The petite purple photosynthetic powerpack

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Abstract
Photoreaction centres are Nature’s solar batteries. These nanometre-scale power producers are responsible for transducing the energy of sunlight into a form that can be used by biological systems, thereby powering most of the biological activity on the planet. Although to the layman the word ‘photosynthesis’ is usually associated with green plants, much of our understanding of the molecular basis of biological transduction of light energy has come from studies of purple photosynthetic bacteria. Their RCs (reaction centres) and attendant light-harvesting complexes have been subjected to an intensive spectroscopic scrutiny, coupled with genetic manipulation and structural studies, that has revealed many of the molecular and mechanistic details of biological energy transfer, electron transfer and coupled proton translocation. This review provides a short overview of the structure and mechanism of the purple bacterial RC, focusing in the main on the most heavily studied complex from Rhodobacter sphaeroides.

Context of the purple bacterial RC (reaction centre)
The RCs found in plants, algae and photosynthetic bacteria use energy derived from sunlight to power a process of membrane-spanning electron transfer [1]. The RC is fed with energy by one or more types of light-harvesting or ‘antenna’ pigment-proteins, and a number of recent reviews have covered the structure and organization of the purple bacterial photosystem [2–6].

The overall electron transfer process is cyclic in purple photosynthetic bacteria, involving the RC, the intramembrane quinone pool, a membrane-embedded cytochrome bc₁ complex and a water-soluble mobile redox protein such as cytochrome c₂. Harvested light energy is used by the RC to power the reduction of quinone to quinol (dihydroquinone) at the so-called Q₈ site on the cytoplasmic side of the membrane and oxidation of cytochrome c₂ at the periplasmic face of the membrane. These products provide a reductant and an oxidant respectively for the cytochrome bc₁ complex [7–10], with quinol oxidation occurring at the so-called Q₉ site on the periplasmic side of the membrane (also referred to as the Q₉α site in some texts). As the sites of quinone reduction/protonation and quinol oxidation/deprotonation are on opposite sides of the membrane, protons are translocated from the bacterial cytoplasm to the periplasmic space, generating an electrochemical gradient of protons (the protonmotive force) that can be used to power reactions such as the synthesis of ATP. The number of protons translocated across the membrane per electron passing through the RC is increased through the operation of a Q-cycle in the cytochrome bc₁ complex [7,11,12].

Structure of the Rhodobacter sphaeroides RC
The R. sphaeroides RC is a membrane-embedded pigment-protein complex made up of three polypeptide chains and ten cofactors (Figure 1A). The X-ray crystal structure is known to a resolution of approx. 2 Å (1 Å = 0.1 nm) [13–15], with multiple entries for wild-type or mutated versions of the protein in the Protein Data Bank (http://www.rcsb.org/pdb/home/home.do). Two of these polypeptides, termed L and M (or PufL and PufM), show sequence similarities that suggest a common evolutionary origin, and X-ray crystallography has revealed that they have a similar fold, with five membrane-spanning α-helices connected by extramembrane loops or short amphipathic helices (Figure 1B). The L- and M-polypeptides are arranged around an axis of 2-fold rotational symmetry that runs perpendicular to the plane of the membrane, and form a scaffold that holds the cofactors in a precise configuration. The structural symmetry displayed by the L- and M-polypeptides is actually a pseudosymmetry, due to sequence differences between the two and asymmetric interactions with the H-polypeptide. The H-polypeptide has a single membrane-spanning α-helix and an extra-membrane domain that caps the cytoplasmic faces of the L- and M-polypeptides (Figure 1B).

The central region of the RC is embedded in a bilayer membrane that forms as an extension of the bacterial cytoplasmic membrane, and is often called the photosynthetic membrane or intracytoplasmic membrane. In R. sphaeroides the photosynthetic membrane comprises approximately spherical invaginations of the cytoplasmic membrane (see [16] for a recent visualization), but a variety of morphologies are found in other species, including tubes and layered

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Abbreviations used: BCH, bacteriochlorophyll; BPhe, bacteriopheophytin; RC, reaction centre.
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sheets. Within the plane of the membrane the RC has a rather elliptical cross section, with major and minor axes roughly 70 and 50 Å in length. The complex is approx. 75 Å at its longest in the direction perpendicular to the membrane, and has a molecular mass in the region of 100 kDa.

The cofactors comprise four BChl (bacteriochlorophyll) \(\alpha\), two BPhe (bacteriopheophytin) \(\alpha\), two ubiquinone-10, a carotenoid and a ferrous non-haem iron atom (Figure 2A). BPhe is chemically identical with BChl, with the exception that the central Mg ion of the latter is replaced by two protons in BPhe. The carotenoid is spheroidene or spheroidenone in RCs from cells grown under illuminated/anaerobic or dark/semiaerobic conditions respectively (see below). The BChl, BPhe and quinone cofactors are arranged at the interface of the L- and M-polypeptides in two membrane-spanning branches that are also related by a 2-fold pseudosymmetry. Two of the BChls (the so-called ‘special pair’) form a dimer near the periplasmic side of the membrane, separated from the adjacent aqueous phase by surface-exposed helices from the L- and M-polypeptides. The dimer BChls are shown with yellow carbons in Figure 2(A) and are labelled \(P_A\) and \(P_B\). Next to the BChl dimer are two monomeric BChls, \(B_A\) and \(B_B\), which are often referred to as ‘accessory’ or ‘voyeur’ BChls and are shown with green carbons in Figure 2(A). These are then followed by the two BPhes (\(H_A\) and \(H_B\), pink carbons) and the two quinones (\(Q_A\) and \(Q_B\), cyan carbons). The single carotenoid (labelled Crt in Figure 2A) breaks the symmetry of the cofactors, being embedded in the M-polypeptide close to the so-called \(B_B\) accessory BChl. The iron is located on the symmetry axis between the two quinones, and its role appears to be primarily structural. The quinone-binding sites are located close to the cytoplasmic side of the membrane but are insulated from the adjacent aqueous phase by parts of the L- and M-polypeptides and the cytoplasmic domain of the H-polypeptide. One possible function of this insulation is to prevent unwanted redox reactions between the quinones and redox centres present in the cytoplasm [17].
Figure 2 | Cofactor structure and absorbance spectrum of the *R. sphaeroides* RC

(A) The BChl, BPhe and ubiquinone cofactors (sticks) form two membrane-spanning branches. For clarity, the hydrocarbon side chains have been removed. Mg atoms of BChl and non-haem Fe are shown as spheres. The axis of 2-fold symmetry is shown and the arrows indicate the route of electron transfer. Atom colours are as in Figure 1. (B) The absorbance spectrum of the purified RC.

A feature of the literature on RCs is the sometimes confusing nomenclature for the various cofactors. The present review uses one of the more common notations where the BChls of the dimer are referred to as P<sub>A</sub> and P<sub>B</sub>, the monomeric BChls as B<sub>A</sub> and B<sub>B</sub> and the BPhe as H<sub>A</sub> and H<sub>B</sub>. However, in many publications, the subscripts A and B are replaced by L and M (i.e. P<sub>L</sub>, P<sub>M</sub>, B<sub>L</sub>, B<sub>M</sub>, H<sub>L</sub> and H<sub>M</sub> respectively), and in some earlier papers, the terms Φ<sub>L</sub> and Φ<sub>M</sub> (or Φ<sub>A</sub> and Φ<sub>B</sub>) are used for the BPhe. Some authors also use D<sub>L</sub> and D<sub>M</sub> (or D<sub>A</sub> and D<sub>B</sub>) for the two dimer BChls, and the dimer is variously referred to as P<sub>L</sub>870 or D<sub>L</sub> (see below). Finally, the two branches of cofactors are labelled as the A-branch and B-branch in Figure 2(A), but are sometimes referred to as the L-branch and M-branch, or the active and inactive branches. Like an island in a sea of potential confusion for the RC novice, the terms QA and QB are used universally for the two quinones.

Spectroscopy of the *R. sphaeroides* RC

The purple bacterial RC has been subjected to a bewildering array of spectroscopic techniques (see [18] for an epic review of many of these). The bacteriochlorin (i.e. BChl and BPhe) cofactors in particular have very distinctive absorbance spectra that provide a very sensitive probe of the structural and functional integrity of the complex, and a means of following the route and rate of light-driven electron transfer.

The absorbance spectrum of the purified *R. sphaeroides* RC is shown in Figure 2(B). Owing to their electronic structure, the BChl and BPhe cofactors give rise to three sets of absorbance bands in the so-called Soret (300–420 nm), Q<sub>x</sub> (500–630 nm) and Q<sub>y</sub> (650–950 nm) regions (see Chapter 4 of [1] for an accessible account of the origins of these). A simplified set of attributions are indicated in Figure 2(B). Molar absorption coefficients (ε) for the prominent bands in the Q<sub>y</sub> region allow the concentration of RCs to be monitored, and a particularly useful feature of the spectrum is that the purity of the complex can be measured from the ratio of protein absorbance at 280 nm to BChl absorbance at 802 nm, with a ratio of 1.3 or below indicating RCs of sufficient purity for crystallization [19]. The structural integrity of the RC can also be assessed through characteristic spectral changes that take place as the protein unfolds and the cofactors are released from their native binding sites (see, e.g., [20]).

Photo-oxidation of the RC is accompanied by distinctive changes in its absorbance spectrum, and in particular the Q<sub>y</sub> absorbance band attributed to the P<sub>B</sub> BChls at 870 nm is lost (the term ‘bleached’ is often used to describe this). The primary donor BChls were first identified through photobleaching of the absorbance band of a BChl species at 870 nm, leading to the moniker P870 (or P<sub>870</sub>). For *R. sphaeroides*, the precise absorbance maximum of this species varies somewhat depending on the environment of the RC, and in some publications it is referred to as P865. In the remainder of this review, the commonly used simpler term P will be employed. Many undergraduate textbooks describe photochemistry in the BChl *b*-containing *Blastochloris viridis* RC, where the primary donor has the moniker P960.

The fact that loss of the electronic ground state of a BChl or BPhe alters its absorbance spectrum, and that charge separation is initiated by light, has allowed a detailed investigation of the route and rate of electron transfer through the RC using ultrafast ‘pump–probe’ absorbance difference spectroscopy (see [21] for descriptions of this technique). This type of spectroscopy can take a number of forms, but in one of the more commonly used approaches, a brief ‘pump’ pulse of light (typically ~100 fs duration in current experimental setups) is used to excite a particular cofactor. The very short duration of this pulse is such that electron transfer is initiated in an approximately synchronous manner in the population of RCs. A second pair of matched femtosecond ‘probe’ pulses is then used to measure the absorbance spectrum of the sample in the region excited by the pump pulse and in an unexcited region, and a difference spectrum is calculated. By varying the distance the pump pulse has to travel before passing through the sample, using moveable mirrors, the time difference between encounter of the excitation and measuring pulses with the sample can be varied with a femtosecond time
resolution, and a series of absorbance difference spectra can be recorded at defined time intervals after excitation. Analysis of these spectra reveals details of the rate at which the electron moves through the RC, and the route taken. To date the main focus of such studies has concerned the visible and near-IR absorbance properties of the RC bacteriochlorins, but attention is now being turned to other regions of the spectrum in order to investigate the dynamics of the protein surroundings of these cofactors on the timescale of electron transfer (see below).

In addition to steady-state and time-resolved measurements based on the absorbance properties of the cofactors, a number of spectroscopic techniques commonly applied to RCs probe the positive and negative charges created during photoinduced charge separation. Examples include EPR and ENDOR (electron nuclear double resonance) [22,23]. Vibrational spectroscopy has also played a major role in RC research, with techniques such as FTIR (Fourier-transform infrared) spectroscopy [24] and resonance Raman spectroscopy [25] providing detailed information on how cofactors, and polar groups in their immediate surroundings, respond to light-induced changes in redox state.

Mechanisms

Transmembrane charge separation

The RC is responsible for using the energy harvested from sunlight to power the formation of an electrochemical gradient of protons across the photosynthetic membrane, a process catalysed in partnership with the cytochrome bc1 complex. Light energy is harvested principally by the BChl and carotenoid pigments of the light-harvesting complexes (see below), and stored in the form of an excited singlet electronic state of a pigment molecule. Once a photon has been absorbed by a BChl in the antenna, excited-state energy is passed between adjacent BChls by a process of resonance transfer until it arrives at the BChl dimer in the RC, where photochemistry is initiated. This transfer involves the passage of energy between BChls, but no exchange of electrons. This terse description does little justice to this subject and the reader is referred to recent reviews for more detailed accounts of light harvesting and energy transfer [26–29].

Photochemistry in the RC is initiated by the formation of the first singlet excited state of the BChl dimer, which is usually given the notation P*. In wild-type bacteria, P* is formed mainly by transfer of excitation energy from the antenna, but in isolated RCs (or antenna-deficient mutants), it can be formed by direct absorption of a photon of appropriate wavelength by the P BChls. In R. sphaeroides, the lowest energy absorbance band of P is centred at 865–870 nm, depending on conditions (Figure 2B). As described in more detail below, acquisition of excited-state energy transforms the P dimer into a powerful reductant, capable of donating an electron to the adjacent B_A BChl in a reaction that has a lifetime of approx. 3 ps, forming the so-called P^+ B_A^- radical pair. The route of electron transfer through the complex is depicted in Figure 2(A). On arriving at B_A, the electron is then passed on to the H_A BPhe in approx. 1 ps, forming the P^+ H_A^- state, and then on to the Q_A quinone to form P^+ Q_A^- in approx. 200 ps (Figure 2A). A recent review of this charge separation process can be found in [30]. Only the A-branch of cofactors is active in membrane-spanning electron transfer, although it has proved possible to engineer partial electron transfer along the B-branch in mutant RCs (see [31] for an overview and [32–36] for recent developments).

The movement of charge through the RC is extremely efficient, in the sense that almost every P* state created produces a P^+ Q_A^- radical pair. As can be seen in Figure 3(A), at each stage in electron transfer the productive forward reaction (black arrows) is much more rapid than competing reactions such as recombination of radical pairs to the ground state (grey arrows). In addition, movement of the electron through the RC involves the formation of radical pairs with progressively decreased free energies (Figure 3A). These features combine to make the overall process extremely efficient. The requirement for a decrease in free energy explains why a special type of bacteriochlorin, BPhe, is employed as the second electron acceptor, as it is easier to reduce than BChl by some 200–300 mV (Figure 3B). In mutant RCs where BPhe is replaced by a BChl, the yield of transmembrane electron transfer is markedly decreased [37].

The first two steps of electron transfer are very rapid, involving cofactors that are touching one another in the structure, with no intervening protein. As the rate of formation of P^+ H_A^- is much faster (3–5 ps) than subsequent formation of P^+ Q_A^- (200 ps), the P^+ H_A^- state builds up to a high level in the RC population (almost 100%) and is easily detected by the type of time-resolved absorbance difference spectroscopy described in the last section. In contrast, the first intermediate in charge separation, the radical pair P^+ B_A^- , has proved rather difficult to characterize due to the fact that the second electron transfer from B_A^- to H_A is somewhat faster than the initial transfer from P* to B_A. The result of this is that the P^+ B_A^- radical pair does not build up at a high level in the RC population, and so is difficult to detect. In a previous review, it has been estimated that the subpopulation of RCs in the P^+ B_A^- state is maximal at approx. 2 ps after photoexcitation but never exceeds 20% (see Figure 5 in [30], where P^+ B_A^- is referred to as the I_2 intermediate). The role of the B_A BChl in this initial charge separation was hotly debated for many years, a debate fuelled by the difficulty in detecting the spectroscopic signature of the B_A^- species, but it is now generally accepted that the P^+ B_A^- state does form, but is very short lived (see [30] for an account of this topic).

The third step in membrane-spanning electron transfer from H_A^- to Q_A takes place with a lifetime of approx. 200 ps, and is therefore much slower that the two preceding steps. One reason for this is the greater distance between the electron donor and acceptor for this reaction (see Figure 1C), compared with the distances involved in the initial reactions. For the third step the BPhe and quinone are not in direct
Figure 3 | Energy and photochemistry

(A) Free energies of the states involved in light-activated charge separation in the RC. (B) Midpoint redox potentials of centres involved in light-driven cyclic electron transfer. Centres are labelled using the convention reactant/product. Cyt bc$_1$ refers to electron transfer through the high-potential chain formed by the Rieske iron-sulfur centre and cytochrome c$_1$.

Why is harvested light energy needed to power this membrane-spanning electron transfer? This question addresses the very heart of photosynthesis, and the answer lies in the redox potentials of the different components (Figure 3B). The midpoint redox potential for one electron oxidation of the P BChls when in the ground electronic state (denoted as P$^+$/$P$ in Figure 3B) is approx. $+$450 mV, whereas that for one electron reduction of the adjacent B$_A$ BChl is approx. $-$900 mV. As a result, the P dimer is not able to donate an electron to B$_A$, and so there is no electron transfer through the complex. However, when P is converted into its first singlet excited electronic state by the absorption of a photon at 870 nm, the change in electronic configuration is accompanied by a dramatic change in its redox properties (Figure 3B). P$^*$ is a powerful reductant, and has a sufficiently negative redox potential (almost $-$1000 mV) to reduce the B$_A$ BChl, triggering the cycle of electron flow outlined above that eventually sees the translocated electron returning to the RC to reduce the oxidized BChl dimer P$^+$ (Figure 3B).

Quinol formation and cytochrome oxidation

The separation of charge across the photosynthetic membrane is followed by microsecond/millisecond timescale reactions to generate the substrates for the cytochrome bc$_1$ complex. On the so-called acceptor side, QA$^-$ reduces the ubiquinone at the Q$_B$ site (Figure 2A), forming a singly reduced semiquinone species, while on the donor side, a reduced cytochrome c$_2$ docks to the periplasmic face of the RC and reduces P$. The latter event reprimes the RC for a second light-induced charge separation to form the P$^+$Q$_A^-$ radical pair. Donation of a second electron from QA$^-$ to the Q$_B^-$ semiquinone is accompanied by a double protonation of the Q$_B$ molecule to form ubiquinol, which then migrates into the membrane interior and is replaced by a new ubiquinone from the intramembrane pool (Figure 2A, dotted arrows). The sequence and energetics of reduction and protonation events at the Q$_B$ site have been subjected to an extremely detailed scrutiny (see [38,39] for reviews). The double reduction and protonation of the Q$_B$ quinone is a key reaction in cyclic electron transfer, as it is the point at which the single electron chemistry of the bacteriochlorin cofactors is converted into the two-electron/two-proton chemistry that is required to couple electron flow to proton translocation in this system.

An intriguing feature of the R. sphaeroides RC is that two chemically identical molecules of ubiquinone-10 are used to catalyse rather different reactions at the Q$_A$ and Q$_B$ sites. The ubiquinone at the Q$_B$ site is capable of accepting two electrons and binding two protons before leaving the RC and being replaced. In contrast, the ubiquinone at the Q$_A$ site is a fixed component and acts as a single electron relay, accepting an electron from the HA BPhe and passing it on to the Q$_B$ site (Figure 2A). This difference in behaviour stems from the different protein environments of the two quinones. The binding pocket for the redox-active head group of the Q$_B$ ubiquinone is open to the membrane interior, facilitating exchange, whereas the head group of the Q$_A$ ubiquinone is clamped in place in the protein interior by residues that interact with that part of the quinone hydrocarbon side chain closest to the head group (this side chain is often referred to as the quinone ‘tail’). The result is that the Q$_A$ ubiquinone remains firmly attached to the RC during all stages in catalysis, and is retained if the RC is removed from the membrane for purification, whereas the Q$_B$ ubiquinone is free to interchage with ubiquinones from the intramembrane pool and is often lost after removal of the RC from the membrane.
The protein environment also imposes the different redox behaviours of the two quinones. In particular, the Q\textsubscript{A} binding site is lined by amino acid residues such as asparagine and glutamic acid, residues that play a role in protonating the ubiquinone in response to reduction [38,39]. As the binding site of the Q\textsubscript{B} head group is buried in the protein interior and is remote from the source of protons in the cytoplasm, protons are delivered to the Q\textsubscript{B} site along chains of hydrogen bonds that can be traced between polar amino acid side chains and embedded water molecules (see [40] for depictions of these). In contrast, the Q\textsubscript{A} site is lined by predominantly hydrophobic amino acid residues and there are no nearby structures for the delivery of protons to the Q\textsubscript{A} head group.

As outlined above the photo-oxidized BChl dimer, P\textsuperscript{+}, is re-reduced by a cytochrome c\textsubscript{2} that docks to the periplasmic face of the RC. This reaction has also been subjected to a detailed scrutiny through a combination of structural studies, mutagenesis, kinetic spectroscopy and molecular dynamics simulations, as it provides a nice example of a transient protein–protein interaction where there are contrasting demands of specificity and looseness of interaction (see [41,42] and references therein). On the one hand, the interaction between the RC and cytochrome c\textsubscript{2} has to be sufficiently specific that the electrons flowing from the cytochrome bc\textsubscript{1} complex get to where they are needed to propagate cyclic electron transfer. It also has to be sufficiently intimate to ensure that electrons are transferred at a rate that is commensurate with the required overall rate of cyclic electron transfer. On the other hand, the interaction has to be sufficiently loose that the oxidized cytochrome can detach from the RC on an appropriate timescale, in order that the flow of electrons from the cytochrome bc\textsubscript{1} complex can be maintained. To facilitate a general interaction the periplasmic face of the RC is decorated with a preponderance of acidic amino acids, whereas the surface of cytochrome c\textsubscript{2}, particularly near the haem group, contains several complementary basic residues. These oppositely charged surfaces bring the cytochrome into a close interaction with the RC, with shorter range van der Waals, hydrogen bond and cation-pi interactions dictating the final bound conformation within which electron transfer takes place (reviewed in [41,42]).

**Roles played by the protein component**

The protein component of the RC plays a very obvious role in holding the bacteriochlorin and quinone cofactors at very precise distances and angles to facilitate the charge-separation process. In addition, the protein plays a number of other roles (see above), including participating in the delivery of protons to the Q\textsubscript{B} site, mediating the transient protein–protein interaction with cytochrome c\textsubscript{2} and tuning the redox potentials of various components. With respect to the latter, there has been extensive analysis of how the protein environment tunes the redox potential of the P BChls in particular, as this can be measured through a simple chemical titration (see [43,44] for reviews).

More difficult questions to address concern possible roles played by the protein during the charge-separation process, including how it responds to the movement of charge between cofactors (sometimes called relaxation events), and the intriguing question of whether the dynamic properties of the protein exert control over charge separation. Two observations in particular have pointed to an influence of protein dynamics on electron transfer. The first is the finding that the decay of the P\textsuperscript{+} state does not follow a single exponential, but rather involves at least two or three exponential components, suggesting a complex scenario where the rate of the reaction is influenced by static inhomogeneity in the population and/or dynamic properties of the system (see discussion in [45]). The second is a finding from experiments involving extremely brief (<30 fs) excitation pulses that spectroscopic signals associated with P\textsuperscript{+} and P\textsuperscript{+}H\textsubscript{2}\textsuperscript{−} are overlaid with oscillatory features arising from nuclear motions, these occurring in a coherent fashion when the excitation pulse is extremely short (see [21] for a review). Much of the application of ultrafast spectroscopy to RCs in recent years has been geared around trying to understand the nature of these spectroscopic signals, and what they indicate about the charge separation process (see, e.g., [46]).

One of the limitations of the type of pump–probe spectroscopy usually applied to the RC is that the visible/near-IR probe pulses interrogate the absorbance properties of the bacteriochlorin cofactors, rather than the protein surroundings. However, recently, attention has begun to turn to UV and IR regions of the spectrum that provide direct information on the protein matrix. For example, Woodbury and co-workers have used visible-pump/UV-probe spectroscopy, analysing ultrafast changes in tryptophan absorbance, to investigate protein structural changes that occur immediately after photo-excitation [47]. The conclusion from this work was that the multiexponential kinetics of the initial charge separation reaction are dictated by the time course of protein dynamics. In addition, visible-pump/IR-probe spectroscopy has been used to investigate the kinetics of charge separation through the spectroscopic signals of vibrational modes that are associated with particular excited or radical pair states [48]. These signals arise from the shift in frequency of a vibrational mode as the RC evolves from one state into the next.

Although many of these signals involve modes internal to the bacteriochlorins, this form of spectroscopy also reveals protein groups that undergo frequency shifts on the formation of a particular state, and so has the potential to throw new light on protein dynamics on the timescale of charge separation (see [49] and references therein).

**Summary and outlook**

Research over the last 30 years or so has provided a detailed description of the structure of the purple bacterial RC and the mechanism of photochemical charge separation. Many of the more accessible secrets of this process have been revealed, but some of the deeper mysteries remain to be solved. In particular, the inherently static nature of most crystallographic data, and the focus of many kinetic spectroscopic techniques on the optical properties of the bacteriochlorins, means that we still have a poor understanding of
the dynamic properties of the protein component of the RC and how they influence the energy transduction process. As a result, spectroscopic attention is increasingly turning to the UV and IR regions of the electromagnetic spectrum in an attempt to probe the kinetic properties of the protein more directly.

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