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Fast phases of the generation of the transmembrane electric potential in chromatophores of the photosynthetic bacterium *Ectothiorhodospira shaposhnikovii*

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Ectothiorhodospira shaposhnikovii **chromatophores were associated with a collodion film and kinetics of generation of the transmembrane electric potential ($\Delta\psi$) were investigated in the 'chromatophore-collodion film' system, using an electrometric technique with a high resolution time (over 200 ns). A generation of $\Delta\psi$ (the chromatophore interior positive) following a laser flash was observed, the kinetics consisting of three components of the following half-times: less than 200 ns (phase 1); 2–7 μs (phase 2); and 120 μs (phase 3). A redox titration of the kinetic phases was performed. Computer analysis of the results has shown that the midpoint potentials (E_m) of the phase 1 at pH 7.5 are +400 mV and −75 mV, whereas those of the phase 2 are +310 mV and +35 mV. The comparison of the kinetic and potentiometric characteristics of the $\Delta\psi$ generation with analogous characteristics of the electron-transport processes, measured by optical spectroscopy, suggested that phases 1, 2 and 3 are associated with the electron transfer from P-890 to the primary quinone acceptor Q_a, from the high-potential cytochrome C_H to P-890, and with the reduction of secondary acceptor Q_b, respectively. From the amplitude characteristics of the $\Delta\psi$ components, a tentative scheme of the intramembrane localization of the electron carriers is presented.**

Introduction

The electron transfer in the photosynthetic reaction center complexes is accompanied by the formation of local and transmembrane electric fields [1–4]. Electrogenic nature of these reactions has been demonstrated by making use of variety of indirect methods (such as monitoring of the absorption changes of the photosynthetic pigments – carotenoids, chlorophylls, pheophytins [1,2,5,6], or externally added oxonol and cyanine dyes [7,8], oxidation–reduction poise shifts between primary electron donor P-870 and cytochrome c_2 [9]) as indicators of light-induced electric potentials.

To avoid some uncertainties in interpretation of experimental data, a direct method to monitor transmembrane electric potential ($\Delta\psi$) has been developed in several groups [3,4,10–13]. A modification of this technique using an association of bacterial chromatophores with a phospholipid-impregnated film can be used [14,15]. By comparing the kinetic, thermodynamic and other characterics of the rise and decay phases of the observed

Abbreviation: DAD, 2,3,5,6-tetramethyl-*p*-phenylenediamine (diaminodurene).

photopotential and the respective electron-transfer characteristics measured by optical methods, it has been possible to identify the stages of $\Delta\psi$ generation and to infer the topology of some electron carriers in the membrane [15,16].

In the present work, this approach was used to study some steps of the photosynthetic electron transfer, in particular the oxidation of cytochromes *c*. In purple bacteria, cytochrome *c* is a donor for photooxidized reaction center pigment, P-870 (P-890 or P-980 in different species) [17,18]. The bacteria *Chromatium vinosum, Chromatium minutissimum, Rhodopseudomonas gelatinoza, Rhodopseudomonas viridis, Ectothiorhodospira shaposhnikovii* * have two types of membrane-bound cytochrome *c* which are closely associated with the reaction center: a high-potential cytochrome C_H (the midpoint potential $E_m = +300$ mV) and a low-potential cytochrome C_L ($E_m \approx 0$–10 mV). The functional characteristics of the two cytochromes have been studied in detail. It has been demonstrated that both the high-potential and low-potential cytochromes *c* can reduce the same photooxidized reaction center bacteriochlorophyll [20,21]: the high-potential cytochrome acting as an intermediate of cyclic electron transport, and the low-potential cytochrome mediating electron flow between the photosystem and a substrate, say H_2S [17].

It is worth mentioning that in the *E. shaposhnikovii, C. vinosum* and other bacteria containing membrane-bound cytochromes *c*, the carotenoid bandshift is much smaller than that in *Rhodopseudomonas sphaeroides* or related species [5,8,22–24]. For this reason it is rather difficult to use the carotenoid bandshift as a probe to study the contribution of the membrane-bound cytochrome *c* into $\Delta\psi$ generation. This difficulty can be overcome by measuring $\Delta\psi$ by the electrochromic response of external dye [8] or by the electrometric method. The latter approach has an unambiguous advantage of direct monitoring a charge movement across the membrane, and it also has sufficiently high time-resolution to study primary reactions of electron transfer in photosynthetic reaction center. This approach was applied in the present work to investigate the kinetics of $\Delta\psi$ generation in *E. shaposhnikovii* chromatophores under varying redox conditions. The results are compared with the kinetics of the electron transfer reactions followed spectrophotometrically.

* According to recent results of DNA–DNA hybridization technique [19], *E. shaposhnikovii* and *E. mobilis* species are very similar. Typical strain of *E. shaposhnikovii* (st. N1) is almost identical to *Ectothiorhodospira mobilis* st. 8115.

Methods

E. shaposhnikovii was grown and chromatophores isolated after ultrasonic disruption of intact cells by the method described elsewhere [25].

Measurements of transmembrane electric potential and oxidation-reduction titrations were done as described previously [3,15,16]. Chromatophores were attached to the surfaces of a collodion film impregnated with a decane solution of asolectin. To this end, a chromatophore suspension was added to one of two buffer solutions of identical composition (40 mM $MgSO_4$/50 mM Tris-HCl, pH 7.5) separated with a collodion film. After a 10–15 h incubation at room temperature the buffer solution without chromatophores and $MgSO_4$ was substituted for the chromatophore-containing mixture. Probing absorption changes and their redox titration were made as described elsewhere [26,27]. A 'Nova 3D' computer was used to analyze the $\Delta\psi$ kinetics and to process experimental titration data.

Results

Kinetics of the rise of the photoelectric response

Fig. 1 shows the rise and decay kinetics of the electric-potential difference induced by a single laser flash in a chromatophore-collodion film system. As is seen, in such a system in the presence of reduced diaminodurene (DAD), with no other additions, the laser flash induces the generation of $\Delta\psi$ with an amplitude of about 10 mV, the chromatophore-free surface of the film positive (curve A). The kinetics of $\Delta\psi$ rise are characterized by a fast phase ($\tau_1 \leqslant 200$ ns) and a slow exponential phase with a τ_2 value of 7 μs. The fast phase kinetics cannot be resolved with our electrometer technique. The addition of ascorbate and vitamin K_3 caused an increase in the amplitude of the fast phase (τ_1), some acceleration of the slow phase

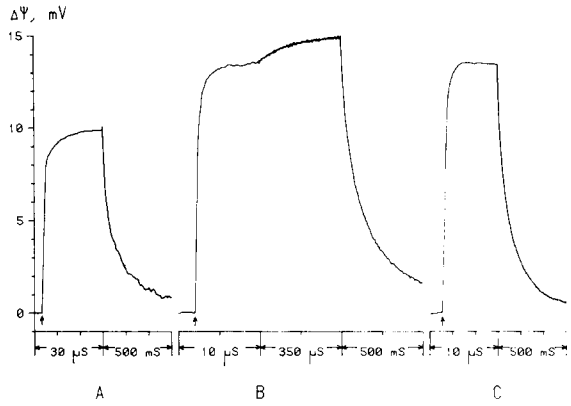

Fig. 1. Kinetics of the laser flash-induced formation of photoelectric potential ($\Delta\psi$) in a chromatophore-collodion film system. Additions: (A) $2 \cdot 10^{-4}$ M diaminodurene (DAD); (B) DAD, $2 \cdot 10^{-4}$ M vitamin K_3 and $2 \cdot 10^{-3}$ M ascorbate; (C) as in (B) plus $2 \cdot 10^{-3}$ M *o*-phenanthroline. Incubation medium: 50 mM Tris-HCl buffer I (pH 7.5). Bacteriochlorophyll concentration, $2 \cdot 10^{-5}$ M. Arrows indicate laser flashes.

(τ_2, 2 μs), and an appearance of a third exponential phase (τ_3, 120 μs) (curve B). The addition of *o*-phenanthroline, an inhibitor of electron transfer between the primary acceptor Q_a and the secondary acceptor Q_b, brings about the disappearance of the slowest (120 μs) phase.

In *E. shaposhnikovii* chromatophores, the decay of $\Delta\psi$ occurs much faster than in *Rps. sphaeroides* and *R. rubrum* chromatophores [15,16], probably due to the higher passive permeability of the *E. shaposhnikovii* chromatophore membrane. It was also shown [25,28] that in these chromatophores one failed to observe such energy-linked reactions as photophosphorylation, and generation of large $\Delta\psi$ under steady-state conditions in the light.

Electron micrographs show that the photosynthetic intracytoplasmic membrane in the whole cells of *E. shaposhnikovii* has lamellar structure [29]. Its disruption may result in the apparent leakiness of *E. shaposhnikovii* membrane particles.

Redox titration of the photoelectric response

As is seen from Fig. 2, the amplitude of the photoelectric response reaches its maximum within the range +100 mV to +250 mV and reduces beyond this range, i.e., when the redox potential of the medium, E_h, is smaller than +100 mV or larger than +250 mV. The amplitude of the photoresponse was measured 20–30 μs after the flash so that only the first two phases were taken into account. Obviously, the results of the redox titration of this biphasic response must be approximated by a curve of four transitions (two on the oxidative and two on the reductive sides). The experimental points were approximated by a computer simulation using a least-squares technique. The results are shown in Fig. 2. The best fit was achieved with a theoretical curve plotted on the basis of the Nernst equation for four one-electron transitions at the following midpoint potentials: $E_{m_1} = -75$ mV (relative contribution, +0.75); $E_{m_2} = +35$ mV (contribution, +0.25); $E_{m_3} = +310$ mV (contribution, −0.35), and $E_{m_4} = +400$ mV (contribution, −0.65).

For comparison, a theoretical curve is presented

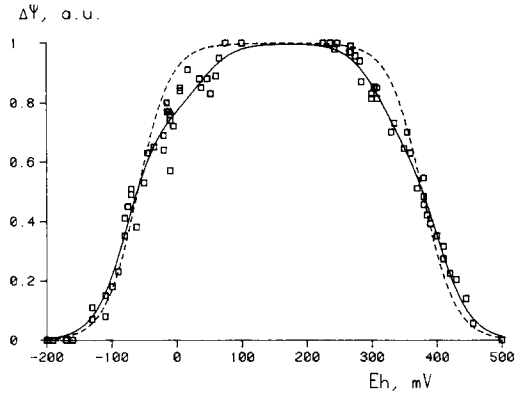

Fig. 2. Redox titration of the amplitude of the photoelectric response in a chromatophore-collodion film system. Incubation medium: 50 mM Tris-HCl buffer (pH 7.5). Redox mediators: 30 μM phenazine methosulfate; 30 μM phenazine ethosulfate; 100 μM 2-CH_3O-1,4-naphthoquinone; 100 μM 1,4-naphthoquinone sulphonate; 20 μM diaminodurene; 100 μM vitamin K_3 (at redox potential of the medium E_h from +150 mV): 150 μM variamine blue, or 20 μm diaminodurene, 100 μM vitamin K_3 (at redox potentials of the medium, E_h from +150 mV to +500 mV). Redox potential of the medium (E_h) was changed under reductive titration by adding sodium ascrobate, NADH and dithionite, or under oxidative titration by adding $K_3[Fe(CN)_6]$. The solid line drawn through the points is a theoretical $n = 1$ line derived from the Nernst equation for four $n = 1$ transitions. The parameters of the transitions (midpoint potential E_m and relative contribution ΔU) were computed by a least-squares techniques: $E_{m_1} = -75$ mV ($\Delta U_1 = 0.75$), $E_{m_2} = +35$ mV ($\Delta U_2 = 0.25$), $E_{m_3} = +310$ mV ($\Delta U_3 = -0.35$), $E_{m_4} = +400$ mV ($\Delta U_4 = -0.65$). For comparison a theoretical computer-simulated curve plotted on the assumption of two transitions with $E_m = -60$ mV and $E_m = +380$ mV is presented (dashed line).

in the figure plotted on the assumption of only two transitions. It is seen that this curve approximates experimental results much poorly.

Fig. 3 shows kinetics of the photoelectric responses for varying redox potnetials of the incubation medium, corresponding to different transitions. Over the redox potentials from +100 mV to +250 mV, the kinetics of the $\Delta\psi$ rise consist of phases 1 and 2 (with τ_1 and τ_2) (Fig. 3B). Beyond this region, the phase characterized by τ_2 shows a gradual decline in amplitude until it disappears completely (Fig. 3A and C). Analysis of the kinetic curves for different redox potentials shows that the transitions with $E_{m_2} = +35$ mV and $E_{m_3} = +310$ mV correspond to the second phase of the $\Delta\psi$ generation ($\tau_2 = 2$–7 μs) and the transitions with $E_{m_1} = -75$ mV and $E_{m_4} = +400$ mV, to the phase of $\tau_1 \leqslant 200$ ns.

Comparison of the kinetic and potentiometric characteristics of the $\Delta\psi$ generation with electron transfer characteristics

To identify mechanisms of electrogenic phases, we have compared their kinetic and potentiometric characteristics with those of the primary electron-transfer reactions available from optical measurements. Laser-flash-induced absorption changes of chromatophores and reaction center bacteriochlorophyll P-890 were measured in the Soret band, as described earlier [15,16]. The kinetic curves are presented in Fig. 4. As demonstrated earlier, the

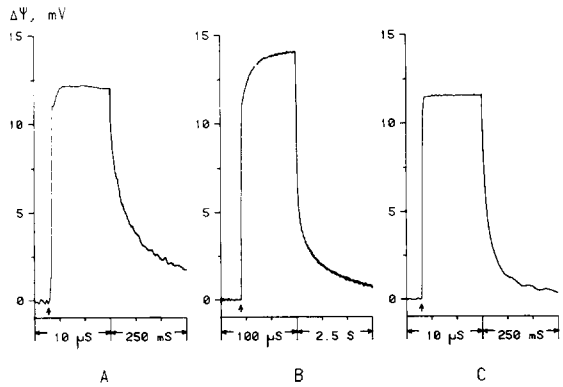

Fig. 3. Kinetics of the photoelectric response under varying redox potentials of the incubation meidum. Conditions as in Fig. 2. (A) $E_h = -10$ mV; (B) $E_h = +215$ mV; (C) $E_h = +350$ mV.

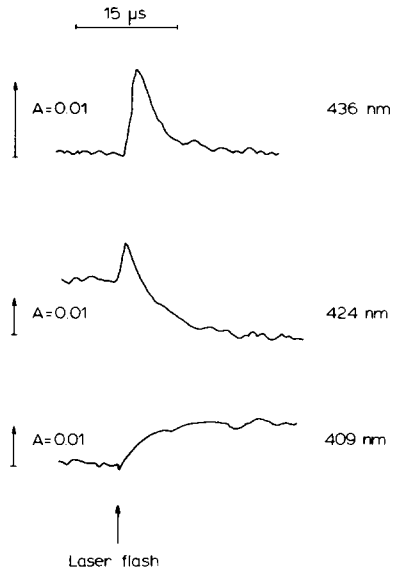

Fig. 4. Kinetics of laser flash-induced absorption changes in a chromatophore suspension.

absorption increase at 436–440 nm is due to P-890 oxidation. The half-time of the rise of this effect is shorter than the recording time scale of the spectrophotometer used (up to 300 ns Fig. 4, upper trace). The absorbance increase at 409 nm is associated with the oxidation of cytochrome *c*. In our experiments, its kinetics ($t_{1/2} = 2.5$–3.5 μs, Fig. 4, lower trace) were the same as those of P-890 reduction, in good agreement with the view that cytochrome *c* is an immediate donor for P-890. The observed 424 nm absorption changes (Fig. 4, central trace) include both the absorbance increase, due to P-890 oxidation, and absorbance decrease, due to its reduction, which goes concomitant with the oxidation of cytochrome *c*.

We performed a redox titration of the P-890 absorption changes (Fig. 5). The experimental points are well approximated by a theoretical curve computed by the Nernst equation for an one-electron transition with midpoint potentials of +400 mV and −90 mV. These agree well with our previous estimates [14,16] and are those that are known to be inherent in P-890/P-890$^+$ and Q_a/Q_a^- couples (400 mV and −90 mV, respectively). It appears that the reduction kinetics of P-890$^+$ coincide very well with the oxidation kinetics of cytochrome *c* over the entire range of the redox potentials studied.

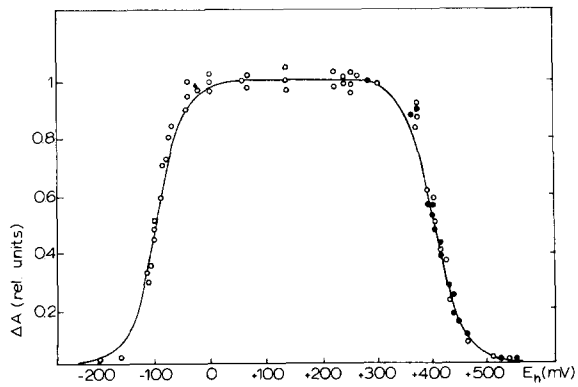

Fig. 5. Redox titration of photo-induced absorption changes at 436–440 nm (○———○) and 890 nm (●———●) in a chromatophore suspension. The 436–440 nm absorption changes were activated by a laser flash and those at 890 nm by continuous illumination. Redox mediators added to the incubation medium: 150 μM variamine blue, 50 μM 2,6-dichlorophenol-indophenol, 50 μM *N,N,N′,N′*-tetramethyl-*p*-phenylenediamine (oxidative part of the curve) and 10 μM phenazine methosulphate, 100 μM indigotetrasulphonate, 100 μM indigodisulphonate (reductive part), pH 7.4. The line drawn through the points is a theoretical $n = 1$ line derived from the Nernst equation for midpoint potentials of +400 mV and −90 mV.

It is worth noting that the absolute rate of the process increases with lowering the redox potential from +100 mV to −50 mV (Fig. 6). In accordance with the generally accepted point of view, one may attribute this effect to the reduction of the low-potential cytochrome C_L ($E_m = +25$ mV, Fig. 6), which reduces P-890$^+$ with a higher rate

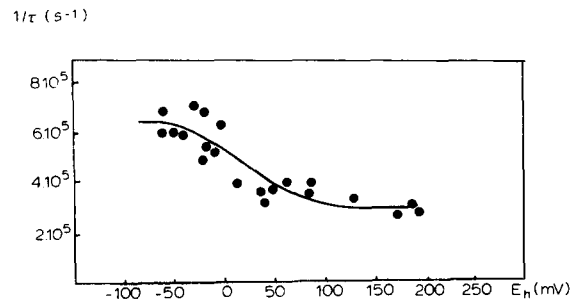

Fig. 6. The characteristic time of flash-induced electron transfer from cytochrome *c* to P-890 as a function of redox potential of the medium. Respective kinetic curves for $E_h = +200$ mV are given in Fig. 4. Redox mediators: 20 μM phenazine methosulphate/50 μM, *N,N,N′,N′*-tetramethyl-*p*-phenylenediamine/100 μM indigodisulphonate/100 μM indigotetrasulphonate (pH 7.0).

than the high-potential cytochrome C_H [10,12,14, 16]. In our earlier work [14], the midpoint potential of the high-potential cytochrome in *E. shaposhnikovii* chromatophores was estimated as +290 mV. We suggest therefore that at redox potentials between +350 mV and +100 mV, it is cytochrome C_H that acts as an immediate donor for P-890$^+$, whereas between +50 and −100 mV this function is performed by cytochrome C_L. Note that as the redox potential is increased from +200 mV to +350 mV, C_H oxidation proceeds at a rate decreased by 2–4 times and the reduction of P-890$^+$ slows to the same extent. The reason for such phenomena are not clear yet. A similar slowing of the cytochrome C_H oxidation was observed under a weak background illumination and after pretreatment with a laser flash. Such exposures cause the oxidation of a part of the cytochrome C_H pool (which may be either chemical, in the case of increasing redox potential, or photoinduced). The observed effect of acceleration of the $C_H \rightarrow$ P-890 reaction between $E_h = +350$ and $E_h = +200$ mV cannot presumably be explained by reduction of two haemes, compared to one, of C_H, because in this case one can expect only doubling the probability of electron donation. In our experiments, however, oxidation rates have been trustworthly changed by a higher factor. It is possible that the observed effect is an expression of the cooperative properties of the reaction involving the C_H cytochrome. The elucidation of this question needs a further study.

Fig. 7 represents results of experiments in which

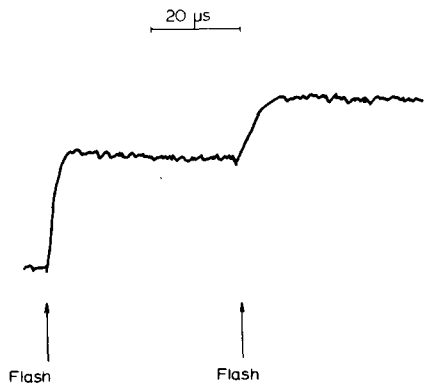

Fig. 7. Kinetics of absorption changes of a chromatophore suspension at 409 nm, induced by successive laser flashes.

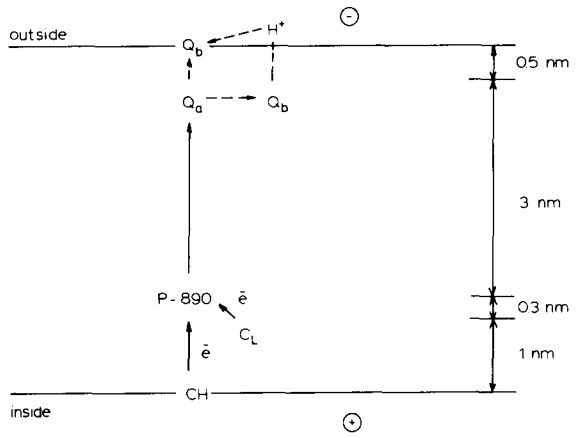

Fig. 8. Localization of some redox components of the electron-transport chain in the chromatophore membrane of *E. shaposhnikovii*. C_H and C_L, high and low potential cytochromes *c*, respectively. Q_a and Q_b, primary and secondary quinones, respectively.

E. shaposhnikovii chromatophores were exposed to two successive laser flashes. As is seen, the first flash of saturating intensity causes the only partial oxidation of the cytochrome *c* pool (that of cytochrome C_H, since E_h was about +200 mV). The second flash added 45 μs after the first flash brings about additional oxidation of the cytochrome. As found [21,22,30], this is due to the fact that a cytochrome molecule has more than one haeme, or that two or more molecules of cytochrome interact with the reaction center. Parson has suggested a method based on this arrangement of cytochromes for estimating the rate of electron transfer from the primary acceptor Q_a to secondary acceptors Q_b [30]. The essence of the method is to vary the dark interval between the first and second flash and measure the extent of cytochrome oxidation, following the second flash, as a function of the dark interval. We have performed such measurements on chromatophores of *E. shaposhnikovii* and obtained τ of approx. 140 μs for this reaction (not shown in the figures) (see also Ref. 31).

Discussion

It has been found in our previous investigations on chromatophores from the photosynthetic bacteria *Rps. sphaeroides, R. rubrum* and *C. minutissimum* [15,16] that the fast phase of the rise kinetics of $\Delta\psi$ (less than 200 ns) is due to electron transfer form P-870 (P-890) to the primary acceptor Q_a and that the slower phase, which is sensitive to *o*-phenanthroline (τ = 100–200 μs), is due to electron transfer from Q_a to Q_b. The findings of the present work are in good agreement with this concept. In fact, the midpoint potentials of the titration curve for the phase 1 are identical close to the P-890/P-890$^+$ (E_m = +400 mV for both cases) and of Q_a/Q_a^- couple (−75 mV and −90 mV, respectively). Hence, one may postulate that the phase 1 is due to the charge separation in the reaction center.

Good agreement exists between the kinetic phase 3 (τ, 120 μs) and the rate of electron transfer from Q_a to Q_b (τ, 140 μs). This fact, together with the sensitivity of the 120 μs phase to *o*-phenanthroline, indicates that it is associated with the reduction of Q_b.

The phase 2 (2–7 μs) is likely to be due to electron transfer from cytochrome C_H to P-890$^+$. An indication of this is evident from the coincidence of the kinetics of the two processes and the similarity of their redox potentials. E_m of C_H^{ox}/C_H^{red} was +330 mV when measured under redox titration of flash-induced cytochrome oxidation [22]; E_m of electrogenic phase 2 was +310 mV. In some experiments, the time-course of the phase 2 was longer (7 μs) than that of oxidation of cytochrome (2.5–3.5 μs). This seeming disagreement may be due to conditions used in electrometer experiments (DAD without other additions, see Fig. 1) in which the cytochrome was not completely reduced. As mentioned above, under oxidizing conditions the rate of electron transfer from cytochrome C_H to P-890$^+$ is 2–4 times slower than under conditions where the cytochrome is completely reduced.

On lowering the redox potential from +100 mV to −50 mV, the phase 2 shows a decline in amplitude (E_m = 35 mV, Figs. 2 and 3). As mentioned, it is in this region of redox potentials that the chemical reduction of the low-potential cytochrome C_L occurs (E_m = 0–25 mV, Fig. 6; see also Ref. 26). Upon reduction, the cytochrome C_L acts as a donor for P-890$^+$. In this conditions the cytochrome C_H does not undergo oxidation after the flash. The conclusion that may be drawn is that the transfer of an electron from cytochrome

C_H to P-890$^+$ is accompanied by the generation of $\Delta\psi$ of much higher magnitude than that coupled with the cytochrome C_L oxidation. From the data, presented at Fig. 2, one can easily calculate that electron transfer from C_L to P-890 is about 1/4–1/3 of that from C_H to P-890 $(\Delta U_3 - \Delta U_2)/\Delta U_3 = (0.35 - 0.25)/0.35 \approx 0.29$. This number is in a good agreement with that (0.26) observed by Itoh, who used merocyanine dye to measure the membrane potential in *C. vinosum* [8]. An observation of this kind has been also reported by Case and Parson for the high- and low-potential cytochromes in *C. vinosum* [5]. In sulphur purple bacteria, to which *C. vinosum* and *E. shaposhnikovii* belong, the photosynthetic charge separation is accompanied only by a negligible absorption shift of carotenoids. Nevertheless, Case and Parson have revealed, using a signal-averaging technique, that in the case when the electron donation to P-890$^+$ is from the high-potential cytochrome *c*-555, the amplitude of the carotenoid absorbance shift is four times higher than when P-890 is reduced by the low-potential cytochrome *c*-553.

The 120 μs phase of $\Delta\psi$ generation may be due to electron transfer from Q_a to secondary quinone acceptor Q_b if Q_a is further from outer surface of the chromatophore membrane than Q_b. If not, electrogenesis may accompany H^+ translocation from the water phase to Q_b. The latter possibility seems to be more adequate because the rate of electron transfer from Q_a to Q_b when measured in the whole *E. shaposhnikovii* cells by the method of successive laser pulses does not depend upon transmembrane electric field [32]. An indication of non-electrogenic nature of $Q_a \rightarrow Q_b$ electron transfer has been recently obtained in *Rps. sphaeroides* [33]. However, at present we cannot completely exclude this possibility in *E. shaposhnikovii* chromatophores.

The measured potential is determined, in the simplest case, by the distance passed by a charged particle (electron or an ion) through the hydrophobic region of the membrane in the direction perpendicular to the membrane plane. Data of the $\Delta\psi$ measurements may provide information on the mutual arrangement of the components of the electron-transport chain. If one assumes that the dielectric constant of the environment is the same for the whole thickness of the membrane, the distance between the electron carriers may be estimated. A tentative scheme of the arrangement of the electron carriers within the photosynthetic membrane in *E. shaposhnikovii* chromatophores is presented in Fig. 8. The estimation of distances is made taking into account the above assumption. The thickness of the hydrophobic layer is taken as 5 nm.

There are different techniques which may be used in an investigation of the localization of photosynthetic components and the distance between them. They are based on immunochemical studies, linear dichroism, ESR, and other methods [35–37]. The results show many similarities with our data, despite the fact that they were obtained by different techniques and for different species. It should be noted, however, that the applicability of each of the above methods is limited, and the interpretatations are not unambiguous sometimes. Only combined analysis obtained by different methods may provide the adequate picture of the topography of the electron carriers in the membrane.

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