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BLUE AND RED SHIFTS OF BACTERIOCHLOROPHYLL ABSORPTION BAND AROUND 880 nm IN *RHODOSPIRILLUM RUBRUM*

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Summary

The redox potential dependence of the light-induced absorption changes of bacteriochlorophyll in chromatophores and subchromatophore pigment-protein complexes from *Rhodospirillum rubrum* has been examined. The highest values of the absorption changes due to the bleaching of *P*-870 and the blue shift of *P*-800 in chromatophores and subchromatophore complexes are observed in the 360—410 mV redox potential range. At potentials below 300 mV (pH 7.0), the 880 nm band of bacteriochlorophyll shifts to shorter wavelengths in subchromatophore complexes and to longer wavelengths in chromatophores.

The data on redox titration show that the red and blue shifts of 880-nm bacteriochlorophyll band represent the action of a non-identified component (C_{340}) which has an oxidation-reduction midpoint potential close to 340 mV ($n = 1$) at pH 6.0—7.6. The E_m of this component varies by 60 mV/pH unit between pH 7.6 and 9.2.

The results suggest that the red shift is due to the transmembrane, and the blue shift to the local intramembrane electrical field. The generation of both the transmembrane and local electrical fields is apparently governed by redox transitions of the component C_{340}.

Introduction

The light-induced absorption changes of purple bacteria in the near infrared region are connected with different processes. The bleaching at 865 nm, which

Abbreviations: CCCP, carbonyl cyanide *m*-chlorophenylhydrazone; TMPD, *N,N,N',N'*-tetramethyl-*p*-phenylenediamine.

was first demonstrated by Duysens [1] in *Rhodospirillum rubrum*, is due to the oxidation of *P*-870 bacteriochlorophyll [2] and is accompanied by the blue shift of *P*-800 [3]. Vermeglio and Clayton [4] assumed that the absorption decrease at 865 and 810 nm reflects the bleaching of the two components of a bacteriochlorophyll dimer, which acts as the primary electron donor. The absorption increase at 790 nm, according to Vermeglio and Clayton [4], 'represents the appearance of a monomeric band in place of the dimer spectrum, as a result of electron donation'.

Along with the bleaching of *P*-870, Vredenberg and Amesz [5,6] detected light-induced shifts of bacteriochlorophyll absorption bands to longer wavelengths in the spectral region of 820—930 nm. These shifts might reflect an energized state of the chromatophore membranes [7] or the action of reaction centers differ from the *P*-870 [8—10].

Our data show that the red shifts of bacteriochlorophyll absorption bands in the cells and chromatophores of purple bacteria [11—13] as well as in the proteoliposomes [14] containing the reaction center plus light-harvesting antenna complexes are due to the light-induced generation of transmembrane electrical potential difference and local intramembrane electrical field. Case and Parson [15] proposed that the light-induced red shifts of bacteriochlorophyll bands in *Chromatium vinosum* chromatophores are accompanied by oxidation of cytochrome *c*-555.

Sybesma and Vindevogel [16] described the shift of 880-nm band of bacteriochlorophyll to shorter wavelengths in *R. rubrum* chromatophores upon the addition of dithionite and/or valinomycin in the dark.

The purpose of the present communication was to set up a study of the blue shift of 880-nm bacteriochlorophyll band and of the relationship between the blue and red shifts of this band in *R. rubrum*.

Materials and Methods

Rhodospirillum rubrum wild type was grown anaerobically in a medium as described by Cohen-Bazire et al. [17] and chromatophores were prepared by ultrasonic treatment of the washed bacterial cells [13]. Subchromatophore particles (*P*-870 reaction center plus light-harvesting antenna complexes) were isolated by solubilization of chromatophores with sodium cholate as described previously [14,18].

The measurements of the absorption changes of chromatophores and subchromatophore particles in the region of 730—930 nm were performed on a single-beam differential spectrophotometer [19]. The absorption changes were induced by actinic light of saturating intensity ($\lambda > 700$ nm).

Oxidation-reduction titration of the light-induced absorption changes was carried out with potassium ferricyanide under aerobic conditions using platinum and Ag/AgCl electrodes. The potential of the reference electrode measured in 100 mM potassium phosphate buffer containing equimolar quantities of potassium ferri- and ferrocyanide was equal to 230 ± 3 mV as described by O'Reilly [20].

Incubation medium for the chromatophores contained 50 mM sodium phosphate (pH 7.0). The subchromatophore particles were incubated in the same

buffer containing 0.5—1.0% sodium cholate. The pH values in some experiments were varied from 6.0 to 8.0 by addition of NaOH and from 8.0 to 9.2 by addition of Tris buffer. The concentrations of dyes used as redox buffers and of other additions are indicated in captions to Figures.

Results

Subchromatophore pigment-protein complexes of *R. rubrum* show the light-induced absorption changes with a positive maximum at 790 nm and with negative maxima at 812 and 865 nm (Fig. 1, line 1). This spectrum is similar to that for chromatophores [11,13]. Addition of TMPD and mammalian cytochrome *c* (E_h = 220 mV) causes a significant change of the difference spectrum. The spectrum observed is characterized by a blue shift of the 880 nm absorp-

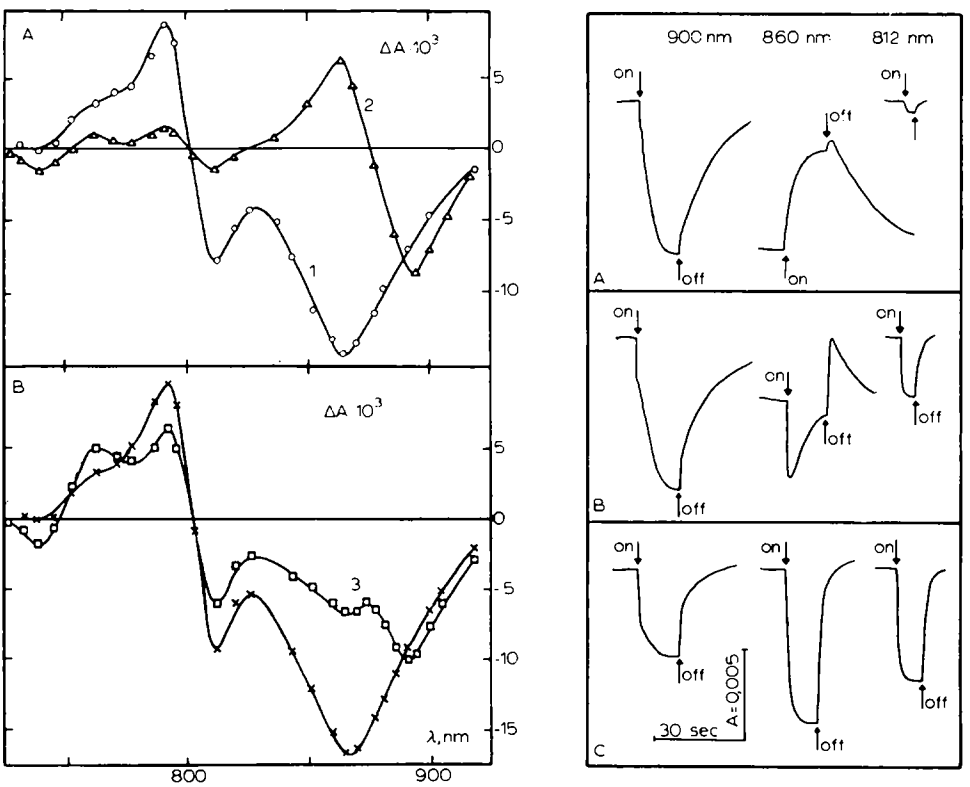

Fig. 1. Light-induced absorption difference spectra of *R. rubrum* subchromatophore pigment-protein complexes at different redox potentials. (1) Without additions; (2) in the presence of 0.3 mM TMPD and 0.15 mM horse heart cytochrome *c* (E_h = 220 ± 10 mV); (3) in the presence of 0.3 mM TMPD, 0.15 cytochrome *c* and 0.15 mM potassium ferricyanide (E_h = 300 ± 5 mV); (4) in the presence of 0.3 mM TMPD, 0.15 mM cytochrome *c* and 0.4 mM potassium ferricyanide (E_h = 360 ± 10 mV). A_{880nm} = 1.0, pH 7.0.

Fig. 2. Kinetics of the light-induced absorption changes of *R. rubrum* subchromatophore pigment-protein complexes at different wavelengths and redox potentials. (A) E_h = 220 ± 10 mV; (B) E_h = 300 ± 5 mV; (C) E_h = 360 ± 10 mV. Incubation mixture contains 0.3 mM TMPD and 0.15 mM cytochrome *c*, A_{880nm} = 1.0, pH 7.0.

tion band of bacteriochlorophyll: by an absorption increase at 865 nm, a bleaching at 895 nm and by an inhibition of the absorption changes near 800 nm (Fig. 1, line 2). *o*-Phenanthroline at a concentration of 2—8 mM does not influence these absorption changes (not shown).

The spectral changes due to the blue shift of bacteriochlorophyll band are monophasic. Half-times ($t_{1/2}$) of the signal appearance upon illumination and of its relaxation in the dark are equal to 2—3 and 6—7 s, respectively (Fig. 2A).

The absorption changes in the region of 840—930 nm are biphasic and in the region of 730—840 nm monophasic, as the ambient redox potential increases from 220 to 300 mV. A $t_{1/2}$ of the rapid phase is 0.5—0.7 s (Fig. 2B). The difference spectrum presented in Fig. 1, line 3 represents only the photobleaching phase at the redox potential of 300 mV; a negative maximum at 865 nm is due to the oxidation of *P*-870, whereas another maximum at 895 nm, to the blue shift of 880-nm bacteriochlorophyll band. The similar absorption changes are observed in the absence of cytochrome *c* as well as with phenazine methosulfate or diaminodurene instead of TMPD (data not shown).

An increase of E_h to 360 mV causes a stimulation of the photobleaching at 860 and 812 nm and a disappearance of the 895-nm band. Under these conditions, the absorption changes at 812, 860 and 900 nm ($t_{1/2}$ of the relaxation in the dark is 0.5—1.0 s) are kinetically similar (Fig. 2C); the spectrum of these absorption changes (Fig. 1, line 4) coincides with that in Fig. 1, line 1. As seen from Fig. 1, a red shift of bacteriopheophytin is observed in a spectral region of 730—780 nm. The absorption changes due to this shift increase when the E_h value is declined.

Thus, the light-induced absorption changes of chlorophyll pigments observed in the subchromatophore complexes in the region of 730—950 nm are dependent on the redox potential and represent the bleaching of *P*-870, the blue shift of *P*-800, the red shift of bacteriopheophytin, as well as the blue shift of 880-nm band of bacteriochlorophyll.

Fig. 3A shows the redox potential dependence (pH 7.0) of the rapid phase of the photobleaching at 860 and 900 nm (*P*-870), of the slow phase of the photobleaching at 900 nm (the blue shift of the bacteriochlorophyll absorption band near 880 nm) and of the photobleaching at 812 nm. Normalized magnitudes of the bleaching at 812 and 860 nm as well as of the rapid phase of the bleaching at 900 nm increases in the 200—360 mV redox potential range and decreases upon the further increase of the E_h to 500 mV. The experimental points fit well the theoretical lines from the Nernst relationship for a one-electron transfer with the E_m values of 307 ± 10 and 445 ± 10 mV, respectively.

A disappearance of the *P*-870 absorption changes at $E_h < 370$ mV is probably due to the reduction of *P*-870$^+$ by TMPD and cytochrome *c* that is more rapid than the *P*-870 photooxidation. Such an effect is not found upon fast time resolution after a flash excitation [23].

A normalized magnitude of the slow phase of the bleaching at 900 nm decreases upon the increase of the redox potential as a theoretical line for an $n = 1$ redox reaction with the E_m of 350 ± 10 mV.

Upon the increase of pH from 7.0 to 9.0 (Fig. 3B), the E_m of the slow phase of the bleaching at 900 nm falls to 238 ± 10 mV, the E_m of the bleaching at 812 and 860 nm and of the rapid phase of the bleaching at 900 nm shifts to

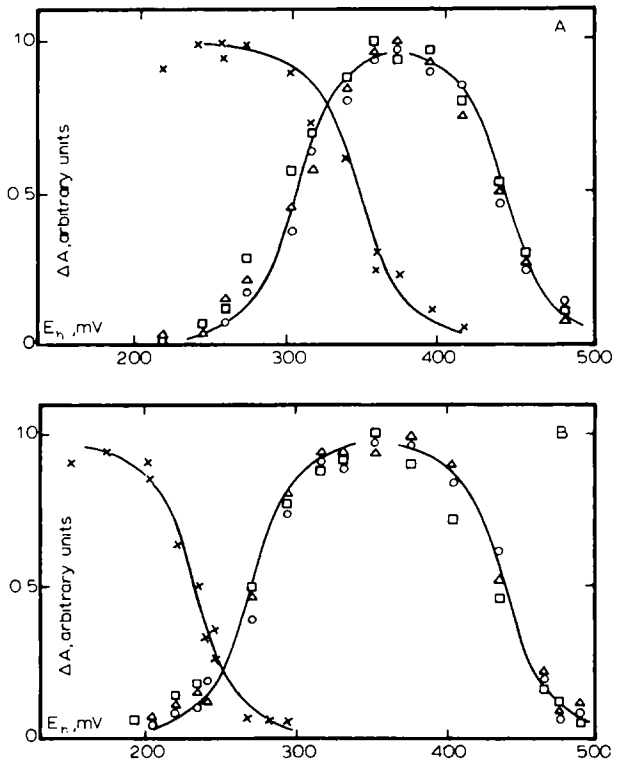

Fig. 3. The redox potential dependency of the light-induced absorption changes of *R. rubrum* subchromatophore pigment-protein complexes. (A) pH 7.0; (B) pH 9.0. ○, the bleaching at 860 nm; △, the bleaching at 812 nm; □, the rapid phase of the bleaching at 900 nm; X, the slow phase of the bleaching at 900 nm; the solid lines reflect theoretical lines for an $n = 1$ redox reaction. Incubation mixture contain 0.3 mM TMPD, 0.15 mM cytochrome *c*, $A_{880nm} = 1.2$.

275 ± 10 mV on the reductive side and remains the same as before on the oxidative side of the titration curve.

The midpoint potential of the slow phase of the bleaching at 900 nm is independent of TMPD concentration in the range from 0.01 to 2.0 mM (Fig. 4). This means that the rate constant for the electron transfer between TMPD and a corresponding electron donor or acceptor is unchanged in this concentration range of TMPD.

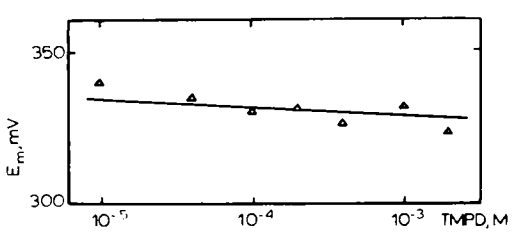

Fig. 4. The equilibrium midpoint potential of the slow phase of the photobleaching at 900 nm in *R. rubrum* subchromatophore pigment-protein complexes as a function of the TMPD concentration. Incubation mixture contains TMPD and 0.15 mM cytochrome *c*, $A_{880nm} = 1.25$, pH 7.0.

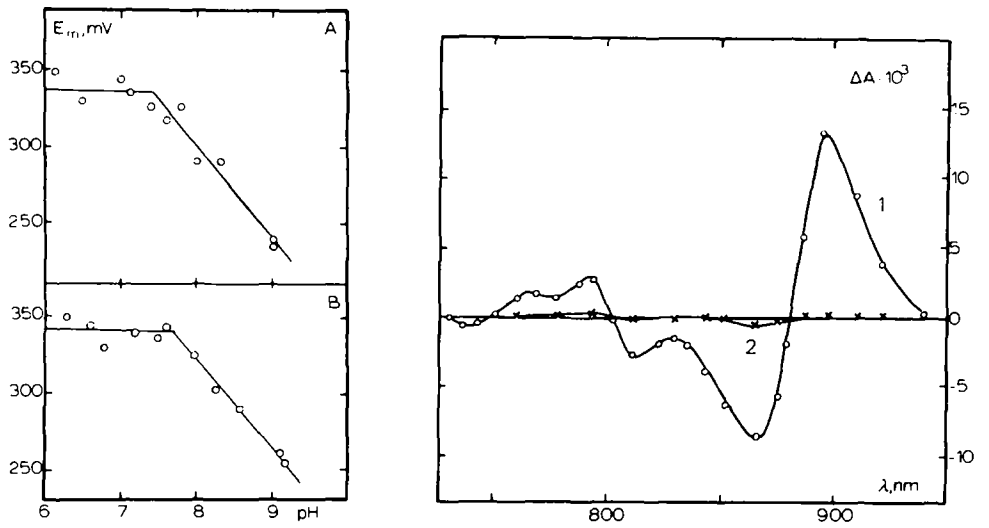

Fig. 5. The equilibrium midpoint potential of the absorption changes due to the blue and red shifts of 880-nm bacteriochlorophyll absorption band as a function of pH. (A) The slow phase of the photobleaching at 900 nm in *R. rubrum* subchromatophore pigment-protein complexes. Incubation mixture contains 0.3 mM TMPD and 0.15 mM cytochrome *c*, $A_{880nm} = 1.2$. (B) The absorption difference (ΔA^{+CCCP}_{895nm} minus ΔA^{-CCCP}_{895nm}) in *R. rubrum* chromatophores. Incubation mixture contains 0.2 mM TMPD, 0.1 mM phenazine methosulfate and 1 mM sodium ascorbate, $A_{880nm} = 1.3$.

Fig. 6. Light-induced absorption difference spectra of *R. rubrum* chromatophores. (1) In the presence of 0.2 mM TMPD, 0.1 mM phenazine methosulfate and 1 mM sodium ascorbate ($E_h = 100 \pm 15$ mV); (2) 1 plus $1 \cdot 10^{-6}$ M CCCP. $A_{880nm} = 1.3$, pH 7.6.

Fig. 5A shows that the E_m of the slow phase of the photobleaching at 900 nm is pH independent at pH 6.0—7.6 and varies by -60 ± 12 mV/pH unit between pH 7.6 and 9.2. The data presented indicate that a component, whose functioning in subchromatophore complexes is reflected by the blue shift of 880-nm absorption band of bacteriochlorophyll, requires one proton per electron reduction. The break at pH 7.6 indicates the functional pK of this component.

In the second series of experiments, we have examined the properties of the light-induced red shift of 880-nm bacteriochlorophyll absorption band in *R. rubrum* chromatophores incubated with TMPD, phenazine methosulfate and ascorbate ($E_h = 100 \pm 15$ mV). As it is shown in Fig. 6 (line 1), the red shift of bacteriochlorophyll in the chromatophores is a mirror image of the blue shift of 880-nm band in the subchromatophore particles (see Fig. 1, line 2).

An addition of the uncoupler CCCP removes the absorption changes due to the red shift of bacteriochlorophyll (Fig. 6, line 2; see also Ref. 11). Under these conditions, there are insignificant absorption changes associated with the photobleaching of *P*-870.

A change of the redox potential from 100 to 380 mV causes an increase in the photobleaching at 860, 895 and 812 nm, which is declines upon a further increase of the redox potential (Fig. 7A). The experimental points measured in the presence of CCCP fit a theoretical line for an $n = 1$ redox reaction with midpoint potentials of 312 ± 10 and 437 ± 10 mV (pH 7.6) on the reductive

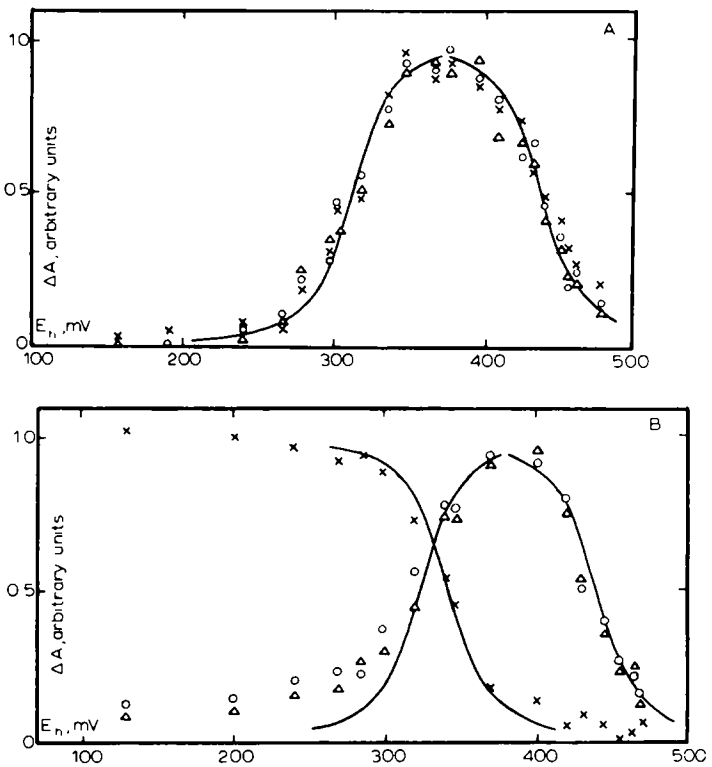

Fig. 7. The redox potential dependency of the light induced absorption changes of *R. rubrum* chromatophores. (A) pH 7.6, in the presence of $1 \cdot 10^{-6}$ M CCCP; ○, the bleaching at 860 nm; △, the bleaching at 812 nm; X, the bleaching at 895 nm. (B) pH 7.6 (○), bleaching at 860 nm in the presence of CCCP; △, bleaching at 812 nm in the presence of CCCP; X, the absorption difference (ΔA^{+CCCP}_{895nm} minus ΔA^{-CCCP}_{895nm}). Incubation mixture contains 0.2 mM TMPD, 0.1 mM phenazine methosulphate and 1 mM sodium ascorbate, $A_{880nm} = 1.3$. The solid lines reflect theoretical lines for an $n = 1$ redox reaction.

and oxidative sides, respectively. These data show that the absorption changes in the region of 770—930 nm observed in the presence of CCCP are caused by the photobleaching of *P*-870 and by the blue shift of *P*-800 only.

In the absence of CCCP, the absorption increase at 895 nm due to the red shift of 880-nm band disappears and interchanges with a bleaching when the redox potential is above 80—100 mV. A superposition of two types of the absorption changes near 895 nm, that are opposite in sign and observed at a time, presents difficulties for their correct redox titration.

In order to determine the true E_h dependency of the absorption changes due to the red shift of 880-nm band, we have measured the redox potential depending of the absorption changes at 895 nm in the chromatophores incubated with and without CCCP. A magnitude of the photobleaching at 895 nm measured in the absence of the uncoupler was subtracted then at the same E_h values from a magnitude of the absorption change observed in the presence of the uncoupler. A difference obtained (ΔA^{+CCCP}_{895nm} minus ΔA^{-CCCP}_{895nm}) provides a correct magnitude of the absorption increase at 895 nm (the positive maximum of the red shift of 880-nm band).

A normalized value of the absorption increase at 895 nm decreases upon the increase of the redox potential as a theoretical line for an $n = 1$ redox reaction (Fig. 7B). The E_m for the red shift of 880-nm band at pH 7.6 is equal to 342 ± 10 mV. Similar values of the E_m were obtained for the light-induced absorption changes due to the red shifts of the bacteriochlorophyll bands in chromatophores of *Chromatium vinosum* [10,15]. When E_h is above 320 mV, normalized magnitude of the photobleaching at 860 and 812 nm observed in the absence of CCCP vary in the same manner as in the presence of CCCP. At potentials below 300—320 mV, these absorption changes do not coincide with a theoretical line for a one-electron transfer. This is connected with the presence of absorption changes sensitive to an uncoupler. The E_m values of the photobleaching at 860 and 812 nm are equal to 320 ± 10 and 440 ± 10 mV (pH 7.6) on the reductive and oxidative sides of the titration curve respectively (Fig. 7B).

At pH 9.2, a character of titration curves remains the same as before. The E_m of the bleaching at 860 and 812 nm shifts to 298 ± 10 mV on the reductive side and is equal to 435 ± 10 mV on the oxidative side. The E_m of the absorption changes at 895 nm shifts to more negative potentials.

The E_m of the red shift in chromatophores, along with the E_m of the blue shift in subchromatophore complexes, is independent of pH in the range from 6.0 to 7.6 (Fig. 5A, B) and varies by −60 ± 10 mV/pH unit upon the increase of pH from 7.6 to 9.2.

Discussion

It was shown by Okayama et al. [21] that a minor band of the photobleaching at 890 nm was observed in *R. rubrum* chromatophores treated with antimycin A. Similar absorption changes arise in the chromatophores incubated without exogenous electron donors upon the addition of uncouplers [11,13]. The results presented in the present paper show that the photobleaching at 890 nm in the chromatophores can be due to the blue shift of 880-nm absorption band (the negative band with the maximum near 895 nm). Sybesma and Vindevogel [16] showed that the blue shift of 880-nm band in *R. rubrum* chromatophores arises in the dark upon the addition of dithionite and also of valinomycin.

The results obtained suggest that these spectral shifts of bacteriochlorophyll represent a oxidation-reduction transition of a non-identified component (C_{340}) of the photosynthetic electron transfer chain.

Case and Parson [15] have demonstrated that the bacteriochlorophyll band shift correlates well with the photooxidation of cytochrome *C*-555 whose E_m is pH independent [22]. The E_m value of the component C_{340} (340—350 mV at pH 6.0—7.6) appears to exclude the cytochrome components as possible candidates for a role of C_{340}. According to Dutton and Jackson [23], the E_m values of cytochromes c_2, *b*, *cc'* and *b* in *R. rubrum* chromatophores at pH 7.2 are equal to 293, 170, −5 and −105 mV, respectively. It was shown that the E_m of cytochrome c_2 in the chromatophores of *Rhodopseudomonas sphaeroides* and *Rps. capsulata* is independent of pH in the range from 5.0 to 11.0 [24].

There are several lines of evidence that the red shift of bacteriochlorophyll in

the chromatophores is due to the transmembrane electrical field (with 'plus' inside):

(1) the red shift arises in the dark upon the addition of ATP, inorganic pyrophosphate or valinomycin in the combination with K^+ [11,13],

(2) the red shift induced by inorganic pyrophosphate is independent of redox potential [25,13],

(3) the light-induced red shift is observed in proteoliposomes containing subchromatophore pigment-protein complexes of *R. rubrum* [14],

(4) the red shift observed upon an energization of the chromatophores is removed by uncouplers.

(5) the absorption changes associated with the bacteriochlorophyll red shift are similar in properties to carotenoid shifts [13] for which there is convincing evidence for the electrochromic in origin [26—33].

Inasmuch as the blue shift of 880-nm bacteriochlorophyll is a mirror image of the red shift observed in the chromatophores and is manifested in both the native membranes and the non-membrane subchromatophore particles (incapable to an exhibition of the uncoupler-sensitive bacteriochlorophyll red shift [14]), it is believed that the blue shift is due to a local intramembrane electrical field arising upon the functioning of photosynthetic redox chain components.

Data on the action of local electric fields on the carotenoid spectral properties are contained in the literature. An illumination or a treatment of the isolation *P*-870 reaction center complexes from *Rps. sphaeroides* by ferricyanide causes the red shift and a treatment by dithionite, the blue shift in the carotenoid spectrum [34]. Authors suggested that the illumination leads to the formation of $P\text{-}870^+ \cdot$ ferroquinone$^-$ electrical dipole, ferricyanide to formation of $P\text{-}870^+$ monopole and dithionite to formation of ferroquinone$^-$ or bacteriopheophytin$^-$ monopole.

By analogy with the view of Cogdell et al. [34] on the shifts in the carotenoid absorption spectrum, we may assume that the *o*-phenantroline-insensitive blue shift of 880-nm bacteriochlorophyll is due to the electrical monopoles of the reduced tightly bound (primary) ubiquinone and of reduced bacteriopheophytin since such an effect is also observed upon a treatment of the *R. rubrum* chromatophores by dithionite [16].

As shown by Shuvalov et al. [35], an accumulation of ubiquinone radical anion is accompanied by the red shift of bacteriopheophytin (see Figs. 1 and 6) upon illumination of *R. rubrum* reaction center complexes.

Thus, the light-induced bacteriochlorophyll absorption changes in the near infrared region represent a superposition of the absorption changes connected with the oxidation of the *P*-870 reaction centers, the red shift of 88-nm bacteriochlorophyll under the action of the transmembrane electrical field, and the blue shift of 880-nm bacteriochlorophyll under the action of the local electrical field. The generation of both the transmembrane and the local electrical field appear to govern by redox transitions of the component C_{340}.

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