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The effects of lithium dodecyl sulfate and sodium borohydride on the absorption spectrum of the B800–850 light-harvesting complex from *Rhodopseudomonas acidophila* 7750

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The effects of the detergent lithium dodecyl sulfate and the reducing agent sodium borohydride on the absorption spectrum of the B800–850 light-harvesting complex from *Rhodopseudomonas acidophila* 7750 were determined. Treatment of B800–850 complex with 0.1% lithium dodecyl sulfate results in an approx. 85% attenuation of the bacteriochlorophyll absorption band at 800 nm and 2–4 nm red-shifts of the bacteriochlorophyll absorption bands at 590 nm and 857 nm and a 4 nm blue-shift of the carotenoid absorption bands. Treatment with sodium borohydride resulted in an attenuation of the bacteriochlorophyll absorption band at 800 nm, a 1 nm red-shift of the bacteriochlorophyll 857 nm absorption band and an attenuation of the carotenoid bands. A comparison of the effects suggests that lithium dodecyl sulfate induces a nonspecific change in the antenna complex, possibly a protein conformational change whereas sodium borohydride chemically modifies both bacteriochlorophyll and carotenoid. The spectral changes are interpreted in terms of alterations in the pigment interactions which are responsible for the native absorption properties of B800–850 complexes.

Introduction

The light-harvesting system of purple photosynthetic bacteria is comprised of discrete pigment-protein complexes which contain noncovalently bound bacteriochlorophyll (BChl) and carotenoid molecules [1]. One of the pigment-protein complexes, denoted B800–850 for its approximate absorption wavelength maxima in the near infrared spectral region, has a bacteriochlorophyll-to-carotenoid ratio of 2 : 1 (Cogdell, R.J. and Evans, M.B., unpublished data; and Ref. 2) per pair of apoproteins. The absorption band at approx. 850 nm has been attributed to an exciton-coupled dimer of BChl molecules, whereas the 800 nm absorption band has been attributed to monomeric BChl [3]. The 800 nm BChl absorption band is red-shifted and more intense by a factor of about 2–3 compared to the corresponding monomeric BChl absorption spectrum in solution. The near infrared absorption maximum of BChl in vitro occurs at approx. 770 nm [4]. The molecular

Abbreviation: BChl, bacteriochlorophyll.

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features which give rise to the spectral properties of BChl in the B800–850 complex are not well understood [5,6]. A complete description of these spectra involves understanding the nature of the pigment-pigment and pigment-protein interactions which exist within the complex.

The pigment interactions which give rise to the in vivo spectral features have been probed by several groups using optical spectroscopic techniques applied to altered B800–850 complexes [3,7–10]. Sauer and Austin [3] discovered that the 800 nm absorption band of B800–850 complex from *Rhodobacter sphaeroides* 2.4.1 could be attenuated by repeatedly freezing and thawing the sample in the presence of strong white light. They observed that the 850 nm absorption and circular dichroism properties were unaffected by the bleaching of the 800 nm absorption band. Cogdell et al. [9,10] reported that proteolysis of chromatophores of *Rhodopseudomonas capsulata* resulted in a loss of the 800 nm BChl absorption band and an approx. 5 nm blue-shift of the carotenoid absorption bands. From this they concluded that the carotenoid associated with the B800–850 complex is located on the same apoprotein as the 800 nm absorbing BChl monomer. Clayton and Clayton [8] reported that the 800 nm absorbance of B800–850 complex from *Rb. sphaeroides* 2.4.1 could be attenuated using lithium dodecyl sulfate (LDS) in an electrophoresis preparation [11]. Dialysis of the sample against Tris buffer containing lauryldimethylamine *N*-oxide (LDAO) reinstated the 800 nm absorption band. They concluded that monomeric bacteriochlorophyll can interact reversibly with a specific binding site on the protein. Kramer et al. [2] extended this work and constructed a structural model for the B800–850 complex based on differences observed in the absorption, fluorescence polarization, linear dichroism and circular dichroism spectra taken from complexes prepared in LDS or LDAO. They proposed that the B800–850 minimal unit consists of regular aggregates of two bacteriochlorophyll dimers, two bacteriochlorophyll monomers and three carotenoid molecules noncovalently bound to two pairs of apoproteins [2]. Based on an observed LDS-induced 30% reduction in the carotenoid-to-bacteriochlorophyll singlet–singlet energy-transfer efficiency they concluded that the carotenoid molecules are divided into two spectrally distinct pools, one-third of the carotenoids being associated with the bacteriochlorophyll monomers and absorbing approx. 4 nm to the red of the remaining two-thirds of the carotenoids which are presumed associated with the bacteriochlorophyll dimers [2]. The sizes of the pools were based on the observation that the carotenoid-to-bacteriochlorophyll singlet energy-transfer efficiency was reduced by approx. 30% in the preparation where the 800 nm absorbing bacteriochlorophyll was dislocated. An assumption in this work was that the preparation of the complex using LDS causes only the dislocation of the monomeric 800 nm-absorbing bacteriochlorophyll molecule and results in a complex that is otherwise structurally identical to B800–850 complex prepared in LDAO.

The use of sodium borohydride as a pigment-specific modifying agent in reaction centers of *Rb. sphaeroides* R26 has recently been demonstrated [12]. The addition of sodium borohydride to the reaction-center preparation converts one of the bound BChl molecules into a bacteriopheophytin derivative [12]. The other pigments and the structure of the protein appear to be unaffected by the procedure [12,13]. Callahan et al. [14] recently reported that upon addition of tetrabutylammonium borohydride to B873 antenna complex from *Rhodospirillum rubrum*, the C_2 acetyl and possibly the C_9 ketyl groups of BChl *a* are reduced. Recently, it has been demonstrated that the 800 nm absorption band in B800–850 complexes may be selectively attenuated upon treatment with sodium borohydride (Steiner, R. and Scheer, H., unpublished data).

In this paper we present an investigation of the magnitude and dynamics of the LDS- and sodium borohydride-induced changes which occur in the absorption spectrum of the B800–850 complex from *Rhodopseudomonas acidophila* 7750. The spectral observations are interpreted in terms of changes in the pigment interactions which are responsible for the absorption properties of the native complex. Part of these results have been reported in preliminary form elsewhere [15].

Materials and Methods

Cells of *Rps. acidophila* 7750 were grown as previously described [16]. The cells were harvested

by centrifugation at 15 000 × *g*. Broken cells were prepared by French pressure disruption according to Cogdell et al. [16]. The B800–850 complex was isolated from *Rps. acidophila* 7750 as follows [17]: broken cells were adjusted to an absorbance of 50 cm^{-1} at the absorbance maximum near 860 nm using 20 nM Tris (pH 8.0). LDAO was added to the broken cells to a final concentration of 1.0% and the mixture was incubated at 26 °C for 5 min. The solubilized membranes were centrifuged at 15 000 × *g* for 10 min. The pellet, which contains cellular debris was discarded, whereas the supernatant, which contains solubilized pigment-protein complexes, was retained. The supernatant was diluted to approx. 4 times the original volume with 20 mM Tris (pH 8.0). The diluted supernatant was applied to a DEAE-Sephacel column (150 ml bed volume) which had previously been equilibrated with 20 mM Tris-HCl (pH 8.0). The column was eluted with buffers containing 20 mM Tris (pH 8.0), 0.1% LDAO and 0–320 mM NaCl (in 40 mM steps). The B800–850 complex was eluted in the fractions which contained approx. 200 mM NaCl. The complex was purified further by a second pass through a DEAE-Sephacel column followed by molecular sieve chromatography on a Sephadex G200 column. Only fractions in which the 857 nm to 280 nm absorbance ratio was greater than 2.3 were used.

B800–850 complex at an optical density of 1 cm^{-1} measured at 857 nm (approx. 8 μM) in 10 mM Tris buffer (pH 8.0) containing approx. 0.07% LDAO was treated with lithium dodecyl sulfate (LDS) by adding 10% aqueous solution of LDS (final LDS concentration was 0.1%) to a cuvette containing 3 ml of B800–850 complex. In the sodium borohydride experiments, B800–850 complex was diluted to an absorbance of approx. 1 cm^{-1} at 857 nm with 100 mM Tris buffer (pH 8.0) containing 0.02% LDAO. A small amount of solid sodium borohydride on the tip of a spatula was added to a cuvette containing 3 ml of B800–850 complex. The pH of the solution was monitored and did not exceed 9.0. The antenna protein solutions in the LDS and sodium borohydride experiments were gently stirred and spectra were recorded at various time intervals after addition of the reactant. Absorption spectra were taken on a Perkin-Elmer Lambda 3B spectrophotometer using a 1 cm path-length cuvette. Fluorescence excitation spectra were taken on a Perkin-Elmer MPS-66 spectrofluorometer using a 0.1 cm path-length cuvette.

Results

Fig. 1 shows the effect on the absorption spectrum of adding 0.1% LDS to the B800–850 complex isolated from *Rps. acidophila* 7750. The BChl dimer absorption band at 857 nm (denoted Q_y) has been red-shifted by approx. 2 nm, attenuated by nearly 10% and broadened by about 0.7 nm (FWHM). The BChl monomer Q_y band near 800 nm has been reduced to less than 15% of its original intensity. Two small broad peaks have grown in at approx. 680 nm and 770 nm. The BChl absorption band near 590 nm (denoted Q_x) has decreased in intensity by approx. 40% and has been red-shifted by about 4 nm. The carotenoid absorption bands have been blue-shifted by approx. 5 nm. The blue-shift in the carotenoid absorption spectrum upon LDS treatment is also accompanied by a 10–15% decrease in intensity of the long-wavelength vibronic band and a comparable increase in intensity of the short-wavelength band. The BChl Soret absorption bands at 373 nm lose approx. 13% of their intensity. The Soret bands also narrow but do not shift their absorption maxima. The protein absorption peak near 281 nm increases in intensity by approx. 4% upon LDS addition.

Overnight dialysis of the LDS treated B800–850

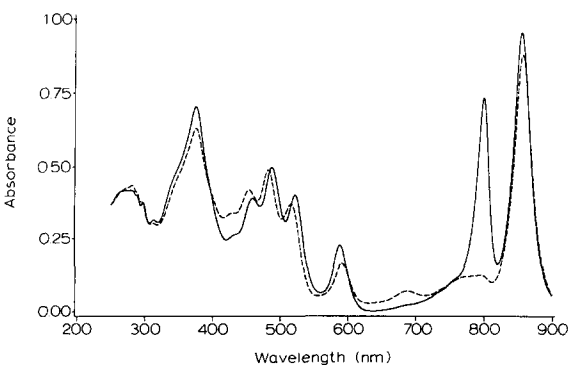

Fig. 1. The effect of LDS on the absorption spectrum of B800–850 complex from *Rps. acidophila* 7750. The spectra were not normalized and were taken from samples having identical protein concentrations.

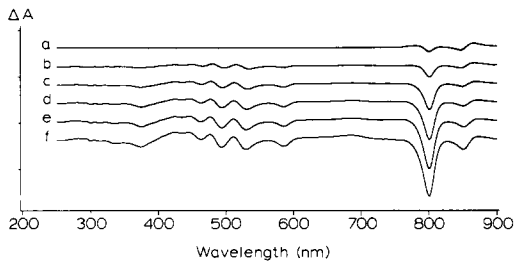

Fig. 2. The dynamics of the LDS-induced changes in the absorption spectrum of B800–850 complex from *Rps. acidophila* 7750. The spectra represent differences in absorbance after the addition of LDS minus the absorbance prior to LDS addition. Times elapsed after the addition of 0.1% LDS are: (a) 1.75 min; (b) 9.38 min; (c) 25.28 min; (d) 40.28 min; (e) 62.12 min; (f) 138.78 min. Each spectrum has been offset for clarity of presentation. The cuvettes were not removed from the spectrophotometer between successive runs.

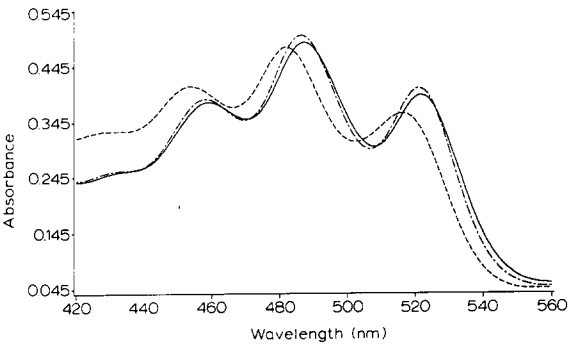

Fig. 3. The effect of LDS on the carotenoid absorption spectrum of B800–850 complex from *Rps. acidophila* 7750. The solid line corresponds to the spectrum prior to LDS addition. The spectrum represented by the alternating dashed and dotted line was taken 4.92 min after LDS addition. The spectrum represented by the dashed line was taken 141.95 min after LDS addition.

complex against 20 mM Tris buffer (pH 8.0) to remove the LDS followed by addition of LDAO (final concentration of 0.3%) resulted in an approx. 70% recovery of the intensity of the 800 nm absorption band and a reduction of the intensity of the small broad peak at 770 nm. The 680 nm absorbing species could be removed by sucrose density gradient centrifugation suggesting it is unbound pigment by-products.

The dynamics of the LDS-induced changes are illustrated in Fig. 2 as a series of difference spectra taken at various time intervals after LDS addition. The loss in intensity of the 800 nm BChl Q_y, the BChl Q_x and the Soret bands, the carotenoid band-shift and the increase in the protein absorbance were found to occur at the same rate ($t_{1/2} = 40 \pm 10$ min). The BChl absorption band at 857 nm exhibited an essentially immediate 1 nm red-shift and a subsequent slower 1 nm red-shift and 10% attenuation. The direction of the spectral shift of the 857 nm absorption band was found to be dependent on LDAO concentration. If the LDAO concentration was reduced to less than 0.01% when 0.1% LDS was added the 857 nm peak exhibited an initial 1 nm blue-shift followed by a subsequent 2 nm red-shift. The spectral changes observed in the other absorption bands were found to be independent of LDAO concentration.

Fig. 3 focuses on the detailed carotenoid absorption changes. There is an initial (time ≈ 295 s) rapid increase in intensity of all three carotenoid absorption bands followed by a slower, more gradual decrease in intensity of the two long-wavelength vibronic bands. The short-wavelength vibronic band increases in intensity throughout the time-course of the experiment. This increase and the blue-shift of the entire carotenoid absorption spectrum occur concomitantly with the decrease in BChl absorption intensity at 800 nm.

Fig. 4 shows the change in the protein absorption region (250–305 nm). After addition of LDS the absorption band increases in intensity between 265 and 295 nm having a maximum at 281 nm.

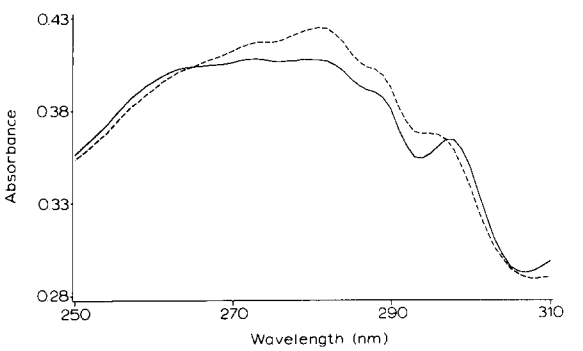

Fig. 4. The effect of LDS in the protein absorption region of B800–850 complex from *Rps. acidophila* 7750. The solid line corresponds to the spectrum taken prior to LDS addition. The dashed line corresponds to the spectrum taken 143.78 min after LDS addition.

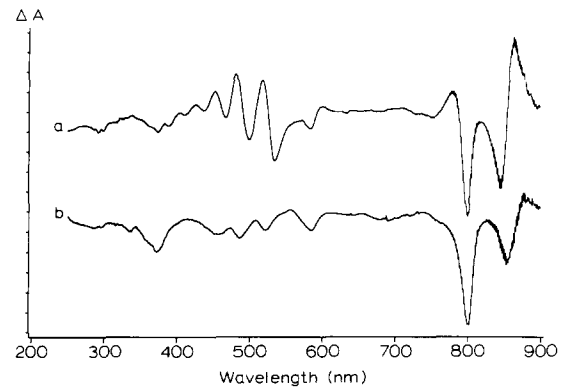

Fig. 5. A comparison of the effect of LDS and sodiumborohydride on the absorption spectrum of B800–850 complex from *Rps. acidophila* 7750. (a) The difference in absorbance 1.75 min after the addition of LDS minus the absorbance prior to LDs addition. (b) The difference in absorbance 1.63 min after the addition of sodium borohydride minus the absorbance prior to sodium borohydride addition.

Fig. 5 compares the LDS induced changes in the B800–850 absorption spectrum to the sodium borohydride-induced effects. The spectra are representative of differences between successive spectral runs. The sodium borohydride-induced difference spectrum is markedly similar to the LDS-induced difference spectrum in the BChl Q_y regions. Both spectra show an attenuation of the 800 nm band and a red-shift of the 857 nm band. In the 857 nm region of the sodium borohydride-induced spectrum, the area of the positive lobe is smaller than that of the negative lobe indicating that the shift in the spectrum is accompanied by an overall loss of intensity in the 857 nm band. The 857 nm region of the LDS-induced spectrum displays approximately equal positive and negative lobe areas indicating little change in the overall intensity of the band upon LDS treatment.

The most striking differences between the LDS-induced and the sodium borohydride-induced absorption changes are seen at 770 nm and in the carotenoid and Soret absorption regions (Fig. 5). In the LDS-induced spectrum an increase in absorbance occurs at 770 nm. This is probably due to the release of BChl. No absorption increase at 770 nm is observed in the sodium borohydride-induced difference spectrum. Decreases in absorbance at 800 nm (Q_y), 590 nm (Q_x) and in the Soret region are observed in the sodium borohydride-induced spectrum, indicating that a chemical reaction with BChl has occurred. The carotenoid bands in the sodium borohydride-induced spectrum are uniformly attenuated indicating that the sodium borohydride is chemically reacting with the carotenoids as well. Addition of sodium borohydride to a solution of β-carotene (approx. 0.1 μM) in 100 mM Tris (pH 8.0) containing 0.3% LDAO resulted in a similar attenuation of the carotenoid absorption bands (Chadwick, B.W. and Frank, H.A., unpublished data). In contrast to the sodium borohydride-induced absorption decreases in the carotenoid region, LDS induces significant blue-shifts in the carotenoid bands as discussed above and which are evident in Fig. 5. The LDS – induced spectral changes also differed from the sodium borohydride-induced spectral changes in the magnitude of the attenuation of the 800 nm BChl absorption band. Addition of LDS resulted in greater than 85% attenuation of the 800 nm absorption band whereas treatment with sodium borohydride resulted in approx. 25% attenuation at 800 nm.

Fluorescence excitation spectra (data not shown) of the lowest energy BChl emission (monitored at 860 nm) for the *Rps. acidophila* 7750 B800–850 complex were used in conjunction with the absorption spectra (Fig. 1) to determine the effect of LDS addition on the efficiency of energy transfer from carotenoid to the 857 nm absorbing BChl. The efficiency of singlet–singlet energy transfer was found to decrease from $51 \pm 3\%$ to $33 \pm 3\%$ corresponding to an approx. 35% reduction after addition of LDS. In a parallel study of the B800–850 complex from *Rb. sphaeroides* 2.4.1, we observed a reduction in the efficiency of energy transfer from $95 \pm 5\%$ to $72 \pm 3\%$ after addition of LDS, in agreement with the previous study by Kramer et al. [2]. The efficiency of singlet–singlet energy transfer from carotenoid to BChl was also found to decrease in the sodium borohydride-treated complex. There was a $9 \pm 2\%$ reduction in energy transfer efficiency in B800–850 complex in which the sodium borohydride-induced attenuation of the 800 nm absorption band was approx. 25%.

Discussion

The changes in the B800–850 absorption spectra induced by the addition of LDS and sodium borohydride may be rationalized in terms of changes in the pigment interactions. A discussion of the effects in each spectral region follows.

Bacteriochlorophyll Q_y and Soret regions

The reduction of the BChl absorbance at 800 nm to less than 15% of its original value is the most pronounced spectral change observed when the B800–850 complex is treated with LDS (see Fig. 1). This effect was found to be approx. 70% reversible upon removal of the LDS by dialysis and subsequent addition of LDAO. Clayton and Clayton [8] also demonstrated that the 800 nm absorption band in B800–850 complex from *Rb. sphaeroides* 2.4.1 could be recovered to approx. 70% of its original intensity by dialysis of the LDS-treated complex overnight against Tris buffer containing 0.1% LDAO. Dialysis of the LDS-treated complex against Tris buffer (0.1% LDAO) which contained 2 μM free BChl facilitated restoration of the 800 nm absorption band [8]. They concluded that the presence of LDS weakens the binding of monomeric BChl to the protein and suggested that the equilibrium for BChl binding shifts towards unbound BChl, while the absence of LDS favors BChl binding to the protein [8]. This conclusion is difficult to reconcile in view of the high reversibility of the effect (more than 70% reported here). In fact Kramer et al. [2] reported a complete (100%) recovery of the 800 nm absorption band upon dialysis against Tris buffer containing 0.1% LDAO. A 100% recovery would not be expected to be observed if BChl is released from the protein in that it would be solubilized during the electrophoresis preparation and not reinstated upon dialysis. A more likely explanation for the LDS-induced effect on the 800 nm BChl absorption band is that the presence of LDS induces a conformational change in the protein resulting in a change in the interaction responsible for the wavelength of the monomeric BChl absorbance. The BChl responsible for the 770 nm absorption band is most likely still bound to the protein via its histidine coordination to the central magnesium [18]. Possibly a change in the BChl functional group binding or changes in the interactions with charged residues [19] affects the absorption band positions so that the BChl absorbs at either 770 nm or 800 nm depending on its position in the protein.

An alternative interpretation for the large LDS induced attenuation of the 800 nm BChl absorption band may be the formation of an oxidized BChl species, analogous to the oxidation of the primary electron donor and concomitant bleaching of the 870 nm absorption band reported in bacterial reaction centers [20]. This explanation is unlikely because: (1) addition of the oxidizing agent, potassium ferricyanide, resulted in an irreversible attenuation of both the 800 nm and 857 nm BChl absorption bands (Chadwick, B.W. and Frank, H.A., unpublished results); and (2) no absorption band was detected in the 900–1100 nm spectral region as expected for oxidized BChl [21].

The greater than 85% loss of absorbtion intensity at 800 nm upon LDS treatment is accompanied by a much smaller increase at 770 nm. This absorption increase is approx. 1/3 of that expected for released BChl based on an analysis of the extinction coefficients [8] of the native (800 nm-absorbing) and released (770 nm-absorbing) species and taking into account the 70% reversibility (Frank, H.A., unpublished results). At the same time the Soret peak decreases by only 13%. If 70% of the 800 nm-absorbing BChl appears at 770 nm after treatment with LDS, one would expect an approx. 30% decrease in the Soret at 373 nm.

Scherz and Parson [5,6] have shown that the formation of oligomers of BChl gives rise to an approx. 80 nm red-shift in the Q_y absorption band and an approx. 50% increase in oscillator strength. They argued that the hyperchromsim of the Q_y band occurs at the expense of the Soret bands which lose oscillator strength upon oligomer formation [5,6]. The fact that there is only a 13% decrease in intensity of the Soret accompanying the greater than 85% decrease in the 800 nm (Q_y) band upon LDS treatment is consistent with, and indicative of, intensity borrowing from the Soret by the 800 nm band in this B800–850 complex.

The 857 nm BChl band is believed to be due to dimeric BChl where the individual molecules are bound to separate subunits of the B800–850 protein [3,22,23]. Clayton and Clayton [8] have pro-

posed that the red-shift, attenuation and broadening of the absorption band near 850 nm is due to a slight structural change of the BChl dimer. Kramer et al. [2] have reported that the circular dichroism of the absorption band near 850 nm is less conservative in the presence of LDS than in LDAO. From this they concluded that in the presence of LDS there is a loss of excitonic interaction between the monomeric BChl which absorbs at 800 nm and the BChl dimer which absorbs near 850 nm [2]. A change in the structure of the BChl dimer brought about by an LDS-induced conformational change of the protein would also be consistent with these results because circular dichroism would also be sensitive to the structure of the BChl dimer. However, the sodium borohydride-induced absorption changes presented in Fig. 5, which show that chemical decomposition of the 800 nm absorbing BChl leads to a shift of the dimeric BChl absorption band, strongly suggest that the 800 nm-absorbing BChl is exciton coupled to the 857 nm-absorbing BChl. Alternatively, the removal of the monomeric BChl by sodium borohydride may induce a protein structural change (perhaps more specific than the LDS-induced change) which affects the absorption spectrum of the BChl dimer near 850 nm.

Bacteriochlorophyll Q_x region

The 4 nm red-shift and 40% attenuation of the BChl Q_x absorption band at 590 nm upon LDS treatment is undoubtedly the result of the loss of the monomeric BChl contribution to this band. Previous linear and circular dichroism analyses of the BChl Q_x (587 nm) absorption spectral region of B800–850 complex from *Rb. sphaeroides* 2.4.1 support this claim [24]. In these analyses Bolt et al. [24] suggested that the band is comprised of two components; a 584 nm contribution attributed to the Q_x transition of monomeric BChl, and a larger 592 nm contribution attributed to the Q_x of the dimeric BChl. A difference spectrum (data not shown) between the LDS-treated and untreated spectra in the Q_x region confirmed the existence of 584 nm-absorbing component.

Protein region

An increase in intensity in the protein spectral region (250–310 nm) occurs concomitantly with the attenuation of the monomeric BChl absorption bands at 800 nm, 590 nm and 373 nm. This increase in intensity is probably the result of an LDS-induced protein conformational change which leads to an increase in the absorbance associated with the aromatic amino acid residues absorbing in this spectral region. Similar effects have been documented for DNA [25]. The absorbance of ordered double-helical DNA is less than that of the free bases or of denatured DNA, suggesting that the absorption intensity of the bases in DNA is dependent on the orientation and interactions of their transition moments within the α helix.

Carotenoid region

The shifts of the carotenoid absorption bands upon exposure to LDS may be further manifestations of a protein configurational change. Kakitani et al. [19] and Wraight et al. [26] have discussed that changes in the distance and/or orientation between the carotenoid and charged amino acid residues affect the position and intensity of the carotenoid absorption bands. Birge et al. [27,28] have shown that the absorption spectra of carotenoids are sensitive to the structure of the carotenoid molecules as well as environmental factors such as solvent polarity and refractive index. Because the initial, rapid bandshift and increase in intensity of the carotenoid absorption occurs much faster than the disappearance of the 800 nm BChl absorption band upon LDS treatment, and because upon treatment of the B800–850 complex with sodium borohydride the 800 nm BChl absorption band is attenuated, and accompanied by no carotenoid band shift (Fig. 5) changes in the interaction between the carotenoid and monomeric BChl absorbing at 800 nm cannot be responsible for the carotenoid band shifts observed upon LDS treatment. More likely, upon LDS addition a protein structural change occurs which alters the interaction of the carotenoid with charged amino acids in the protein, or induces a carotenoid configurational or conformational change which would affect the carotenoid absorption properties.

Kramer et al. [2] suggested that the LDS-induced reduction in carotenoid-to-BChl singlet–singlet energy-transfer efficiency is a result of a dislocation of the monomeric BChl rendering its

associated carotenoid pool incapable of energy transfer to it in the B800–850 complex. A plausible alternative explanation is that a protein structural change induced by the presence of LDS alters the distance and/or orientation between the carotenoid and the dimeric BChl resulting in a reduction in the carotenoid-to-BChl singlet energy transfer efficiency. The present work suggests that the effect of sodium borohydride on the absorption spectrum of the B800–850 complex is to alter BChl and carotenoid chemically. In these samples the sodium borohydride-induced reduction in energy-transfer efficiency is due to the chemical modification of the pigments. In contrast, LDS appears to induce nonspecific changes in the antenna complex, possibly a conformational change in the protein, which alters the energy-transfer efficiency and the BChl, carotenoid and protein absorption properties of the complex.

Acknowledgements

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