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STUDIES OF PHOTOSYNTHETIC ENERGY CONVERSION

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ABSTRACT

(Progress since Dec. 1, 1977 is indicated by vertical lines in the margin.)

The fragments of bacterial photosynthetic membranes known as chromatophores can be oriented by drying them so that they lie flat on glass slides. Photochemical reaction centers (RCs) from these chromatophores can be oriented in stretched gelatin films. Measurements of polarized optical absorption (linear dichroism) in these preparations give angles made by electronic transition moments of pigments in relation to the plane of the membrane or to the axis of stretching in gelatin. The technique of photoselection in which photochemistry is elicited with polarized light and the consequent changes of optical absorbance are also measured with polarized light, gives angles between selected pairs of transition moments. By combining these sources of information we have developed a three-dimensional picture of the orientations of the photosynthetic pigments, bacteriochlorophyll (bchl) and bacteriopheophytin (bph), in relation to the membrane. We have thus begun to elucidate in detail the architecture of the photosynthetic membrane. These studies have also led us to reinterpret some of the well known absorbance changes in terms of photochemical oxidation of bchl in the RC.

Carotenoids, bchl and bph in the photosynthetic membrane show absorption band shifts related to the separation of electric charge in the RCs and across the membrane. These electrochromic effects have been used as probes of the distribution and movement of charge, but these responses are subject to many environmental factors that make specific interpretations uncertain. We have learned how to use variations of the bph band shifts to monitor the movement of an electron from "primary" to "secondary" ubiquinone (UQ) in the RC. We are trying to learn which carotenoid pigments respond in what ways to the movements of electrons and protons in and near the RCs in the photosynthetic membrane. Our aim is to rationalize these band shifts so that we

can map electric fields in the RC and its neighboring electron carriers, in a variety of states of oxidation or reduction of the components. This may give us information about the translational coordinates of the components, to supplement our new knowledge of the rotational coordinates and thus to complete the construction of a three dimensional model of the photosynthetic membrane.

By studying the altered optical and photochemical properties of RCs when they are dehydrated, we have shown that some anomalies in fluorescence and in photochemical kinetics, in the range 200-260°K, are related to phase transitions involving bound water. Now that we can eliminate these anomalies we can obtain more extended and meaningful data on the temperature dependence of photochemical and secondary electron transfer; these data when interpreted in terms of quantum mechanical tunneling may give estimates of the distances between bchl, bph and UQ (both primary and secondary) in the RC.

We have found that in isolated RCs and in chromatophores under suitable conditions, the molecules of UQ that serve as primary and secondary photochemical electron acceptors show binary oscillations in their redox states after consecutive flashes of light. The primary UQ, receiving an electron, is reduced to $UQ^{\cdot-}$ and no further. This electron is passed to secondary UQ, which on receiving a second electron enters the doubly reduced form $UQ^{\equiv}$. The binding of two protons forms UQH_2 . Elaborations of these observations show how the two-electron chemistry of quinones is linked to the one-electron chemistries of chlorophylls and cytochromes, and promises to clarify the electron transport cycles by which protons are translocated across the photosynthetic membrane.

New studies of RCs from Rhodopseudomonas gelatinosa and Rp. viridis indicate that these differ markedly in their protein composition from those isolated from Rp. sphaeroides, Rhodospirillum rubrum and Chromatium vinosum.

RCs from the latter three are closely similar although they exist in widely differing genera of photosynthetic bacteria. This raises questions as to the requirements for a unique molecular architecture in the photosynthetic membrane and as to the appropriateness of the genus Rhodopseudomonas as a taxonomic and phylogenetic entity.

We have isolated a specific major antenna pigment-protein complex from photosynthetic membranes, and have recombined this complex with purified RCs so as to reconstitute energy transfer with efficiency comparable to that in the intact bacterium. In doing so we have gained new information about the rate at which RCs trap excitation energy from the antenna, in both active and photochemically inactive states of the RC.

We have begun a basic photochemical characterization of phycochromes, photoconvertible pigments that may be the receptors for chromatic adaptation in blue-green algae. The response to lowering the temperature is unique: the reaction (photoconversion between "green" and "red" states) is reversible at room temperature but becomes unidirectional below 260°K. If the living algae show a correspondingly unusual chromatic adaptation response after a light program at low temperature, this will strengthen the identification of phycochrome as the trigger for chromatic adaptation.

Bacteriorhodopsin, a close analog of the visual pigment of higher animals, supports light-dependent ATP formation in halophilic bacteria by effecting the photochemical pumping of protons across the cell membrane. By studying the fluorescence of this pigment as a function of temperature we have augmented our knowledge of the physical states involved in the photochemistry.

ACCOMPLISHMENTS: RESEARCH IN OUR LABORATORY SINCE 9/1/75

(Progress since 12/1/77 is indicated by vertical lines in the margin)

Orientations of components of the photosynthetic membrane.

A. Vermeiglio showed in our laboratory (40) that chromatophores (vesicular photosynthetic membrane fragments) from Rp. sphaeroides, when dried onto glass slides, show linear dichroism in the absorption spectra of pigments of both the antenna and the reaction centers. The same technique could be applied to chromatophores in which the antenna pigments had been irreversibly bleached by exposure to chloroiridate, leaving the absorption spectrum of the RCs more clearly exposed. We assume that the chromatophores were flattened so that the plane of the membrane was predominantly parallel to the slide, and that this orientation was responsible for the linear dichroism. Analysis of dichroic ratios, with the electric vector of the measuring light polarized either parallel to or at an angle with the plane of the slide, gave some indications of the orientations of various optical transition moments relative to the membrane. Some of these findings were not novel (47), but we were led to reinterpret the light-induced absorbance changes of RC bchl in the near infrared. The absorption spectrum of these RCs shows bands at 870, 800 and 760 nm. The 870 nm band is identified with the "special pair" (photochemical electron donor), the 800 nm band with the two molecules of bchl in each RC that do not participate in electron donation ("voyeur" bchl or P800), and the 760 nm band with the bph of the RC. The light-induced changes appear superficially to be a bleaching of the 870 nm band (oxidation of the special pair), and a blue-shift of the band at 800 nm, previously attributed to an electric field effect on the P800. Changes in dichroic ratios near 800 nm led us to conclude that the "800 nm blue-shift" is actually the bleaching of one band at 810 nm and the appearance of a new band at 795 nm. The 810 and 870 nm bands, which are reversibly bleached by light, can be regarded as the expected exciton

components of the Q_y transition of a dimer, the bchl special pair. The new band at 795 nm then represents a monomer-like transition of the singly oxidized special pair, B_2^+ . The 870 and 795 nm transitions are oriented predominantly in the plane of the membrane; the 810 nm transition and also the 760 nm Q_y transitions of bph are oriented out of the plane. A more refined analysis by Vermeglio et al. has shown that the changes near 800 nm include both phenomena: bleaching of a component at 810 nm coupled to appearance of a new band at 795 nm (special pair), and also some blue-shift of the 800 nm band (48). Vermeglio et al. used the technique of photoselection: analysis of absorbance changes using polarized actinic light and a polarized measuring beam, applied to a frozen suspension of RCs. By this method they also determined angles that some of the transition moments make with each other.

C. N. Rafferty introduced a new orientation technique in our laboratory: RCs in solution with gelatin were dried, forming films that resemble Kodak-Wratten optical filters. When these films were humidified, stretched and redried, the RCs in them were found by their linear dichroism to be highly oriented, as if an axis of symmetry in the RC became aligned with the direction of stretching. The optical quality of these films allowed reliable measurements throughout the visible as well as in the near infrared (41). We detected for the first time the second of a pair of bands at 600 and 625 nm, identified as the dimeric Q_x transitions of the special pair bchl (42). In retrospect the 625 nm band is discernible in light-induced absorption difference spectra of RCs in solution, resolved from the much larger 600 nm band. Analysis of the linear dichroism of RCs in stretched gelatin films allowed us to compute the angles that several optical transition moments make with an axis of symmetry in the RC. These include the bchl "special

pair" transitions at 600, 625 and 870 nm, the Q_x transitions of the two molecules of bph (at 532 and 547 nm), and the average of the unresolved Q_y transitions of the two bphs at 760 nm. By combining this information with Vermeglio's recent photoselection data (48) we were able to compute angular coordinates for each of these transition moments and thus to specify their orientations in a polar coordinate system with the axis of symmetry of the RC as the pole (this axis is defined operationally as the axis of alignment in a stretched gelatin film)(43). From the directions of the transition moments we can make inferences about the orientations of the molecules themselves, for the bph and for the special pair bchl. With the help of new photoselection measurements on chromatophores we are finding how this three-dimensional construction of the RC is related to the plane of the membrane (49).

We and Vermeglio have data for RCs and chromatophores of Rhodopseudomonas viridis as well as for those from Rp. sphaeroides, but we have not yet correlated the data on Rp. viridis in the foregoing way.

As part of a continuing collaboration, we have sent a graduate student (Yoram Barouch) to Vermeglio's laboratory for four months. They are studying the orientations of the quinones associated with RCs, using optical measurements on cells and chromatophores of various species of photosynthetic bacteria, with orientation induced by magnetic and electric fields. We are also repeating the experiments on RCs in stretched gelatin films, using the smaller but still photoactive LM particle, derived from the complete RC by removing the heaviest ("H") polypeptide (10).

Several extensions of these techniques for orientation and analysis by polarized light will be mentioned under "Proposed Research".

Absorption band shifts in relation to the movement of electric charge in photosynthetic membranes and RCs.

Band shifts of the carotenoid (antenna) pigments in chromatophores have been ascribed to the formation of electrochemical gradients across the membrane, either through photochemistry or by the artificial creation of ionic gradients (31-33). We found that in a mutant of Rp. sphaeroides that lacks RCs, in contrast to the wild type, the generation of ionic gradients (as by adding KCl to chromatophores in the presence of valinomycin) does not cause a band shift of the carotenoids (34). We concluded that the RCs are somehow associated with the shift, even in a context in which light is not involved and in which it is supposed that a diffusion potential has been generated across the entire membrane. Later work by DeGrooth and Ames (50) showed that the light-induced carotenoid shift is a property of only a relatively small fraction (the "shifting pool") of the total carotenoid content of the membrane. RCs purified from wild type Rp. sphaeroides retain one molecule of the carotenoid sphaeroidene for each RC (51), whereas the "shifting pool" in chromatophores represents a larger proportion of the total carotenoid. It is not yet certain whether the shift, when generated by light on the one hand or by an artificial ionic gradient on the other, involves the same complement (perhaps a special complement) of the carotenoids of the antenna. We also do not know whether the change of peak wavelength is graded or is "all-or-none" when weak and strong stimuli are compared, using light and artificial ionic gradients respectively (see 50,52,53). We are exploring these questions by comparing weak and strong carotenoid shifts in chromatophores from Rp. sphaeroides, using materials in which the preponderant antenna carotenoid is varied by mutation or by growth conditions.

Studying RCs purified from wild type Rp. sphaeroides, we found that the carotenoid (sphaeroidene) shows a red-shift in its absorption bands of about 1 nm when the special pair bchl is oxidized, either photochemically or chemically in the dark (29). Reduction of the UQ (primary or secondary) does not cause a carotenoid shift, and does not modify the shift caused by oxidation of the bchl.

Shifts of the absorption bands of bchl and bph in RCs are caused by oxidation of the special pair bchl and also by the reduction of UQ (12,30,54). These shifts show interesting variations (30): The 800 nm band of bchl is blue-shifted when special pair bchl is oxidized. The 810 and 870 nm (special pair) bands are blue-shifted when the primary UQ is reduced, but when an electron moves from primary to secondary UQ the 870 nm shift disappears and the 810 nm shift is reversed, becoming a shift to greater wavelengths. The 760 nm band of bph is shifted to a greater wavelength when bchl is oxidized and also when either primary or secondary UQ is reduced; this shift becomes smaller when an electron moves from primary to secondary UQ. The 532 and 547 nm bands of bph are red-shifted at room temperature, but the 547 nm band shift is reversed, becoming a blue-shift, at liquid nitrogen temperature.

The changing pattern of bchl and bph band shifts when an electron moves from primary to secondary UQ allowed us to monitor the kinetics of this electron transfer; we found a half-time of 200 μ s (30), in rough agreement with a value inferred by Parson, using chromatophores of Chromatium vinosum, from changes in the fluorescence of antenna bchl (55). Aside from that, we have done little to exploit these potentially useful optical signals.

Fluorescence, energy transfer and photochemical efficiency in reaction centers.

RCs exhibit a fluorescence band at 900 nm (f900), associated with the 870 nm absorption band of special pair bchl. The yield of this fluorescence in photochemically active RCs is 3×10^{-4} , corresponding to an excited state lifetime of 7 psec (16). This emission may come partly through a reversal of the earliest photochemical step:

as well as from the initially photo-excited special pair, B_2^* . Its yield is independent of temperature from 35K to 200K; if any of it comes through the back reaction, this lack of temperature dependence implies that the state B_2^+, P^- has nearly the same energy (within 10^{-3} electron volt) as the state B_2^*, P (56). More likely, B_2^+, P^- is at a lower energy, and emission through the back reaction occurs only at temperatures above 200K. But between 200K and 300K there are anomalous variations of f900, probably associated with a phase transition involving water bound to the RCs (see later), and this makes an interpretation of the temperature dependence uncertain. Temperature-independence of f900 below 200K is consistent with the observed temperature-independence ($\pm 15\%$) of photochemical efficiency (22).

There are fluorescence bands, ascribed to emission by bph and bchl, at wavelengths below 900 nm, but these are due mainly to the presence of contaminating pigments that can be removed or denatured, or their fluorescence suppressed by drying the RCs as films on quartz slides (56,57). In such films, f900 is at least ten times more intense than any other component of fluorescence above 700 nm. A suggestion of a band at 820 nm at low temperature is actually an artifact caused by

reabsorption of emitted light, in samples that retain contaminating fluorescence between 750 and 850 nm. Curiously there is no detectable emission associated with the 800 nm band of bchl, even when the 810 and 870 nm bands have been bleached by oxidation of the special pair.

We measured the photochemical quantum efficiency in RCs from Rp. sphaeroides to be greater than 98% with actinic light absorbed directly by the special pair at 880 nm. With 800 nm actinic light (absorbed principally by P800) the efficiency was 7% less (a surprising result, if it can be believed, in view of the absence of fluorescence from P800), and with 760 nm light (absorbed by bph) the efficiency was about 15% less (58). These measurements were made with RCs that probably retained about 15% extraneous (contaminating) bph and no more than 1% contaminating bchl. Allowing for this, we cannot be sure whether or not energy transfer from bph and from P800 to the special pair proceeds with efficiency close to 100%. This is an important question, bearing as it does on the strength of exciton interactions between these chromophores. We plan to explore these points more carefully so as to gain information about energy transfer and spatial relationships among the chromophores of the RC.

Quinones in relation to the transport of electrons and protons in the photosynthetic membrane.

In RCs and chromatophores from Rp. sphaeroides the primary and secondary UQ can be removed selectively, either by extraction with organic solvents or by exposure to high concentrations of orthophenanthroline and of the detergent lauryl dimethyl amine oxide (11,59). Milder treatments remove secondary UQ and harsher treatments

remove the primary UQ. Thus one can prepare RCs that contain no UQ, or only the primary one (UQ_a), or the primary and one secondary one (UQ_a and UQ_b), or these plus a pool of excess UQ. The removal of all but UQ_a by low concentrations of orthophenanthroline may explain the action of this inhibitor in blocking electron transport beyond the primary quinone in photosynthetic bacteria.

We have studied electron transport among these quinones by observing light-induced changes, especially at 450 and 280 nm, that indicate interconversions between UQ, $UQ^{\cdot-}$, and $UQ^=$ or (with H^+ uptake) UQH_2 . We also measured H^+ uptake with the help of pH indicator dyes added to the preparation. RCs were prepared with UQ_a , with or without UQ_b and an external pool of UQ. We added an electron donor (ascorbate, diaminodurene or cytochrome *c*) in excess to cause rapid re-reduction of B_2^+ and thus to suppress absorbance changes due to oxidized bchl. From observations of such RCs exposed to consecutive flashes of light (24), Vermeglio in our laboratory traced the pattern of electron movement among the quinones. In the following reaction sequences I have omitted for simplicity the steps involving bph and the transitory presence of oxidized bchl ($B_2^{\cdot+}$) before it is re-reduced by the donor.

No secondary quinone

No further reaction until $UQ_a^{\cdot-}$ has given an electron to the oxidized donor, thus returning to UQ_a .

ONE SECONDARY QUINONE

No further reaction until $UQ_a^{\cdot-}$ has reverted to UQ_a by reacting with oxidized donor. $UQ_b^{\cdot-}$ might fall off, leaving the RC without secondary UQ after the second flash.

With an added pool of UQ, the fully reduced $UQ_b^{\cdot-}$ (but not the singly reduced $UQ_b^{\cdot}$) can pass its electrons to the pool, perhaps by coming off and being replaced from the pool (unpublished suggestion by M. Y. Okamura). Under these conditions the absorbance at 450 nm, indicative of the presence of $UQ^{\cdot-}$, showed pairwise oscillations after consecutive flashes: the first flash caused an increased absorbance, the second flash abolished this increase, and so forth. These observations with isolated RCs show how the obligate "one-electron" chemistry of UQ_a can be linked to the two-electron chemistry of secondary UQ.

We then sought evidence for this pattern in chromatophores of Rp. sphaeroides; specifically the pairwise oscillations of 450 nm absorbance and also the pattern of H^+ uptake (27). With chromatophores from the carotenoidless mutant R-26 we observed the pattern of oscillating 450 nm absorbance, with H^+ uptake only after even-numbered flashes (when $UQ^{\cdot-}$ has been formed). We did not see such "periodicity of two flashes" in 450 nm absorbance or in H^+ uptake when we examined chromatophores of strains of Rp. sphaeroides that contain colored carotenoids. We had no explanation for this difference associated with the presence of carotenoids. Meanwhile deGrooth et al. (60) reported pairwise oscillations of 450 nm absorbance in cells and chromatophores of Rp. sphaeroides and Rhodospirillum rubrum, but only when the preparations were aerated. No such oscillations were observed under anaerobic conditions. We are thus led to implicate differences in the

ambient redox potential in the presence or absence of "quinone oscillations".

These considerations may be related to the report by Dutton et al. (61) that in chromatophores, a single turnover of the RC in response to a brief flash can cause the translocation of two protons across the membrane. They suggested a mechanism based on a secondary cycle of electron transport involving cytochrome b. In highly truncated form,

By such a mechanism, every flash causing a single turnover of the RC can effect the translocation of $2H^+$ and singly reduced UQ appears only as a transient entity. No oscillations on consecutive flashes are expected. But if the "cyt b cycle" were interrupted, for example at a redox potential high enough to keep the cyt b in its oxidized form, two consecutive electrons from the RC would be needed to convert the secondary UQ to its fully reduced form and thus to allow the binding of $2H^+$. In nature the bacteria may resort to this less efficient pattern ($2H^+$ moved for two turnovers of the RC) when they are exposed to aerobic conditions.

We are beginning to repeat our studies of UQ reduction and H^+ uptake on consecutive flashes with chromatophores exposed to controlled ambient redox potentials.

Miscellaneous.

Dehydration of reaction centers: When RCs from Rp. sphaeroides are dried onto glass slides in air, their absorption spectra and reaction kinetics are similar to those of RCs in solution. If the air-dried RCs are then dehydrated, as by pumping against a cold trap, several changes occur (44). There is a loss of 870 nm absorbance and an increase at 795 nm, as if some of the special pair bchl has been converted to a monomeric state by the removal of water. There is no change at 1250 nm, indicating (20) that none of the special pair has become oxidized. About half of the RCs that retain their 870 nm absorbance become photochemically inactive and the remainder has impaired photochemical efficiency. The back reaction, return of an electron from reduced UQ to oxidized bchl, shows an altered pattern of temperature dependence. In hydrated RCs that lack secondary UQ the half-time is about 60-80 ms at room temperature, falling to about 25 ms as the temperature is lowered to about 220K. As the temperature is lowered to 50K the half-time declines more gradually to 15 ms. In dehydrated RCs the half-time of the back reaction is about 25 ms, independent of temperature between 300K and 50K. All of these effects of dehydration are reversible upon adding back water vapor. If D₂O vapor is added in place of H₂O the results are the same within the precision of measurement. We suppose that the change in reaction kinetics with temperature in hydrated films is related to a phase transition involving water bound to the RCs. This can also account for anomalous changes in the yield of 900 nm fluorescence between 300K and 200K. The anomalous changes in reaction kinetics and fluorescence with temperature can thus be avoided by studying

dehydrated RCs, but these RCs are not in an optimal state for photochemistry.

Reaction centers from Rhodopseudomonas gelatinosa and Rp. viridis:

We have isolated RCs from Rp. gelatinosa (35) and have developed an improved RC preparation from Rp. viridis (37). The most striking property of these RCs is their polypeptide composition. When RCs from such diverse photosynthetic bacteria as Rp. sphaeroides, Rs. rubrum and Chr. vinosum are compared, their polypeptide components are closely similar (9,10): three polypeptides in the range 18-30 kdalton as estimated by polyacrylamide gel electrophoresis. The RC from Rp. gelatinosa shows just two polypeptides, about 25 and 33 kdalton (35). The RC from Rp. viridis shows polypeptides of apparent weights 41 and 30 kdalton, and a lesser one at 37 kdalton. One or more of these three components might be attributed to cytochrome 553 or cyt 558 bound to the RC of Rp. viridis. It appears that the RCs of three species within the single genus Rhodopseudomonas differ widely in their polypeptide components, whereas more distant relatives (Rhodospirillum and Chromatium) are closely similar to Rp. sphaeroides in this respect. This raises evolutionary and taxonomic questions and suggests that efficient RCs can be made by binding the same chromophores, in similar configurations, to quite different protein substrates.

Reconstituted energy transfer from antenna to reaction centers.

By mixing antenna pigment-protein isolated from Rp. sphaeroides (38) with purified RCs in the presence of a detergent, and then dialyzing away the detergent, we have reconstituted efficient transfer of excitation energy from the antenna to the RCs (39). We measured antenna fluorescence (both steady state and the variable component at

the onset of illumination) and also the quantum efficiency of photochemical bchl oxidation in the RCs. The RCs could be present in their photochemically active state or in the inactive ("closed") state in which the primary UQ has been reduced chemically. The trapping of excitation energy by the RCs was consistent with our expectations drawn from the quenching of excitation energy by isolated RCs: Active RCs quench the energy three times more rapidly than closed RCs. The yield of antenna fluorescence followed the same pattern in these reconstituted model systems as in chromatophores: About 10% in antenna without RCs after dialysis to remove excess detergent (and the same in chromatophores from a mutant of Rp. sphaeroides that lacks RCs), about 3% in antenna with closed RCs (or in normal chromatophores in which the RCs are closed), and about 1% in antenna with active RCs, or in normal chromatophores with active RCs. These findings may eventually become useful in solar cell technology. For the present, we have learned that the lifetime of singlet excited states in closed RCs is the same, about three times that in active RCs, whether the RCs have been closed by reducing the primary UQ or by oxidizing the special pair bchl.

Phycochromes. In collaboration with Drs. I. Ohad and L. Bogorad we have studied the photochemistry of a photoconvertible pigment from blue-green algae, possibly allophycocyanin, known generically as phycochrome (46). Partially purified preparations of this pigment show a bleaching centered at 620 nm, induced by red (640 nm) light and reversed by green (550 nm) light:

with P_r having the greater absorbance at 620 nm. In preliminary studies (62) we have found two components or states of this pigment. One component

reacts reversibly at temperatures between 307K and 200K. The other component is active for the green light effect ($P_g \longrightarrow P_r$) but inactive for the $P_r \longrightarrow P_g$ reaction. As the temperature is lowered, the proportion of "unilaterally active" pigment grows larger, up to a maximum of about 70% at 260K and below. The change from reversible to unilateral activity, induced by lowering the temperature, is itself reversed without hysteresis when the temperature is raised. The block in the $P_r \longrightarrow P_g$ reaction in the unilateral condition appears not to be due to a temperature dependent intermediate step. We know of no other photoconvertible pigment (phytochrome, rhodopsin, etc.) that shows such a unilateral temperature dependence. This curious dependence on temperature may help us to design experiments to establish or disprove a connection between this pigment and the phenomenon of chromatic adaptation in the living algae.

We have also estimated the quantum efficiency of $P_g \longrightarrow P_r$, and of $P_r \longrightarrow P_g$ in the reversibly active state, to be about 10% or more.

Bacteriorhodopsin. In collaboration with Prof. A. Lewis (45) we have measured the quantum efficiency of fluorescence from bacteriorhodopsin, an analog of the visual pigment of higher animals. The temperature dependence of the fluorescence yield, coupled to information about the lifetime of the emitting state, has given new information about the physical states involved in fluorescence and photochemistry of this pigment:

At low temperature the entry into the metastable state is blocked and fluorescence from the "allowed" excited state may be observed.

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PUBLICATIONS

Eighteen publications during the current three year DOE Contract period, from Sept. 1, 1975 to date, are indicated by * or ** in the REFERENCES. Six additional ones are listed below. Abstracts are not included. Publications during the current contract year, since 12/1/77, are shown by **; reprints or preprints of these are appended to this report.

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