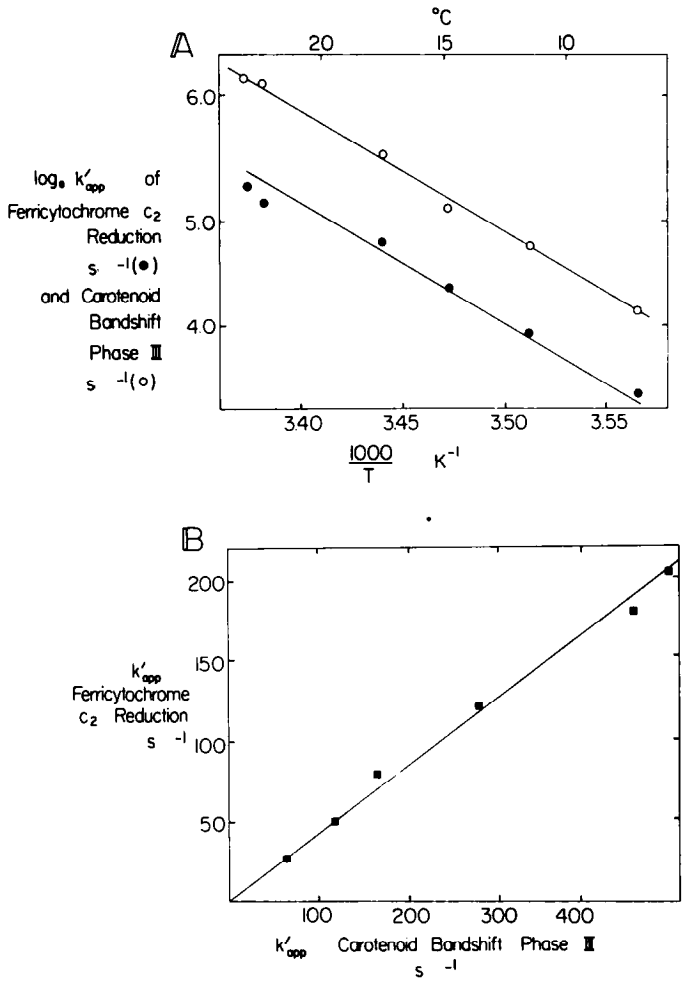

Fig. 6. The effect of temperature on electron flow through the ubiquinone-cytochrome b/c_2 oxidoreductase. Chromatophores (137 nM reaction centers) were suspended in a medium similar to that of Fig. 1. The pH was 6.8 and the E_h was 95 ± 5 mV. The Arrhenius plot (part A) indicates an activation energy of 10.3 kcal/mol for both reactions, and the ferricytochrome reduction reaction extrapolates to a rate of $1.1 \cdot 10^{10}$ $M^{-1} \cdot s^{-1}$ at infinite temperature.

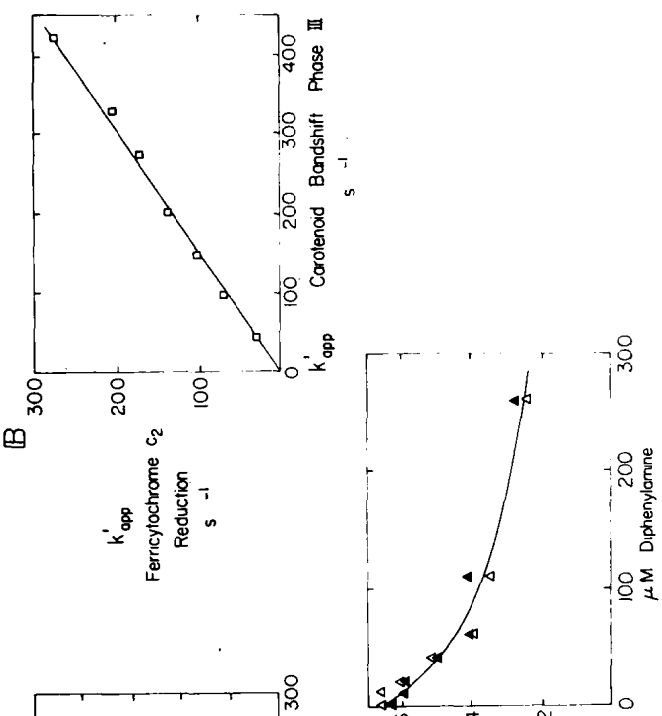

Fig. 7. The effect of diphenylamine on electron flow through the ubiquinone-cytochrome b/c_2 oxidoreductase. Chromatophores (165 nM reaction centers) were suspended in a medium similar to that used for Fig. 2. The pH was 7.0, the temperature 21°C and the E_h 85 ± 10 mV. Diphenylamine (Sigma), made up as a 1 M solution in ethanol, was added as indicated.

did not alter dramatically with pH; a 1000-fold change in proton concentration caused less than a 10-fold change in reaction rate. Although the absolute rates of ferricytochrome c_2 reduction and phase III differ, correlation plots (Fig. 5) reveal that both reactions seem to be intimately related at each pH. The k'_{app} plots for both carotenoid bandshift phase III and cytochrome c_2 reduction extrapolate to a zero rate at pH 4.6. It is noteworthy that the pH dependencies of the midpoint potentials of cytochrome c_2 and Z suggest that they would be equipotential at this pH [6,16].

The temperature dependence of reactions in the ubiquinone-cytochrome b/c_2 oxidoreductase is shown in Fig. 6. As before, phase III has a significantly higher k'_{app} than ferricytochrome c_2 reduction, but the correlation plot reveals that both reactions have a very similar temperature dependence. Indeed, the activation energy for both reactions is 10.3 kcal/mol between 5 and 25°C, which is close to that found for other membrane-associated reactions and indicates the lack of lipid phase transitions or phase separations in this temperature range [17,18].

The effect of diphenylamine on ferricytochrome c_2 reduction and carotenoid bandshift phase III is shown in Fig. 7. Diphenylamine is a well known inhibitor of carotenoid [19] and ubiquinone [20] synthesis during the growth of photosynthetic bacteria, but it is also an inhibitor of the ubiquinone-cytochrome

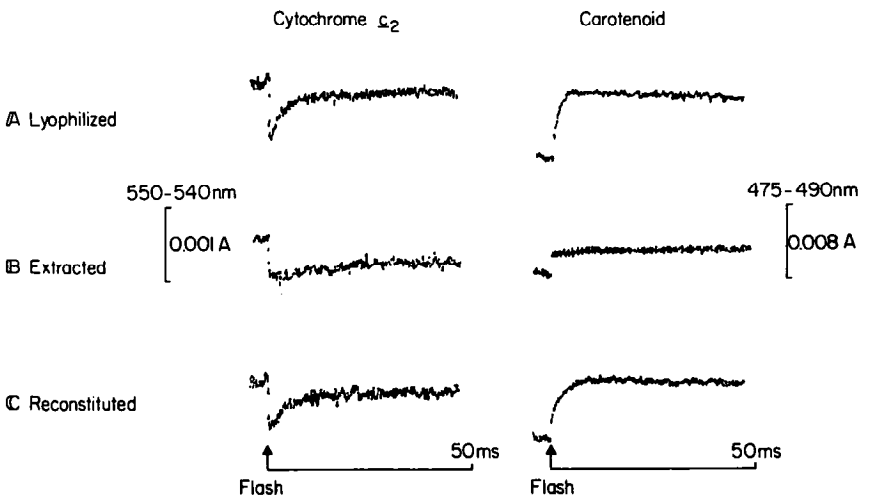

Fig. 8. The effect of removal and reconstitution of ubiquinone on electron flow through the ubiquinone-cytochrome b/c_2 oxidoreductase. Three separate samples of chromatophores were used for this experiment. All had been lyophilized; sample A was then resuspended in buffer, while samples B and C were extracted with isooctane. Sample B was then resuspended in buffer, while sample C had pure ubiquinone (30-fold excess over the reaction center concentration) added before resuspension. The chromatophores (200, 130 and 150 nM reaction centers, respectively) were suspended in a buffer similar to that used for Fig. 1, except that only N-phenylphenazonium methosulfate, N-ethylphenazonium ethosulfate and 2,3,5,6-tetramethylphenylenediamine were used as redox mediators, at a concentration of 5 μM; 100 μM ferrocyanide was also present. The pH was 7.0, the temperature 21°C, and the E_h 100 ± 5 mV. The scale for the carotenoid traces is correct for the extracted and reconstituted samples. However, the extraction with isooctane removes some carotenoid with the ubiquinone, and the bandshift is correspondingly much smaller than in unextracted controls. In fact, the trace for the lyophilized, unextracted sample (top right) is shown at only half the amplification of the other traces.

b/c_2 oxidoreductase in vitro (Fig. 7). Increasing concentrations of diphenylamine have two effects: cytochrome c_2 reduction and carotenoid shift phase III are slowed down in parallel (Fig. 7A and B) and the extent of the carotenoid bandshift is decreased. This latter effect (Fig. 7C) is apparently a general effect on the carotenoids, because the extents of phases I plus II and phase III decrease concomitantly. Antimycin also inhibits both ferricytochrome c_2 reduction and carotenoid banshift phase III, but this will be dealt with in detail in a forthcoming paper (van den Berg, W.H. et al., in preparation).

Baccarini-Melandri and Melandri [9] have presented evidence that ubiquinone extraction inhibits the reduction of ferricytochrome c_2. Fig. 8 demonstrates that such extraction also prevents the formation of carotenoid bandshift phase III. Furthermore, both ferricytochrome c_2 reduction and carotenoid bandshift phase III are restored by the addition of ubiquinone to the extracted chromatophores. This work will also be reported in greater detail elsewhere (Takamiya, K. and Dutton, P.L., in preparation); it is presented here to demonstrate another situation where ferricytochrome c_2 reduction and carotenoid bandshift phase III are perturbed in a parallel fashion by a specific experimental procedure.

Discussion

The work described here was designed to investigate earlier suggestions that the third phase of the carotenoid bandshift was obligatorily linked to the reduction of flash-generated ferricytochrome c_2 in coupled chromatophores [5—8,14], and the results provide strong evidence consistent with the proposition. Both ferricytochrome c_2 reduction and the formation of phase III are similarly affected by the concentrations of ferricytochrome c_2 and ZH_2 (Figs. 2, 3 and 4), pH (Fig. 5), temperature (Fig. 6), the inhibitor diphenylamine (Fig. 7), the inhibitor antimycin (van den Berg, W.H., et al., unpublished) and the presence of ubiquinone (Fig. 8). Nevertheless, phase III formation always appears to be faster than ferricytochrome c_2 reduction by a factor of two to four. However, this discrepancy may arise from the treatment of the data (Fig. 1). The apparent rate constant for cytochrome c_2 reduction was always measured assuming that all the ferricytochrome was being reduced by the same process. This assumption may not necessarily be valid because some of the ferricytochrome might not be reduced by ZH_2 [1,6] because of 'damage' during the preparation of the chromatophores. For example, even though whole cells seem to have two molecules of cytochrome c_2 attached to each reaction center, the preparation of chromatophores always results in some reaction centers (typically 15—40%) losing their cytochrome complement. If similar 'damage' occurred in the ubiquinone-cytochrome b/c_2 oxidoreductase, some ferricytochrome will be reduced by alternative, and at this stage unknown, electron donors. If these considerations are correct, our calculations might consistently underestimate the rate constants of ferricytochrome c_2 reduction. In contrast, we measure the third phase of the carotenoid bandshift in a way which might lead to an overestimation of the rate constant of this phenomenon. Phase II of the carotenoid bandshift [14], which is linked to the oxidation of ferrocytochrome c_2 by the photo-oxidized reaction center

bacteriochlorophyll dimer, has kinetics which overlap with the onset of phase III [4,14]. This could cause a consistent overestimation of the initial rate of phase III. Furthermore, any collapse of the membrane potential during the rise of phase III would lead to an underestimation of the extent of this phase, which in turn would result in a larger k'_{app}. In view of the remarkable similarity of the behavior of ferricytochrome c_2 reduction and the formation of phase III of the carotenoid bandshift, during seven different experimental procedures, we believe that the reactions are indeed obligatorily coupled, and that the discrepancy in the rate constants reflects systematic factors in the measurements.

There has been considerable speculation as to how ferricytochrome c_2 reduction is coupled to carotenoid bandshift phase III [1,5—8,14]. Phase I of the bandshift is coupled to charge transfer within the reaction center from the bacteriochlorophyll dimer, which is apparently in the middle of the membrane dielectric, to the 'primary acceptor', which is close to the outer membrane-aqueous interface [4,14,21]. The subsequent phase II is coupled to the oxidation of ferrocytochrome c_2, which is at the inner membrane-aqueous interface [22], by the oxidized reaction center bacteriochlorophyll dimer [4,14,21]. Together, these two phases of the bandshift appear to register the electrogenic movement of a single electron across the entire membrane dielectric. Phase III of the bandshift is approximately as large as the sum of phases I plus II [5,14], and perhaps the simplest explanation is that it reflects the movement of one other electron from the inside to the outside of the chromatophore membrane (see for example the models in refs. 5—8, 14, 23, 24), although an alternative possibility is that it could reflect the electrogenic movement of a cation from the outside of the membrane. Whatever the mechanism, phase III can occur even when there is a pre-existing membrane potential (generated by the reaction center events) of some 100 mV [21]. Thus, providing that phase III reflects a transmembrane potential rather than a strictly local event [25], there must be a considerable amount of free energy available for the electrogenic reaction. It is remarkable that this free energy is available over such a wide range of conditions. For example, the reaction occurs rapidly at pH 5.2 and at pH 9.3 (Fig. 5) and even at pH 11 [6]. The equilibrium midpoint potential of the Z/ZH_2 couple varies from 265 to −85 mV over this range, while that of cytochrome c_2^{3+}/c_2^{2+} apparently varies only from 315 to 265 mV [16]. It thus seems unlikely that the difference between the equilibrium E_m values of these two couples is always the major source of the free energy available for phase III. However, the light reaction seems to generate a redox potential difference within the reaction center (between the $(BChl)_2^+/(BChl)_2$ and QFe/Q^-Fe) of some 630 mV [2]. This would be sufficient to drive all the reactions in the cyclic electron transfer chain, even when some individual steps may be unfavorable.

Appendix

The theoretical behavior of the halftime of a second-order reaction

Consider the reaction

$$A + B \rightarrow P \qquad (1)$$

and let us use capital letters to signify the initial concentrations of the reactants and lower case letters for the concentrations at any other time. The rate of product formation is given by

$$\frac{dp}{dt} = k_2 ab \tag{2}$$

The halftime ($t_{0.5}$) for the reaction can be obtained from the integrated form of Eqn. 2, for which two cases must be considered:

Case 1, A = B
Integration of Eqn. 2 yields

$$k_2 t = \frac{p}{A(A-p)} = \frac{p}{B(B-p)} \tag{3}$$

at the halftime, $p = A/2 = B/2$ and substitution in Eqn. 3 gives

$$t_{0.5} = \frac{1}{k_2 A} = \frac{1}{k_2 B} \tag{4}$$

Case 2, $A \neq B$
Integration of Eqn. 2 yields

$$k_2 t = \frac{1}{A-B} \ln \frac{B(A-p)}{A(B-p)} \tag{5}$$

and the halftime can be obtained for two different conditions:
(i) $A > B$, in which case $p = B/2$ at $t_{0.5}$ and substituting in Eqn. 5 gives

$$t_{0.5} = \frac{1}{k_2(A-B)} \ln \frac{2A-B}{A} \tag{6}$$

(ii) $A < B$, in which case $p = A/2$ at $t_{0.5}$ and substituting in Eqn. 5 gives

$$t_{0.5} = \frac{1}{k_2(A-B)} \ln \frac{B}{2B-A} \tag{7}$$

The solutions of Eqns. 4, 6 and 7 are illustrated in Fig. 9; k_2 was set arbitrarily at a value of 10^9 $M^{-1} \cdot s^{-1}$ and B at a value of 10^{-6} M. A logarithmic scale was employed for the abscissa to illustrate the behavior of the halftime over a wide range of concentration of reactant A.

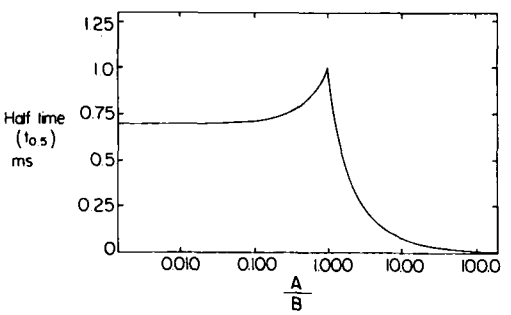

Fig. 9. Theoretical behavior of the halftime of a second-order reaction.

Acknowledgements

We are indebted to Heather Bonner for preparing the chromatophores and to Peggi Mosley and Barbara Bashford for preparing the manuscript. The work was supported by a grant No. GM 12202 from the United States Public Health Service. P.L.D. acknowledges his Research Career Development Award 1-K4-GM 70771.

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