Quantum scattering model of energy transfer in photosynthetic complexes

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Received 26 July 2015, revised 31 August 2015
Accepted for publication 2 September 2015
Published 29 October 2015

Abstract
We develop a quantum scattering model to describe the exciton transport through the Fenna–Matthews–Olson (FMO) complex. It is found that the exciton transport involving the optimal quantum coherence is more efficient than that involving classical behaviour alone. Furthermore, we also find that the quantum resonance condition is easier to be fulfilled in multiple pathways than that in one pathway. We then definitely demonstrate that the optimal distribution of the pigments, the multitude of energy delivery pathways and the quantum effects are combined together to contribute to the perfect energy transport in the FMO complex.

Keywords: quantum scattering model, photosynthetic complexes

Online Supplementary data available from stacks.iop.org/LPL/12/125201/mmedia
(Some figures may appear in colour only in the online journal)

I. Introduction

Photosynthesis is a fundamental biological process that harvests solar energy to power life on Earth. It starts with the absorption of a photon of sunlight by the antenna molecules, followed by transfer of the energy to the reaction centres. Remarkably, the energy transfer from the antennas to the reaction centres is almost perfectly efficient [1]. Then an intriguing question arises: what makes the energy transfer so efficient? To date, there are two acceptable contributing factors [2]: the first one is the optimal space distribution of the pigments in light-harvesting complexes [3], where the optimal space is just close enough to enable fast energy transfer, but far enough apart to prevent the molecular orbital of the pigments from overlapping. The second factor is the supramolecular organisation of the photosynthetic apparatus, which allows the multiple energy delivery pathways to connect to the reaction centres [4].

Recently, the experimental and theoretical studies have shown that there exists a long-lived quantum coherence in this energy transfer in several photosynthetic complexes [5–12], which suggests that quantum coherence could be a third factor in optimising energy transfer efficiency. However, to what extent quantum effects contribute to the efficiency of the energy transfer is largely unknown. Therefore, it would be of significant importance to establish quantitatively whether or not the photosynthetic light harvesting that involves quantum coherence is truly more efficient than it would be using classical mechanisms alone [2].

In this paper, we develop a quantum scattering model to describe the exciton (the energy carrier) transport in the FMO complex. We explore, respectively, the quantum and classical transports of the exciton in one, two and multiple pathways and show that the quantum transport under the resonant condition can lead to perfect efficiency. Since the resonance is due to the quantum coherence and is impossible in classical physics, we thus demonstrate definitely that the exciton transport involving optimal quantum coherence is more efficient than that for the classical case. We show that the resonant transport occurs with perfect efficiency when the quantum phase of the
exciton accumulated in the pathways is fulfilled with the resonant condition. Since the phase of the exciton is determined by the space distribution of the pigments, the optimal distribution of the pigments is then indeed significant in the near-unity transfer efficiency. Although the perfect efficiency is also possible for one pathway alone, multiple pathways are essential because the resonant region in multiple pathways is much larger than that in one pathway. The large resonant region is the mechanism that the excitons with a broad range of the spectrum (electrons absorbing different colours of light) can transport with perfect efficiency. Therefore, the three above-mentioned contributing factors, the optimal distribution of the pigments, the multitude of energy delivery pathways and the quantum effects, are combined together in our proposed model to contribute the perfect energy transport in FMO.

II. Quantum scattering model of the FMO complex

The architecture of antenna light-harvesting complexes varies widely among photosynthetic organisms. A well-studied example is the water-soluble FMO complex of the green sulfur bacteria. As shown in figure 1, the FMO complex comprises three identical monomers, each containing eight pigments. The eight pigments (figure 1(b)) can be combined into two major energy transport pathways [13]. The chlorosome antenna could absorb light to create a quasi-particle called exciton, which can be considered as the energy carrier in light-harvesting complexes. The exciton then transports to the reaction centre through FMO with nearly perfect efficiency.

In the previous theories [9, 10, 14], each pigment was usually modelled by a two-level molecule, and then the FMO complex is described by some coupled two-level molecules interacting with their environmental phonons. One may model the FMO as a network of $N$ sites with each site as a pigment. The network is a collection of $N$ connected nodes which may support excitations exchanged between lattice sites by hopping [15, 16]. In this paper we propose a different model, the scattering model [17, 18] (see the brief review in supplementary material (stacks.iop.org/LPL/12/125201/mmedia))3, to explain the transmission efficiency of FMO. Roughly speaking, one may consider the suggested scattering model as a special quantum network with an additional phase factor on the hopping term. There are two basic elements in the scattering model, the scatterer and the ideal channel; they are connected with certain orders to form a quantum network. We denote the transfer matrix for the $n$th scatterer as $M_n$, and the transfer matrix for the ideal channel with the length $l$ as $U_l$. They can be written as

$$M_n = \begin{pmatrix}
\frac{1}{t_n} & r_n^+ \\
\frac{r_n}{t_n} & \frac{1}{t_n}
\end{pmatrix}, \quad U_l = \begin{pmatrix} e^{-ikl} & 0 \\
0 & e^{ikl}\end{pmatrix}.$$  

where $t_n = \frac{1}{Fj} e^{i\phi}$, $r_n = -i Fj e^{i\phi}$, $T_n$ is the transmission probability of the $n$th scatterer, $R_n = 1 - T_n$ is its reflection probability, $\phi$ is the phase change in the transmitted wave and $k$ is the wave number of the exciton.

The transport of FMO can be well explored with the help of the transfer matrices in equation (1) as well as the junctions $S$ and $G$ to be defined below. Each pigment can be thought of as a potential well and there exists a potential barrier between two nearest neighbour pigments along the pathways. The potential barrier can be well described by the transfer matrix of the scatterer defined in equation (1). The wave function of the exciton in pigment $j$ could be written as $\psi_j(x) = C_j e^{ikx} + D_j e^{-ikx}$, where $C_j$ and $D_j$ are the amplitudes of the wave function. The amplitudes $C_j$ and $D_j$ are related to its nearest neighbour pigment through the transfer matrix of the scatterer between the two pigments. In addition, the transfer matrix of the pigment is the one as the ideal channel defined in equation (1). Therefore, we can describe the exciton transmission through the whole FMO complex with the following three steps: (i) the two major energy transport pathways in each monomer are described by two different scattering pathways $L_A$ and $L_B$, as shown in figure 2(a). (ii) Each monomer is represented by a ring with two branches $L_A$ and $L_B$, and is connected to two leads through two junctions $S$. The transfer matrix of the monomer $j$ ($j = 1, 2, 3$) is denoted as $F_j$, as shown in figure 2(b). (iii) The transport of the whole FMO can be described in figure 2(c), where three monomers represented by $F_j$ are connected to the antennas and the reaction centre through two junctions $G$. The exciton created at the antennas injects into FMO with $l = 1$ through the G junction connected with the antennas. For simplicity, we assume that there is no reflection from the reaction centre (the amplitude $O$ in figure 2(c) vanishes); In this case, the transmission coefficient of the whole FMO complex is then determined by the probability $|O|^2$ indicated in figure 2(c).

3 See supplementary material (stacks.iop.org/LPL/12/125201/mmedia) for reviewing some basic results of the quantum scattering model developed in the condensed matter physics.
where $l$ is the distance between the adjacent scatterers. The pathway $L_B$ is composed of four branches connected by two $S$ junctions ($\circlearrowleft$ and $\circlearrowright$). For each branch, we have

$$
\begin{pmatrix}
    p^R_m \\
    Q^R_m
\end{pmatrix} = \Gamma_m
\begin{pmatrix}
    p^L_m \\
    Q^L_m
\end{pmatrix} (m = 1, 2, 3, 4)
$$

where $\Gamma_1 = U_{l1} M_1$, $\Gamma_2 = U_{l1} M_2$, $\Gamma_3 = U_{l3} M_3 U_{l1} M_3$, $\Gamma_4 = U_{l3} M_3 U_{l3} M_3$, and $\Gamma_5 = U_{l3} M_3 U_{l3} M_3 U_{l3}$. Here $l_m$ is the distance between the scatterers or the distance between the scatterers and the junctions for the $m$th branch. The amplitudes of the three outgoing waves of the junction $S$ are related by a $S$ matrix to the amplitudes of the three incoming waves, i.e.

$$
\begin{pmatrix}
    Q^L_1 \\
    P^L_2 \\
    P^L_3
\end{pmatrix} = S
\begin{pmatrix}
    Q^R_1 \\
    Q^R_2 \\
    Q^R_3
\end{pmatrix},
\begin{pmatrix}
    P^R_1 \\
    P^R_2 \\
    P^R_3
\end{pmatrix} = S
\begin{pmatrix}
    Q^L_1 \\
    Q^L_2 \\
    Q^L_3
\end{pmatrix}
$$

where $S$ is a $3 \times 3$ unitary matrix and its detailed form is given by equation (14) in supplementary material (stacks.iop.org/LPL/12/125201/mmedia)$^4$.

From equations (1)–(4), the amplitudes $C^L_\alpha$, $D^L_\alpha$ of the wave function on the left of the pathway and the amplitudes $C^R_\alpha$, $D^R_\alpha$ on the right of the pathway can be related by the transfer matrices $L_\alpha$, that is,

$$
\begin{pmatrix}
    C^R_\alpha \\
    D^R_\alpha
\end{pmatrix} = L_\alpha
\begin{pmatrix}
    C^L_\alpha \\
    D^L_\alpha
\end{pmatrix}.
$$

Therefore, instead of an array of the scatterers, each pathway may be replaced by an effective transfer matrix.

We now study the exciton transport in one monomer of the trimer. The schematic representation of the monomer is shown in figure 2(b). Two pathways $L_A$ and $L_B$ form a ring and are connected to two leads through two $S$ junctions ($\circlearrowleft$ and $\circlearrowright$). With the help of the effective transfer matrix for the pathway $\alpha$ of the monomer $j$, we can obtain

$$
\begin{pmatrix}
    C^R_{j,\alpha} \\
    D^R_{j,\alpha}
\end{pmatrix} = L_{j,\alpha}
\begin{pmatrix}
    C^L_{j,\alpha} \\
    D^L_{j,\alpha}
\end{pmatrix},\ (j = 1, 2, 3)
$$

$^4$ See footnote 3.

Figure 2. The quantum scattering model we proposed to describe the excitation transmission of FMO. (a) The scattering matrix representation of two major pathways $L_A$ and $L_B$. (b) Each monomer is represented by the symbol $F_j$ made up of a ring with two branches $L_A$ and $L_B$ and connected to two leads. (c) The scattering matrix representation of the whole FMO complex. The symbols near the arrows denote the corresponding transmitted and reflected amplitudes.

III. Transfer matrices of the FMO complex

We now turn to study the transfer matrices of the basic elements $L_A$, $L_B$, $F_j$ and the whole FMO complex. The pathway $L_A$ is represented by three scatterers connected to two ideal channels, and its transfer matrix is then given by

$$
L_A = M_3 U_2 M_2 U_1 M_1,
$$

We now study the exciton transport in one monomer of the trimer. The schematic representation of the monomer is shown in figure 2(b). Two pathways $L_A$ and $L_B$ form a ring and are connected to two leads through two $S$ junctions ($\circlearrowleft$ and $\circlearrowright$). With the help of the effective transfer matrix for the pathway $\alpha$ of the monomer $j$, we can obtain

$$
\begin{pmatrix}
    C^R_{j,\alpha} \\
    D^R_{j,\alpha}
\end{pmatrix} = L_{j,\alpha}
\begin{pmatrix}
    C^L_{j,\alpha} \\
    D^L_{j,\alpha}
\end{pmatrix},\ (j = 1, 2, 3)
$$

$^4$ See footnote 3.
where \( L_{i,\alpha} = U_{i\alpha} M_{i\alpha} U_{i\alpha} \), and \( L_{j,\alpha} \) is the distance between the scatterers and \( S \) junctions for the pathway \( \alpha \) of the monomer \( j \).

The amplitudes of the three outgoing waves are related to the amplitudes of the three incoming waves through the \( S \) matrix given by

\[
(C^L_{j,A}) = S \left( \begin{array}{c} x_j^L \\ y_j^L \end{array} \right), \quad \left( \begin{array}{c} x_j^B \\ y_j^B \end{array} \right) = S \left( \begin{array}{c} x_j^C \\ y_j^C \end{array} \right).
\]

(7)

From equations (6) and (7), the amplitudes of the wave function on the left of the monomer \( j \) and the amplitudes on the right are related by the matrix \( F_j \) given by

\[
\left( \begin{array}{c} x_j^R \\ y_j^R \end{array} \right) = F_j \left( \begin{array}{c} x_j^L \\ y_j^L \end{array} \right)
\]

(8)

Similar to the transmission of one monomer, we can describe the exciton transport through FMO by two \( G \) junctions, as shown in figure 2(c). The amplitudes of the four outgoing waves of the junction \( G \) are related by a \( G \) matrix to the amplitudes of the four incoming waves

\[
(P') \left( \begin{array}{c} x_j^L \\ x_j^S \\ x_j^T \\ x_j^L' \end{array} \right) = G \left( \begin{array}{c} I \\ y_j^1 \\ y_j^2 \\ y_j^3 \end{array} \right), \quad \left( \begin{array}{c} O' \\ y_j^4 \\ y_j^5 \\ y_j^6 \end{array} \right) = G \left( \begin{array}{c} 0 \\ x_j^R \\ x_j^R \\ x_j^R \end{array} \right)
\]

(9)

where \( G \) is a 4 x 4 unitary matrix given by equation (20) in supplementary material (stacks.iop.org/LPL/12/125201/mmedia)\(^5\). By solving equation (9) with \( I = 1 \) and \( O = 0 \), one can obtain the transmission coefficient \( T_{FMO} = |O|^2 \) of the FMO complex.

To understand the features of the transmission, we compare the transmission coefficients for different numbers of pathways. For simplicity, we assume that all the scatterers have the same transmission probability \( T_s = T \) and the phase change in transmitted wave \( \phi_s = 0 \). Furthermore, we compare the transmission difference between the classical and quantum cases. As for the classical transmission, it means that the exciton is a classical particle without a wave-like phase and thus the particle probability is determined by the addition of the probability from different pathways and not the amplitudes of the wave function; in addition, the scatterer is determined uniquely by the transmission probability \( T \).

IV. Transmission of the FMO complex

IVA. Transmission of the pathways \( L_A \) and \( L_B \).

Based on equations (1), (2) and (5), we can obtain the total transmission probability \( T_A = |C_{R0}^L|^2 \) for pathway \( L_A \) under the conditions \( C_A^C = 1 \) and \( D_A^C = 0 \),

\[
T_A = T^3 / [2R \cos 4\phi_A + 4R(1 + R) \cos 2\phi_A + 5R^2 + 1],
\]

(10)

where \( \phi_A = kl \). It is notable that the resonant tunnelling \( T_A = 1 \) appears under the condition \( \phi_A = \pi/2 - \arccos(T^2 - 1) \). However, as for the classical case, after considering the multi-reflection between the scatterers, we may obtain the total transmission probability \( T_A^C < \frac{T}{T^2} \).

Figure 3(a) shows the total transmission probability as a function of the path phase for both the quantum and classical cases at strong scattering limit \( T = 0.01 \). For classical case, \( T_A^C < 5 \times 10^{-3} \), it is impossible for the particle to pass through the system at the strong scattering limit. However, for the quantum case, there exist four resonant peaks at which the total transmission probability takes its maximal value \( T_A = 1 \). Therefore, the transport involving optimal quantum coherence is more efficient than that involving the classical behaviours alone.

For pathway \( L_B \), we set \( C_B^L = 1, D_B^R = 0, kl_2 = kl_3 = \phi_B \) and \( kl_1 = kl_4 = \phi_B' \). From equations (2)–(5), the total transmission probability \( T_B = |C_{R0}^L|^2 \) is given by

\[
T_B = T^4 / [(P^2 + Q^2)],
\]

(11)

where \( P = (1 + R) [\cos \gamma + R \cos(\gamma - 2\phi_B)] + 4R \cos \phi_B \), \( Q = T \sin\gamma + R \sin(\gamma - 2\phi_B) \), \( \gamma = 3\phi_B + 2\phi_B' \), the resonant tunnelling \( T_B = 1 \) will happen under the conditions \( \phi_B = \pi \) and \( \phi_B = \frac{1}{2} \arccos(-R) \).

The path phases \( \phi_A, \phi_B \) and \( \phi_B' \) denote the distance between the neighbouring scatterers or the distance between the scatterers and the junctions, which is determined by the space distribution of the eight pigments. When the pigments are optimally spaced such that \( \phi_A = \frac{1}{2} \arccos(T^2 - 1) \) for \( L_A \) and \( \phi_B = \frac{1}{2} \arccos(-R) \) or \( \phi_B' = \frac{1}{2} \arccos(-R) \) for \( L_B \), the quantum resonant tunnelling will happen and the exciton can pass through the barriers with perfect efficiency. Therefore, we have theoretically demonstrated that optimally spaced pigments in light-harvesting complexes can facilitate the energy transfer.

IVB. Transmission of one monomer

From equations (6)–(8), we can obtain the total transmission probability of one monomer \( T_M = \left|x_j^R\right|^2 \) at \( x_j^L = 1, \ y_j^R = 0 \), \( kl_{j,A} = \phi_A \) and \( kl_{j,B} = \phi_B \), which is given by

\[
T_M = H^2 / [P^2 + Q^2],
\]

(12)

where \( H = \sqrt{2} / (2\sqrt{R + \sin 2\phi_A + \sin 2\phi_B}), \ P = 2 \sin^2(\phi_A + \phi_B) \sin(\phi_B - \phi_A), \ Q = \sin(2\phi_A + 2\phi_B), \) \( R = \cos 2\phi_A + 2\phi_B \). We can find that the resonant tunnelling \( T_M = 1 \) under the conditions \( \phi_A + \phi_B = \frac{\pi}{2} \) and \( \phi_A = \frac{1}{2} \arcsin (\sqrt{T^2 - T^2}) \). In contrast, the classical transmission probability \( T_M^C \) is less than its upper bound \( \frac{T}{T^3} \).

Figure 3(b) shows the total transmission probability of one monomer versus the path phases at \( T \leq 0.01 \). For the classical case, \( T < 0.029 \), the particle passes through the monomer with a very small probability. However, for the quantum case, there
are eight resonant regions where the particle can pass through the monomer with perfect efficiency. Compared with the single pathway, the resonant regions for two pathways become larger, and then it is much easier for the exciton that absorbed different colours of light to pass through the monomer.

IV.C. Transmission of the whole FMO complex

From equations (6)–(9), we can obtain the total transmission probability $T_{\text{FMO}} = |O|^2$ of the whole FMO complex. For simplicity, we assume $k_{l,A} + k_{l,B} = \frac{1}{2}$ (which means that the quantum resonant tunnelling occurs in each monomer) and the phases accumulated between $G$ and $S$ are an integer of $2\pi$. Then we have

$$T_{\text{FMO}} = H^2|Q|^2,$$

(13)

where $H = 6\sqrt{T}q_1g_1\left(3R + 2p_1\sqrt{R} + \frac{1}{2}p_1^2 - \frac{1}{2}p_2^2\right)$. Here $p_0 = \sin 2\phi_1 \sin 2\phi_2 \sin 2\phi_3$, $p_n = \sin^n 2\phi_1 + \sin^n 2\phi_2 + \sin^n 2\phi_3$ ($n = 1, 2, 3, 4$), and $q_j = \sin 2\phi_1 + \sqrt{R}$ with $\phi_j = kl_{l,A}$. It is found that the exciton can resonantly pass through FMO when $\phi_1 = \phi_2 = \phi_3 = \frac{1}{2}\arcsin (\sqrt{T} - \sqrt{R})$. In contrast, the total classical transmission probability $T_{\text{FMO}}^c$ is less than its upper bound $\frac{9\pi}{1 + 8\pi}$ figure 3(c) shows the quantum transmission of the whole FMO complex for fixing $\phi_3 = \frac{1}{2}\arcsin (\sqrt{T} - \sqrt{R})$ and $T = 0.01$. Compared with the transmission of double pathways shown in figure 3(b), the resonant region of the whole FMO becomes larger. However, the transmission $T_{\text{FMO}}^c < 0.083$ for the classical case, which is pretty small.

Figure 3. The transmission probability as a function of the path phases at $T = 0.01$. (a) Single pathway $L_A$ for both the quantum and classical cases. (b) A monomer with double pathways. (c) The whole FMO with multiple pathways at $\phi_1 = \frac{1}{2}\arcsin (\sqrt{T} - \sqrt{R})$. (d) The resonant structures: (I) one pathway $L_A$, (II) two pathways at $\phi_B = \frac{1}{2}\arcsin (\sqrt{T} - \sqrt{R})$, (III) multiple pathways at $\phi_1 + \phi_2 = \pi/2$ and $\phi_3 = \frac{1}{2}\arcsin (\sqrt{0.12T} - \sqrt{R})$. 
V. Concluding remarks

Here we make several remarks on the main results that can be obtained from the scattering model: (i) the mechanism underlying the perfect energy efficiency is the resonant transmission induced by the quantum coherent effects, which is impossible for the classical mechanism. (ii) The multi-pathway plays a significant role in achieving the remarkable efficiency of the energy transfer. To understand this point, we plot in figure 3(d) the transmission coefficients for one, two and multiple pathways. The resonant regions for FMO with multiple pathways occupy almost all the parameter space, which ensures that the exciton can pass through FMO with perfect efficiency. The large resonant region means that the exciton that absorbed different colours of light can still pass through FMO with high efficiency. (iii) The resonant conditions are determined by the space distribution of the pigments. When the pigments are optimally spaced such that the quantum resonant tunnelling will happen, the exciton can pass through FMO with perfect efficiency. Therefore, our results prove the conjecture that quantum coherence might ‘wire’ together the final energy acceptors in antennas, thus compensating for the relatively weak coupling between the pigments in FMO [2, 8]. In addition, FMO with multiple pathways has a fault-tolerant function. When one pathway or one subunit is blocked, the exciton can still pass through other pathways.

The FMO experiment was usually described by the quantum network (graphs). Before ending, we compare the scattering model with the quantum network (graphs) studied in the previous literature [15, 16]. One usually models a FMO with a network with two parameters: the local site excitation energies \( \omega_k \) and the hopping rate \( v_{k,l} \) of an excitation between the sites \( k \) and \( l \). It has been shown that the efficiency of the energy transport on such quantum graphs can be larger than that in the corresponding classical model [15]. The scattering model proposed here is actually a special quantum network with a constant \( \omega_k \) (since for simplicity we have assumed that all potentials in the wells are the same, this assumption can be released) but \( v_{k,l} \) is analogous to the tunnelling rate \( T_{k,l} \). Compared with the previous literature, an essential difference in this paper is that we have a phase factor in the scattering model, which is equivalent to adding a phase \( \varphi_{k,l} \) to the hopping term in the quantum graphs. This phase factor has been ignored in previous studies; however, it indeed has an important impact [19] since the phase factor is a fundamental element in quantum theory. The phase factor is determined by the structure of FMO, such as the length of the pigment as well as the barrier between the pigments. Although the phase factor is usually complicated, it can be directly measured with some devised interference experiments. Essentially because of this newly introduced phase factor, we have obtained one of the main conclusions that all three aforementioned factors are perfectly combined together to contribute the perfect energy transport.

In summary, we have proposed a scattering model to compare the quantum and classical energy transfer in FMO. We found that the aforementioned three factors, the optimal space distribution of the pigments, multiple pathways and quantum effects, are combined together to ensure the high efficiency of the energy transfer in FMO. Although we only studied the transport process through the FMO complex, the methods and conclusions can be extended to the other photosynthetic light-harvesting complexes. Therefore, we can definitely demonstrate that the quantum coherence with optimal pathways is a factor for highly efficient energy transport in photosynthetic light-harvesting complexes. As we know, the biological system governed by Darwinian selection usually has the optimal structure, which can ensure that the quantum coherence occurs in the optimal pathways.

Acknowledgments

This work was supported by the NNSFC (Nos. 11575064, 11175067, and 11125417), the NBRPC (No.2011CBA00302), the SKPBR (No.2011CB21204), the PCSIRT (No. IRT1243), and the NSF of Guangdong (No. 2014A030313426)

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