

The model of photoinduced changes in the pigment-protein complex of reaction center

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Summary. The slow dynamics of isolated complexes of the chlorophyll containing membrane proteins in photosynthetic reaction centers (RCs) in *Rb. sphaeroides* R-26 which is induced by light flows has been studied experimentally. The changes of the RC solution absorption have been analyzed theoretically in terms of the three-level model. The equation that has been obtained determines the ratio between the population of electron levels of the primary and secondary chinons. The solution of this equation even for stationary case has been found to bear non-Boltshman character and depend on the intensity of the excitation light. The suggested model of level dynamics in RCs takes into account the probability of polarization processes in the vicinity of the secondary chinon Q_B in the result of numerous photoinduced electron transitions. All the RCs are assumed to have identical structural deformation but may be in different states whose characteristics depend on time duration after light quantum absorption as well as on viscosity and elasticity of the Q_B surrounding.

Keywords: reaction center, photoinduced electron transition, theoretical model.

Introduction. It is well known that when a light quantum is absorbed by a reaction center (RC) in photosynthetic purple bacteria the primary donor of bacteria chlorophyll dimmer electron (P) is photooxidized and then transferred first to primary (Q_A) and next to final chinon acceptor (Q_B) [1-3]. At each of the cofactors in the chain of the electron transfer it is stabilized due to the structure and dynamics of an RC molecular complex. In particular the localization of the electron on chinon acceptors is determined by the state of interprotein hydrogen bonds (whose formation involves water mole-

cules as well) and by protogeneity of the ionogenic groups of the nearest amino acid residues, which is accompanied by conformational reconstruction of the RC molecular complex [2-5]. To find out the mechanisms of the photoinduced conformational transitions in biomolecules is not only of theoretical but also of practical interest. On the one hand the molecule bioactivity depends largely on its conformation, on the other hand the control over conformational transitions makes it possible to apply them in molecular electronics.

Despite a great number of researches in photoinduced processes in RCs their theoretical interpretation is far from complete. In particular, no adequate model has been suggested so far to describe the electron intermolecular dynamics under the action of light. The difficulty in

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developing such a model is caused by multistage electron transfer within RC complexes as well as the variety of transition channel inside RCs themselves. As the simplest case an RC may be presented as a protein matrix with built-in molecules (redox-cofactors) which show donor-acceptor properties with respect to photoexcited electron. Through a number of intermediate states and primary quinon Q_A the electron is transferred from dimmer bacteriochlorophyll donor P to the distance of 30–40 Å and is stabilized at the secondary acceptor Q_B , thus forming a potential difference at a photosynthesizing membrane. The electron transfer initiated by light quantum absorption can be described in terms of a three level model in which the energy level corresponding to acceptor Q_B is presented as gradually changing in the process of electron transfer [5]. The energy level change depends on conformational transitions in the RC and polarization processes around it. It is obvious that the change of energy characteristics of the RC should result in different velocity constants of photoinduced electron transitions. Since the problem of electron transport in RCs is rather complicated, it has been analyzed by using two-level model with additional simplifying assumptions [2, 5, 7]. In particular the conformational motion of the RC is assumed to be a continuous diffusion in the potential well of small depth [8], RCs are assumed to be characterized by a certain dispersion of structural changes, which involves the availability of the whole complex of the photoinduced electron transition velocity constants, and, finally, the ratio of electron population on Q_A and Q_B quinons is assumed to be quasi-equilibrium and independent of the inducing light intensity. However, the validity of these assumptions requires further verification.

In our work we suggest a model of photoinduced structural changes in the aggregations of molecular complexes of RCs with small dispersion. All the molecules in RCs are assumed to be the same, i.e. with the same dynamics of structural changes described by one and the same electron transition velocity constant which depends on the time of the process. As a result the permanent configuration of RC is formed due to multiple electron transitions and the RC macromolecule deformation in its turn influ-

ences the velocity of electron transitions deforming the electron levels of the reaction [9]. We also analyze the three-level set of ballast equations and take into account the influence of the light intensity on the relation between electron population of P, Q_A and Q_B .

The three-level model of electron dynamics in RC. The conformational transitions may be detected either directly (by using x-ray or photoluminescence analysis) or indirectly — by means of interferometry, and photoacoustic or optical methods [2, 5–7].

We shall analyze the problems arising in the researches of electron transport dynamics in RCs by investigating the absorption dynamics of optical spectrum at the wavelength of $\lambda_0=865$ nm [1–7]. This approach is possible because the cross-section of interaction of photons with λ_0 wavelength depends on the electron state of an RC complex which changes under exposure of the sample with RCs to excitation light with intensity I and wavelength λ_0 . When the electron escapes the bacteriochlorophyll dimmer, the RC becomes incapable of absorbing light with λ_0 wavelength. Thus, the difference in (A) absorption is proportional to the different probability $p(t)$ of electron availability on the bacteriochlorophyll [2, 5] at the moment of observation:

$$\Delta A(t) \sim p(t) \quad (1)$$

According to the results reported in [5], it follows from correlation (1) that velocity constant k_{21} of the electrons returning from the other parts of RC (Q_A , Q_B is the generalized acceptor) to P (donor) can be determined from the correlation:

$$k_{21}(t) = -\frac{1}{A(t) - A(0)} \cdot \frac{\Delta A(t)}{\Delta t} \quad (2)$$

The set of equations [5] will describe the electron transfer in this system:

$$\begin{aligned} \frac{dp(t)}{dt} &= -k_{PA} \cdot p(t) + k_{AP} \cdot q_A(t) + k_{BP} \cdot q_B(t); \\ \frac{dq_A(t)}{dt} &= k_{PA} \cdot p(t) + k_{BA} \cdot q_B(t) - k_{AP} \cdot q_A(t) - k_{AB} \cdot q_A(t); \\ \frac{dq_B(t)}{dt} &= k_{AB} \cdot q_A(t) - k_{BA} \cdot q_B(t) - k_{BP} \cdot q_B(t) \end{aligned} \quad (3)$$

where k_{ij} is the constant of transition velocity between levels $i \rightarrow j$. The processes in the RC molecule are initiated by the excitation light, therefore k_{PA} parameter depends (proportionally) on the intensity of the light I; $q_A(t)$ is the

probability of electron location on the primary chinon acceptor Q_A ; $q_B(t)$ is the probability of electron location on the final chinon acceptor Q_B .

The set of equations (3) should be complemented by the correlat

$$p(t) + q_A(t) + q_B(t) = 1 \quad (4),$$

which shows the RC system closeness.

As shown in [2, 5, 7] the transition velocity constants are of the following order of magnitude: $k_{AP} \sim 10 \text{ s}^{-1}$, $k_{BP} \sim (0,02-0,2) \text{ s}^{-1}$, $k_{AB} \sim 10^4 \text{ s}^{-1}$, $k_{BA} \sim 10^3 \text{ s}^{-1}$.

Now we shall determine the ratio of electron populations on Q_A and Q_B :

$$f(t) = \frac{q_A(t)}{q_B(t)} \quad (5).$$

By using this quantity we can obtain:

$$\frac{dq_B(t)}{dt} \cdot f(t) + q_B(t) \frac{df(t)}{dt} = k_{PA} \cdot p(t) + k_{BA} \cdot q_B(t) - (k_{AP} + k_{AB}) \cdot f(t) \cdot q_B(t) \quad (6).$$

By substituting (6) in the last equation of the system (3) we obtain

$$[k_{AB} \cdot f(t) - k_{BA} - k_{BP}] \cdot q_B(t) \cdot f(t) + q_B(t) \frac{df(t)}{dt} = k_{PA} \cdot p(t) + k_{BA} \cdot q_B(t) - (k_{AP} + k_{AB}) \cdot f(t) \cdot q_B(t) \quad (7),$$

from which it follows that after cancelling $q_B(t)$ in the right and left sides of the equation:

$$[k_{AB} \cdot f(t) - k_{BA} - k_{BP}] \cdot f(t) + \frac{df(t)}{dt} = k_{PA} \cdot \frac{p(t)}{q_B(t)} + k_{BA} - (k_{AP} + k_{AB}) \cdot f(t) \quad (8).$$

Therefore under the sample exposure to excitation light even in stationary case the ratio of electron population on levels Q_B and Q_A is not described by Boltzman correlation but depends on the intensity I . The equation for the electron population ratio on Q_A and Q_B acquires especially simple form without sample exposure to excitation light ($k_{PA}=0$) and should be as follows:

$$\frac{df(t)}{dt} = k_{BA} + (k_{BA} + k_{BP} - k_{AP} - k_{AB}) \cdot f(t) - k_{AB} \cdot f^2(t) \quad (9).$$

To solve equation (8) it is necessary to specify the value of $f(t)$ at a certain (initial) moment of time and a natural choice should be the moment of switching off the light. Therefore in the region of transitional time, even with the switched off light, $f(t)$ function depends on the intensity of the excitation light. Equation (9) is the precise consequence of the balance equations of three-level system (3) and the condition of system closeness (4). The analysis carried out with taking into account the above values of

transition velocity constants has shown that if we do not take into consideration the range of time ($0 \div 10^{-3}$) sec., we can use instead of (9) its stationary and linear variant

$$0 = k_{BA} + (k_{BA} + k_{BP} - k_{AP} - k_{AB}) \cdot f(t) \quad (10)$$

or

$$f(t) = \frac{k_{BA}}{k_{AP} + k_{AB} - k_{BA} - k_{BP}} \approx \frac{k_{BA}}{k_{AB}} \quad (11).$$

Expression (11) agrees with that reported in [5], but it can be used for describing the processes taking place in the RC only after switching off the light. To obtain the approximation of expression (11) we use the above mentioned values of transition velocity constants. From equation (11) we can write:

$$q_A(t) = \frac{k_{BA}}{k_{AB}} \cdot q_B(t) \quad (12).$$

Now we shall use equation (12) to analyze the first equation from the system (3) describing the case without the excitation light ($k_{PA}=0$) together with equation (4). In the result we have:

$$\frac{dp(t)}{dt} = k_{AP} \cdot q_A(t) + k_{BP} \cdot q_B(t) = k_{AP} \cdot \frac{k_{BA}}{k_{AB}} \cdot q_B(t) + k_{BP} \cdot q_B(t)$$

$$(k_{AP} \cdot \frac{k_{BA}}{k_{AB}} + k_{BP}) \cdot q_B(t) = \frac{k_{AP} \cdot k_{BA} + k_{AB} \cdot k_{BP}}{k_{AB}} \cdot q_B(t) \quad (13),$$

$$p(t) + \frac{k_{BA}}{k_{AB}} \cdot q_B(t) + q_B(t) = p(t) + \frac{k_{BA} + k_{AB}}{k_{AB}} \cdot q_B(t) = 1 \quad (14).$$

Taking into consideration that $k_{AB} \sim 10^4 \text{ s}^{-1} \gg k_{BA} \sim 10^3 \text{ s}^{-1}$ is typical for RC instead of (14) we can use:

$$p(t) + q_B(t) = 1 \quad (15).$$

This expression allows us to write (13) in the following form:

$$\frac{dp(t)}{dt} = \frac{k_{AP} \cdot k_{BA} + k_{AB} \cdot k_{BP}}{k_{AB}} \cdot (1 - p(t)) \quad (16).$$

Equation (16) together with the initial condition

$$p(t=0) = p_0 \quad (17)$$

describes the kinetics of the RC system after switching off the light. The included in (17) parameter p_0 determined by the electron population of donor at the moment of switching off the light. Correlations (16, 17) make it possible to describe the RC system as a two-level system if the results obtained by using this model are not used for time intervals smaller than 0,001 s. In this case transition velocity constant k_{21} of the electron from acceptor (which is a dynamic unity Q_A and Q_B — level 2) to donor (P — level 1) is determined from the following equation:

$$k_{21} = \frac{k_{AP} \cdot k_{BA} + k_{AB} \cdot k_{BP}}{k_{AB}} \quad (18).$$

Thus, to investigate the absorption relaxation dynamics in an RC solution with the precision in time no smaller than 0,001 s we can use the equation:

$$\frac{dp(t)}{dt} = k_{21} \cdot (1 - p(t)) \quad (19).$$

The expression for the velocity constant k_{21} of the electron return is given by correlation (18). Equation (17) is used as initial condition. Therefore the quantities k_{21} and p_0 are the only characteristics that can be determined experimentally (formula 2) by investigating the absorption relaxation of RC solution which occurs after terminating the exposure to excitation light.

The repeated analysis for the case when $I \neq 0$ shows that the kinetics of electron population P can be described by the equation

$$\frac{dp(t)}{dt} = -I \cdot \alpha \cdot p(t) + k_{21}(t) \cdot (1 - p(t)) \quad (20),$$

where α is the absorption cross section depending on I ; $k_{21}(t)$ coefficient in this case should be obtained by using equation (8). However, the optional assumption given in [5, 7] is that the cross section is independent of time. Thus, the given model describes the peculiarities of RC kinetics by modeling the reverse transition of k_{21} which depends on time.

The processes taking place in RC complexes with the switched off light are described by equation (19) in which correlation (17) is used as initial condition.

In order to obtain the direct information about the transition velocity constant in the RCs from experimental data on $k_{21}(t)$ we shall use formula (18) and the assumption that electron transition from Q_B directly to donor P is highly difficult, therefore we assume $k_{BP}=0$. In this case the following equation is valid:

$$k_{21}(t) = \frac{k_{AP} \cdot k_{BA}}{k_{AB}} \quad (21).$$

According to the reported data [4-7] the velocity constant k_{AP} is a quantity that does not depend on time and therefore the kinetics of $k_{21}(t)$ is totally determined by the velocity constants of k_{BA} and k_{AB} electron transitions between Q_A and Q_B chinons.

Experimental results and their discussion. In

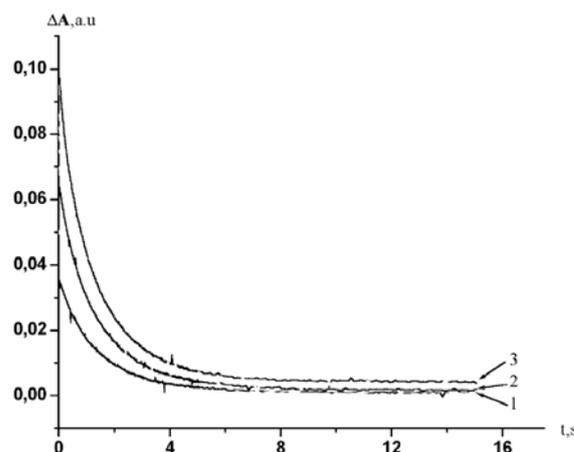


Fig. 1. The experimentally obtain dependence of light absorption by water solutions with RC complexes separated from the photosynthetic cell membranes of *Rhodospirillum rubrum* at the moment of switching off the excitation light $t=0$ for different time exposures: 1 s (curve 1), 50 s (curve 2) and 300 s (curve 3).

our experiments we used isolated protein-pigmented complexes (RCs) obtained by the researchers of biophysics department of Moscow State University from photosynthetic membranes of *Rhodospirillum rubrum* cells by using laurilmethylaminoxide (LDAO) detergent. The long-term stability of RCs parameter was insured by using water solution of 0.01 M sodium phosphate buffer with pH 7.2 and additional 0,05 % of the detergent. The dimensions of measuring cell were 3x5x2,5 cm and quartz wall thickness 1 mm.

The RC solution of concentration $\sim 10^{-6}$ M was exposed for no less than 12 hours in darkness at room temperature (darkness adapted state). The darkness adapted state was obtained by illuminating the RC solution with light impulses of varied duration and intensity [1-7]. The spectral range of the excitation light diode covered the larger part of the absorption band of RC's «aerial». The relative number of the centers as well as the velocities of transition from one state into another was determined from the kinetics of optical spectrum absorption at $\lambda_0=865$ nm by using equation (19).

The measurement data are given in Fig. 1, 2, which shows the kinetics of RC absorption relaxation after switching off ($t=0$) the excitation light (865 nm) of different duration and intensity. As seen from Fig. 2 the absorption

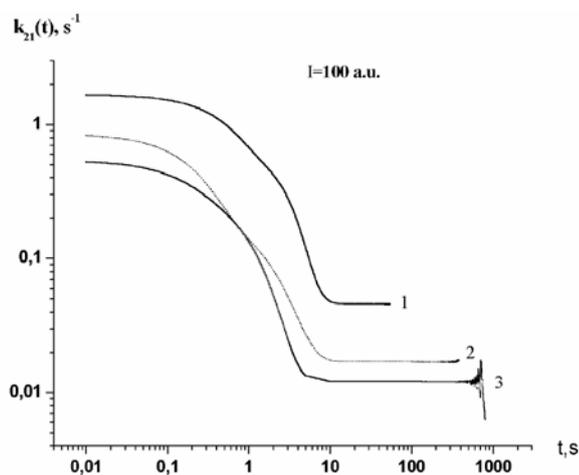


Fig. 2. The time dependence of light absorption by water solutions with RC complexes separated from the photosynthetic cell membranes of *Rhodospira rubra* at the moment of switching off the excitation light $t=0$ with intensity $I_0=100$ a.u. and different time exposures: 1 s (curve 1), 50 s (curve 2) and 300 s (curve 3).

becomes stationary within 10 s after switching off the light. The difference of the values ($A_{(t=0)} - A_{(t>10\text{ s})}$) increases with the increase of RC light exposure. The intensity I of the excitation light is given in apparatus units (700 units correspond to 20 W/m^2).

The experimental data were calculated by using correlation (18) and the results are given in Fig. 2 and 3, which shows the velocity constant kinetics $k_{21}(t)$ for RC relaxation to darkness adapted state after switching off excitation time of different intensity and duration. The results allow for the following conclusions:

1) during the first 0,1-2 s the value of $k_{21}(t)$ is maximal and weakly changes with time. Within the next time interval $\sim 1-3$ s the value of $k_{21}(t)$ decreases by 2-3 orders after which it remains stable as well. This fact testifies about the stability of RC properties in this time interval;

2) the decreased exposure of the sample to the excitation light or the increase of light intensity results in the decreased values of parameter k_{21} .

This kind of $k_{21}(t)$ dependence for RC relaxation should be the consequence of polarization peculiarities in the vicinity of Q_B resulting from viscous-elastic properties of the medium.

The kinetics of electron level Q_B in darkness.

To explain the peculiarities of the parameter k_{21} behavior we suggest a model in which the corre-

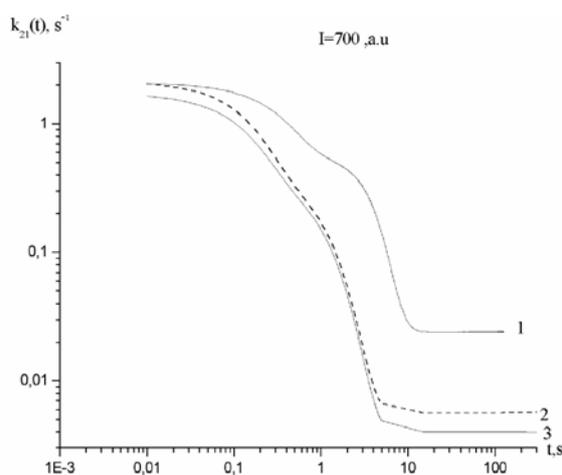


Fig. 3. The time dependence of light absorption by water solutions with RC complexes separated from the photosynthetic cell membranes of *Rhodospira rubra* at the moment of switching off the excitation light $t=0$ with intensity $I_0=700$ a.u. and different time exposures: 1 s (curve 1), 50 s (curve 2) and 300 s (curve 3).

lations between the values obtained from experimental measurements are taken into account. The model's scheme is shown in Fig. 4.

When the excited electron is on chinon Q_A it is located in the vicinity of point y_A . We place this point at the beginning of the coordinate system and thus assume $y_A=0$. The change of the electron potential energy when it deviates from the equilibrium state we describe by potential energy $U_A(y)$. In case of electron transition to chinon Q_B its equilibrium center is shifted to point y_B . It is obvious that due to this transition the electron surrounding changes and therefore, to put it generally, the interaction between the RC skeleton and the electron should also change. Thus the expression describing the electron potential energy on Q_B will be different, as should be the shape of potential curves $U_A(y)$ and $U_B(y)$ (Fig. 4). The minimal potential energy of the electron on Q_B is determined by E_B . Taking into account [2, 8, 10-11] that the location of neighboring electrons is not strictly fixed, when arriving to Q_B the electron interacts with its surrounding thus causing the polarization in the vicinity of its localization that changes with time. Therefore y_B , E_B (and $U_B(y)$ in general) should, generally speaking, depend on time. For the simplicity we shall take into account only $y_B(t)$ and $E_B(t)$.

To explain the peculiarities of $k_{21}(t)$ kinetics we shall dwell on the investigation of electron

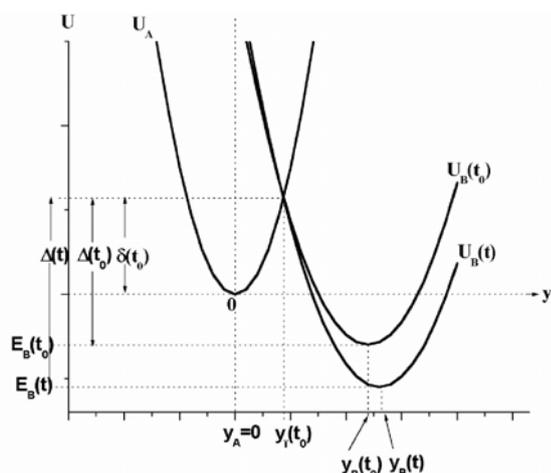


Fig. 4. The scheme of electron transitions between chinons Q_A and Q_B . $UB(y)$ function is plotted for the two moments of time: $t=t_0$ corresponds to the moment of switching off the light and $t>t_0$. The heights of potential barriers Δ and δ , which prevent electron transition $Q_B \rightarrow Q_A$ and $Q_A \rightarrow Q_B$, depend on time; y is the nucleus coordinate.

transition $Q_B \leftrightarrow Q_A$. Fig. 4 shows the scheme of electron transitions in the two-level acceptor system. The light is switched off at the moment t_0 . The time $t>t_0$ corresponds to RC exposure in the darkness. It should be noted that, under the assumption about the activation mechanism of overcoming the barrier which separates the energy levels of the electrons on Q_A and Q_B [5], k_{21} is determined by the barrier height in the correlation:

$$k_{BA}(t) = v \cdot \exp\left(-\frac{\Delta(t)}{k_B \cdot T}\right) \quad (22).$$

Here v is the frequency of electron approaches to the barrier in $\Delta(t)$ which includes the transition matrix element $2 \rightarrow 1$, k_B is Boltzman constant, T is absolute temperature of the sample. In case of the tunnel mechanism of the barrier overcoming, correlation (22) should be substituted by the corresponding expression given in [12]. The quantity k_{AB} is determined by using expression analogous to (22):

$$k_{AB}(t) = v \cdot \exp\left(-\frac{\delta(t)}{k_B \cdot T}\right) \quad (23).$$

δ (Fig. 4) is the height of energy barrier which is overcome by the electron in transition from chinon Q_A to chinon Q_B .

When deriving formulas (22) and (23) we assumed that $Q_A \leftrightarrow Q_B$ electron transitions are activational. For the sake of simplicity we also assumed that the frequency of hops during

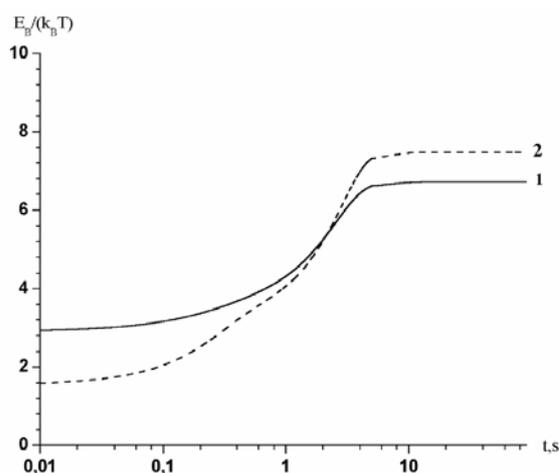


Fig. 5. The time dependence of potential differences between energy levels Q_A and Q_B at different light intensities: $I=100$ (curve 1) and $I=700$ a.u. (curve 2). The time of exposition is 300 s.

$Q_A \leftrightarrow Q_B$ electron transitions is the same. Using (21), (22) and (23) we obtain the following expression:

$$k_{21}(t) = k_{AP} \cdot \exp\left(-\frac{E_B(t)}{k_B \cdot T}\right) \quad (24).$$

It should be mentioned again that E_B is the depth of the potential well in which electron is found on chinon Q_B and which is relative to the minimal possible energy of the electron on chinon Q_A (Fig. 4). From formula (24), experimental data given in Fig. 2 and 3 as well as approximated correlation $k_{AP} \sim 10^{-1}$ s we can obtain information about the kinetics of the electron level on Q_B relatively electron level on Q_A :

$$\frac{E_B(t)}{k_B \cdot T} = \ln \frac{10c^{-1}}{k_{21}(t)} \quad (25).$$

The behavior of (25) is illustrated by Fig. 5 where the time dependence of E_B is shown for two values of the excitation light intensity. As seen from the figure, E_B depends on I , which testifies about the mutual influence of polarization processes and rheological parameters of RCs [13].

Conclusions.

1. The velocity constant of electron transition from acceptor to donor has been found to depend considerably on time after switching off the excitation light. This $k_{21}(t)$ dependence displays S-like character, which can be explained by the distortion of the electron level at final acceptor Q_B in the result of polarization effects due to multiple photoinduced electron transitions in RC macromolecule.

2. During the first 0,1-2 s the magnitude of electron transition velocity constants is maximum and weakly depends on time. Further, in the next time interval of ~3 s. The constant value decreases by 2-3 orders of magnitude, after which it remains stable testifying to the stability of RC properties in this time interval.

3. The theoretical model has been suggested that describes the process of photoinduced electron transition in the aggregation of similar RCs. The model takes into account the dependence of

the ratios between electron populations of Q_B and Q_A acceptors on the intensity of excitation light.

4. A single combination of velocity constants for electron transitions in RCs has been found, which is calculated by using experimental data about RC behavior after switching of the light. The electron level kinetics of chinon Q_B has been found in relation to the electron level of chinon Q_A .

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Модель фотоіндукованих змін у пігмент-білковому комплексі реакційного центру

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Резюме. Експериментально досліджено повільну динаміку ізольованих комплексів хлорофілвісних мембранних білків фотосинтетичних реакційних центрів (РЦ) *Rb. sphaeroides* R-26, індуковану світловими потоками. Проведено теоретичний аналіз зміни поглинання розчину РЦ у рамках трьохрівневої моделі. Отримано рівняння, яке визначає відношення заповнених електронних рівнів першого та другого хінонів. Розв'язок цього рівняння навіть у стаціонарному випадку не має бальцманівського характеру і залежить від інтенсивності збуджувального світла. Запропонована модель динаміки рівнів РЦ ураховує можливість поляризаційних процесів в околі другого хінона Q_B як результат багатократних фотоіндукованих переходів електрона. Припускається, що всі РЦ мають однакову структурну деформацію, але можуть знаходитися в різних станах, характеристики якого залежать від часу, що пройшов після поглинання кванта світла, а також від в'язкості та пружності оточення Q_B .

Ключові слова: реакційний центр, фотоіндукований електронний перехід, теоретична модель.

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