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Electron transport in *Heliobacterium chlorum* whole cells studied by electroluminescence and absorbance difference spectroscopy

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An electric field pulse induced luminescence signal was observed in suspensions of whole cells of the photosynthetic green bacterium *Heliobacterium chlorum*. This signal is associated with electron transport in the reaction center. The dependence of the electroluminescence on the delay between the flash and the pulse and the absorbance kinetics at 800 and 553 nm revealed the following properties of electron transport in whole cells: (1) most of P-798$^+$ was rereduced by cytochrome *c*-553 in two phases with half-times of 0.11 and 0.7 ms and equal amplitudes (this is considerably faster than the times reported for membrane fragments); (2) if reduced cytochrome *c*-553 is not available, P-798$^+$ reacts back with a reduced acceptor in 20 ms; (3) oxidized cytochrome *c*-553 is rereduced in about 20 ms, presumably by an external donor, because it does not take place after resuspension of the cells in Tris buffer. In membrane fragments, spheroplasts and cells stored at −20 °C, cytochrome oxidation is inhibited and no electroluminescence can be observed.

Introduction

The kinetics of charge recombination of charge pairs which span the photosynthetic membrane can be altered by external electric fields. Studies of these effects may reveal information on electrogenic, kinetic and thermodynamic properties of the electron-transport reactions involved. In order to significantly alter the free energy of the back-reaction, membrane potentials in the order of hundreds of millivolts must be applied. Popovic and co-workers [1,2] achieved by this incorporating isolated *Rhodobacter sphaeroides* reaction centers into Langmuir-Blodgett films. A different method is to use a suspension of large membrane vesicles which allow the generation of high field strengths in the membrane. The pulse-induced change in redox state may be detected in fluorescence [3] or absorbance [4]. The stimulated charge recombination during the pulse can be monitored by delayed luminescence, called electroluminescence [5–7]. This phenomenon has been subject to study almost exclusively in osmotically swollen chloroplasts called blebs. However, photosynthetic bacteria may be large enough to detect electroluminescence. The recently discovered green photosynthetic bacterium *Heliobacterium chlorum* is rod-shaped, with a width of about 1 μm and a length of up to 10 μm [8]. It displays a relatively simple and undifferentiated internal structure. No membranes within the cells have been observed [9,10]. The photosynthetic pigment-protein complexes must be located in the cell membrane. This implies that the photosynthetic reaction centers are located in closed and unfolded membrane systems of relatively large dimensions, which makes it possible to apply reasonably high electric fields over a part of the reaction centers in a suspension of *H. chlorum*. The present study was undertaken to verify the possibility to induce electroluminescence in *H. chlorum*. The signals observed did not agree with earlier reported electron-transport properties, which were therefore reinvestigated.

Little is known about the electron transport chain of *H. chlorum*. All investigations hitherto reported have been performed on isolated membrane fragments. Like the major antenna pigment, the primary donor, P-798, is probably a bacteriochlorophyll *g* species [9]. Forward electron transport from the primary acceptor, possibly a BChl *c*-like species, occurs in about 500 ps [11]. EPR studies have demonstrated the light-induced reduction of iron-sulfur clusters [12,13]. Reduction of the primary donor at room temperature has been reported to occur mainly in about 10 ms [9,12,14] with a small, much slower component. Oxidation of a *c*-type cytochrome in

Abbreviations: BChl, bacteriochlorophyll; P-798, primary electron donor; PS, Photosystem.

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the same time-range has also been observed, although to different extents [11,12,14].

Membrane fragments may possess modified electron-transport properties compared to intact cells, due to loss or alteration of redox components. The results presented in this paper were obtained with freshly harvested cells. It will be shown that the kinetics of electron transport in those cells indeed deviate considerably from those in membrane fragments.

Materials and Methods

H. chlorum was grown in medium 1552 of the American Type Culture Collection containing 0.5 g/l ascorbate in an anaerobic hood under continuous stirring. This is a medium used for culturing *Heliobacillus mobilis*, a recently discovered bacterium closely related to *H. chlorum* [15]. It was observed that this medium yielded a higher amount of *H. chlorum* (absorbance at 788 nm = 1.6 cm^{-1} in 48 h) and a lower concentration of degradation products ($A788/A670$ about 6 in whole cells, cf. Ref. 9) than when it was cultured in medium 112 of the American Type Culture Collection as described previously [8,14] (Van de Meent, E.J., personal communication). Also, cultures grown in medium 1552 contained a very low concentration of spheroplasts, i.e., cells of which the cell wall had been disrupted (see Ref. 8).

Cells were harvested by centrifugation and washed in a buffer (pH 8.0) comprising 10 mM Tris/10 mM ascorbate/2 mM dithiothreitol. The cell suspension was kept in the dark on ice and was used within 10 h after harvesting, unless indicated otherwise. Just prior to measurement, the suspension was diluted about 100-times in a buffer (pH 8.0) containing 1 mM Tris. The final absorbance of the sample (1 cm) was about 0.4 at 788 nm. In some measurements (indicated in the figure legends) cells were kept at 30 °C in the growth medium, diluted to an absorbance of about 0.9 cm^{-1} at 788 nm. Routinely, no special care was taken to keep the cell samples anaerobic. However, it was checked that samples in which glucose, glucose oxidase and catalase were added did not yield significantly different results.

Electroluminescence and absorbance kinetics were measured as described before [4]. Flash illumination at 532 nm (15 ns half-width) was generally provided by a Nd-YAG laser (JK lasers). For the absorption measurements at 553 nm a Xenon flash lamp (13 μs half-width) was used with a Schott RG715 cut-off filter. The luminescence photomultiplier was protected by a Schott RG9 filter or by Balzer interference filters in the spectral measurements. For the measurements at high electric-field strengths (greater than 1600 V/cm) a cuvette with a 5-times smaller electrode spacing (2 mm) was used. Here, special care was taken to collect the maximum amount of emitted light by placing the cuvette in one focus of an ellipsoidal mirror and the photomultiplier in the other focus.

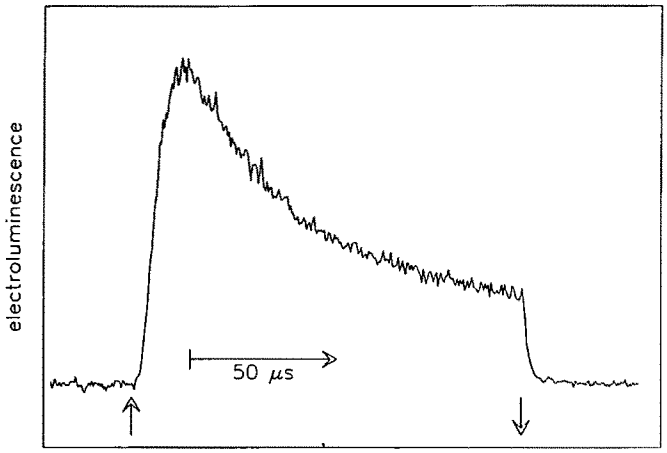

Fig. 1. Electroluminescence signal induced by a pulse of 1600 V/cm given 220 μs after a saturating flash. Average of five traces. The arrows indicate the onset and offset of the pulse.

The measurements with cells suspended in growth medium were performed at 30 °C; all other measurements were performed at 20 °C. For each measurement a new sample was taken, except for those in growth medium.

Results

A typical electroluminescence signal obtained with a suspension of fresh *H. chlorum* cells resuspended in 1 mM Tris (pH 8.0) is depicted in Fig. 1. Its general shape, characterized at maximal field strengths by an initial peak and a much slower decay, at first view resembles that of PS II [4,6,16].

The electroluminescence spectrum (Fig. 2) consists of a band of about 40 nm width around 815 nm. It

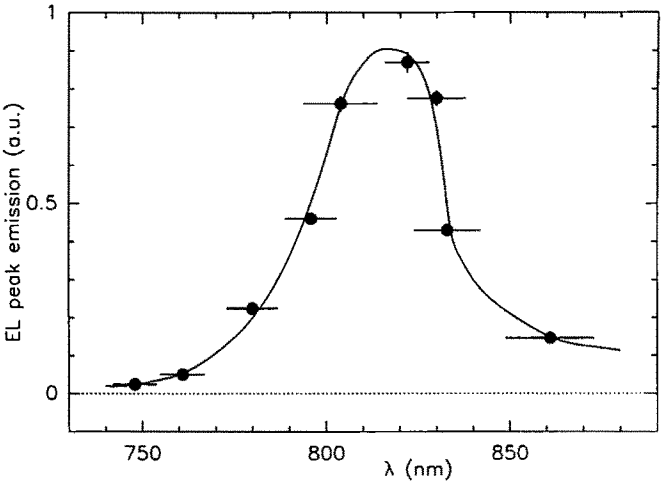

Fig. 2. Spectrum of the electroluminescence induced by a pulse of 1600 V/cm given 0.8 ms after the flash. The signals were detected through interference filters (bandwidths indicated by horizontal bars) and corrected for photomultiplier sensitivity and filter transmittance.

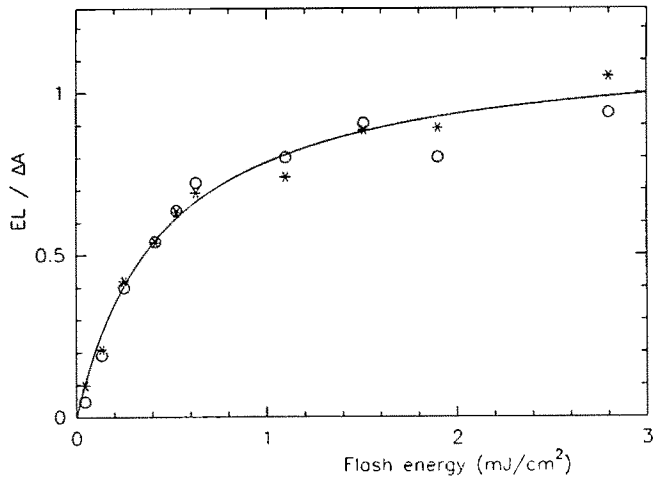

Fig. 3. Saturation characteristics of the electroluminescence induced by a pulse of 1500 V/cm given 220 μs after the flash (*) and of the initial flash-induced absorbance change at 800 nm (○). The intensity of the flash was varied by neutral density filters.

strongly resembles the room temperature fluorescence spectrum of *H. chlorum* [17]. The flash saturation characteristics of the electroluminescence are similar to those of the initial absorbance change at 800 nm associated with photooxidation of P-798 (Fig. 3). Both features indicate that the observed electroluminescence signal is associated with *H. chlorum* reaction center activity.

At lower field strengths, the peak emission during the pulse shifts towards later times (data not shown), as was also observed with electroluminescence in blebs [6]. The electric-field dependence of the time-integrated electroluminescence is shown in Fig. 4. Its general shape, an almost linear field-dependence from a certain threshold value, is similar to that of corresponding curves of PS I and PS II [4]. Even at very high field strengths, up to 5500 V/cm, saturation is not reached.

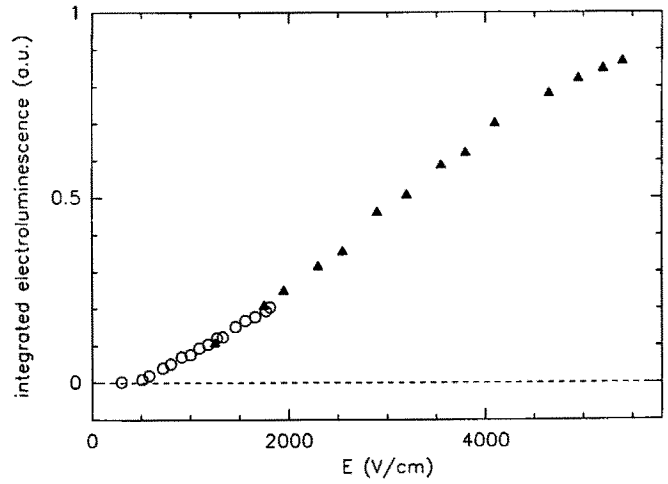

Fig. 4. Integrated electroluminescence induced by a 100 μs pulse given 0.5 ms after the flash as a function of the external electric field strength. Cuvettes with an electrode spacing of 9.0 mm (○) and of 2.0 mm (▲) were used.

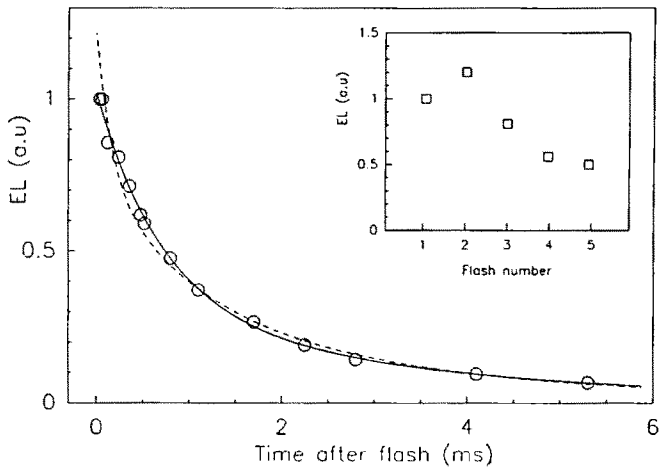

Fig. 5. Dependence of the electroluminescence peak emission on the time-delay between the flash and the pulse (1600 V/cm). The solid line is the best fit to a biexponential decay with half-times of 0.5 and 2.4 ms and an amplitude ratio of 7:3. The dashed line is a best fit to a triexponential decay with the half-times (0.11 and 0.7 ms) and relative amplitudes (1:1) of two phases constrained. This yielded a third exponential decay with a half-time of 2.2 ms and an amplitude 25% of the total electroluminescence at $t = 0$. Inset: dependence on the flash number of the electroluminescence, induced by a pulse given 120 μs after the last flash, when a series of flashes spaced at 40 ms was given.

The dependence of the signal on the time delay between the flash and the external field pulse is shown in Fig. 5. This dependence was characterized by a biphasic decay with half-times of about 0.5 ms and about 2.4 ms. The fast phase accounted for approx. 75% of the decay. A few % of the signal decayed with a half-time of more than 10 ms (not visible within the range of Fig. 5).

The electroluminescence changed when a number of preflashes was given before the measuring flash (Fig. 5, inset). After two flashes it was larger than after one flash and after even more flashes it decreased with flash number. Also, the kinetics of the precursor changed: the relative amplitude of the 2.4 ms phase increased with flash number (not shown).

The kinetic properties of the electroluminescence precursor state as described above indicated that the oxidized primary donor P-798 was involved in this state and that its reduction by cytochrome *c*-553 was largely responsible for the decay. For convenience, flash-induced absorbance changes measured under the most physiological circumstances in the medium and at the temperature of growth (30 °C) will be presented first.

The kinetics at 800 nm, which reflect the reduction kinetics of the oxidized primary donor P-798, are depicted in Fig. 6A. To fit these, three exponential decays were needed with half-times of 0.11, 0.7 and 20 ms and relative amplitudes of about 3:3:1. The kinetics at 553 nm, reflecting the kinetics of cytochrome *c*-553 oxidation, are depicted in Fig. 6B. They can also be fitted with biphasic rise kinetics with half-times of 0.11 and

0.7 ms and relative amplitudes 1 : 1, followed by a decay with a half-time of 20 ms. These results suggest that cytochrome *c*-553 biphasically rereduces about 90% of the flash-formed P-798$^+$ and is reduced itself in 20 ms. The latter reduction time was only observed in batches in which virtually no spheroplasts were present. Its time-constant also varied considerably from batch to batch and was not correlated with the time-constant of the slow (20 ms) decay phase at 800 nm. When a series of five flashes spaced at 40 ms was given, the initial absorbance after the first flash was restored upon each flash at both wavelengths (data not shown). At 553 nm the kinetics after the flashes remained equal, but the total amplitude decreased somewhat because 40 ms was too short to allow complete rereduction between the flashes, whereas at 800 nm the 20 ms component increased somewhat after subsequent flashes. This suggests that the latter component is due to charge recombination in those centers where no reduced cytochrome *c*-553 is available.

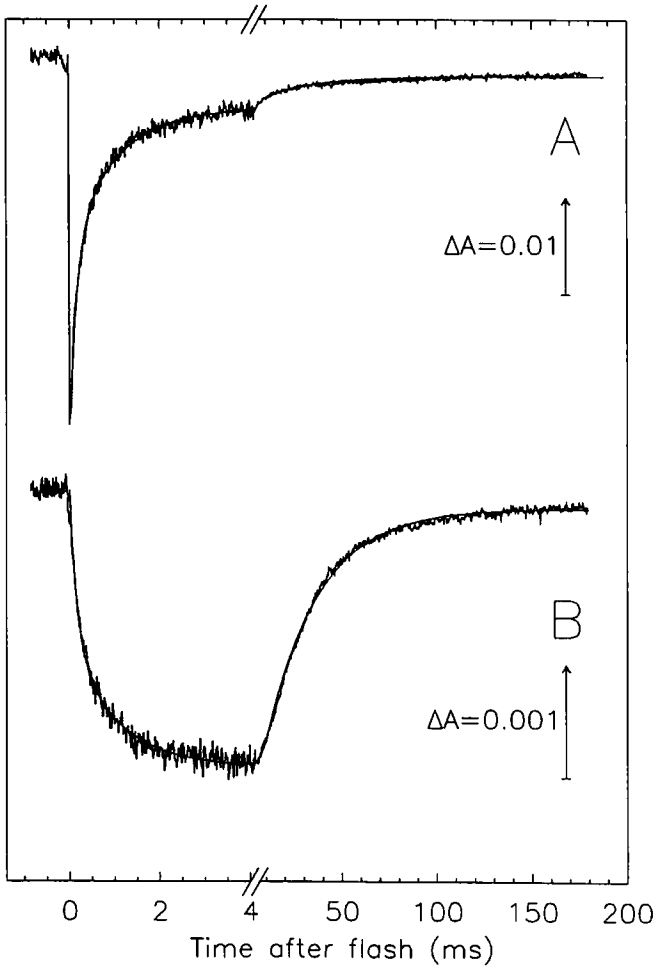

Fig. 6. Kinetics of absorbance changes measured in whole cells in growth medium at 30 °C. The absorbance was 0.9 in 1 cm at 788 nm. Note the different time-scales. Average of 20 traces. The band-width of the measuring light was 5 nm. After every 10 traces the sample was renewed. (A) 800 nm. The curve is a best fit to a biexponential decay (0.11 and 0.7 ms half-time, fast part) and a monoexponential decay (20 ms, slow part). (B) 553 nm. The curve is a best fit to a biexponential rise (0.11 and 0.7 ms, fast part) and one exponential decay (20 ms, slow part). See text for the amplitudes of the phases.

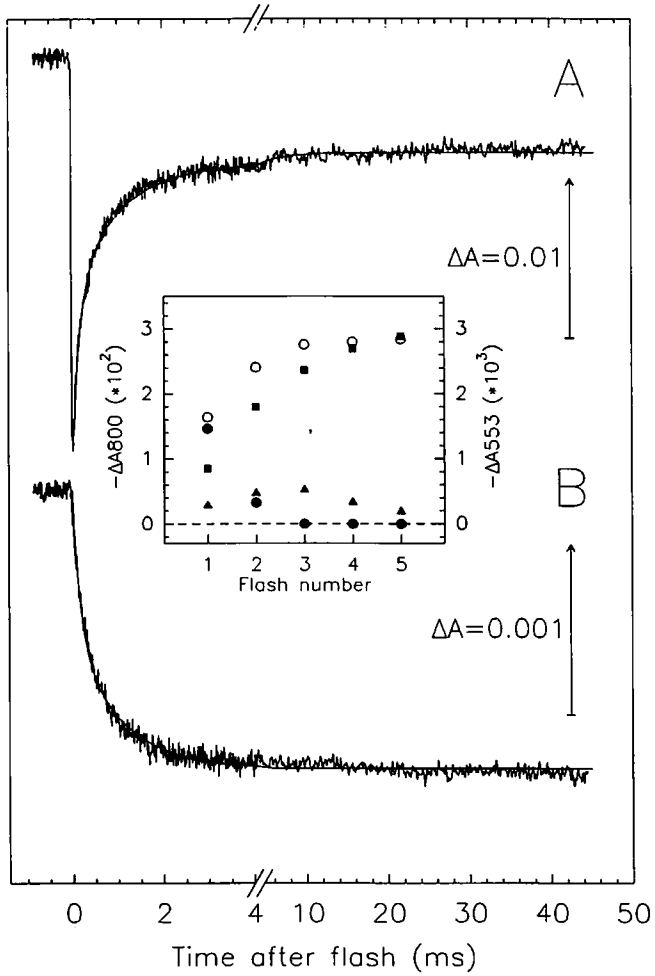

Fig. 7. Kinetics of absorbance changes measured in whole cells in 1 mM Tris (pH 8.0). Note the different time-scales. Average of 20 traces. (A) 800 nm. Absorbance of 0.32 in 1 cm at 788 nm. The curve is a best fit to a triexponential decay (half-times 0.11, 0.7 and 2.2 ms constrained) and an offset. (B) 553 nm. Average of 30 traces. Absorbance of 0.49 in 1 cm at 788 nm. The curve is a best fit to a biexponential rise (half-times 0.11 and 0.7 ms constrained). See text for amplitudes of the phases. Inset: dependence of the amplitude of the different phases on flash number when five flashes, spaced at 40 ms, were given. 800 nm: sum of the 0.11 and 0.7 ms phases (●), 2.2 ms phase (▲) and cumulative irreversible phase (■). 553 nm: total absorbance change (○).

The partial irreversibility of the electroluminescence signal (Fig. 5, inset) suggests that electron-transport properties under these conditions deviate from those in growth medium. For this reason the absorbance kinetics of whole cells in the 1 mM Tris solution were monitored as well. Three decay phases and an irreversible phase were needed to fit the kinetics at 800 nm after one flash (Fig. 7A). With fixed half-times of 0.11, 0.7 and 2.3 ms a good fit was obtained with amplitude ratios of 4 : 4 : 1 : 2. The kinetics at 553 nm (Fig. 7B) could also be fitted with rise-times of 0.11 and 0.7 ms and equal

amplitudes of both phases. No decay on a longer timescale could be observed. So in these preparations cytochrome *c*-553 is also oxidized with biphasic kinetics; however, the oxidation is irreversible. Also a fair amount of flash-induced P-798$^+$ is not reduced within seconds after the flash. When a flash series was given on the same sample, the amount of stable P-798$^+$ increased (up to more than 90% after five flashes) and the submillisecond decay phases were almost completely absent after more than three flashes (inset Fig. 7). The 2.2 ms phase increased at the second and third flash and then decreased after subsequent flashes.

The kinetics of the electroluminescence decay as a function of time between the flash and the pulse can also be reasonably fitted with a biphasic decay of 0.11 and 0.7 ms half-times and equal amplitudes instead of the 0.5 ms decay component (Fig. 5, dashed line). Thus the main and most rapid part of this decay can be ascribed to reduction of P-798$^+$ by cytochrome *c*-553. The slower 2.2 ms decay phase is also found in the kinetics of P-798$^+$ reduction, albeit to a much smaller extent. However, the relative amplitude of this electroluminescence phase corresponds well with the sum of the 2.2 ms and the irreversible phase after the first flash in P-798$^+$ kinetics (both about 25%). It may thus be ascribed to reoxidation of an acceptor both by forward electron-transport and charge recombination.

When cells were stored at $-20\,^\circ$C the cytochrome *c*-553 oxidation was decelerated to a half-time of about 5 ms in a few days. This half-time corresponds to the time-range reported for cytochrome *c*-553 oxidation in membrane fragments [9,14] which are usually also stored at $-20\,^\circ$C before use. Similar times were observed in a suspension of spheroplasts separated from intact cells on a phycol gradient. Storage of whole cells at $-20\,^\circ$C also yielded a considerable decrease in electroluminescence, whereas in suspensions of spheroplasts no electroluminescence was observed.

Discussion

The electroluminescence signal as depicted in Fig. 1 clearly originates from the reaction center of *H. chlorum*. Its spectrum (Fig. 2) is similar to the fluorescence spectrum of *H. chlorum* [17] and its illumination saturation characteristics are the same as those of P-798 oxidation (Fig. 3), indicating that both phenomena are strongly related.

The observability of the signal presumably is due to the specific structure of *H. chlorum*. It has a relatively large size and its photosynthetic apparatus is located entirely in the cell membrane [8,10]. In membrane fragments the signal was not observed. It can be calculated that in ellipsoidal closed membrane systems the externally built up membrane potential V_m is given by

$$V_m = -\alpha \vec{E} \cdot \vec{x} \qquad (1)$$

in which $\vec{E}$ is the external field, $\vec{x}$ the place on the membrane relative to the center and α a shape factor. For highly eccentric ellipsoids, i.e., for long thin rods, $\alpha = 1$. This can be derived analogously to the case of an ellipsoidal body in a magnetic field, taking eccentricity 0 [18]. For a length/diameter ratio of 10, the deviation is about 1%. For blebs, i.e., spherical closed membrane systems which do disturb the external field, $\alpha = 1.5$ [16,19]. Also *H. chlorum* cells (length up to 10 μm [8]) are considerably smaller than blebs (diameters up to 20 μm [6]). These two factors both imply that the field-induced membrane potentials must be considerably smaller in *H. chlorum* cells than in blebs, which may explain the lack of saturation with field strength (Fig. 4) in contrast to PS I and PS II electroluminescence in the same range of applied field strength [4]. It should be kept in mind, however, that these arguments may only be used in a qualitative way, since the photosystems involved may be quite different.

From Eqn. 1 it can be calculated that in rods with a length of 10 μm the maximum membrane potential in an external field of 1600 V/cm, as in Fig. 1, is 800 mV. The decay of the electroluminescence during the pulse takes about 30 μs (Fig. 1), presumably reflecting the exhaustion of the precursors. Charge recombination of the precursors in the absence of an external field takes about 20 ms. Thus the electrical field stimulates back reaction by about three orders of magnitude.

The kinetics of absorbance change detected in whole cells in the growth medium at $30\,^\circ$C (Fig. 6) reveal a consistent picture of electron transport at the donor side of the reaction center of *H. chlorum*. The initial absorbance change at 800 nm (the Q_y peak of the bleaching of P-798) was -0.039 with an absorbance of 0.9 at 788 nm (the Q_y peak of the antenna absorption). The bandwidths of these Q_y band are, respectively, 21 [9,11] and 60 nm (whole cells, [8]), so the ratio of the areas under the Q_y bands is 1 : 65 (assuming equal oscillator strengths this would indicate that 1 P-798 per 65 BChl *g* is oxidized). The same number can be derived from picosecond data obtained in membrane fragments by Nuijs et al. [11] ($\Delta A = -0.028$ after the decay of the antenna bleaching with an absorbance of 0.8 at 788 nm) taking into account that the band width of the antenna absorbance in membrane fragments is 50 nm [17]. Thus we conclude that all of P-798 is observed in Fig. 6A. The bulk part of the photo-oxidized primary donor P-798$^+$ is rereduced biphasically with half-times of 0.11 and 0.7 ms by cytochrome *c*-553. Cytochrome *c* oxidation times of about 0.1 ms have been found in green sulfur bacteria as well [20,21]. The biphasic nature of the reaction in *H. chlorum* suggests that two types of cytochrome *c* are involved, the slower reductor acting as a donor in the absence of the fast reductor. A similar mechanism has been proposed for cytochrome *c* oxidation in the green sulfur bacterium *Chlorobium limicola f.*

thiosulphatophilum and in purple bacteria [21–23]. In our preparations cytochrome *c*-553 was rereduced monophasically with a half-time of 20 ms by an as yet unidentified donor. The facts that this process could occur several times within 200 ms and that cytochrome *c*-553 remained oxidized after illumination in the absence of growth medium (Fig. 7B) suggest that this donor is part of, or is rapidly derived from, an external pool. This would indicate that photosynthetic electron transport in *H. chlorum* is mainly noncyclic. An overall turnover time under physiological conditions of 20 ms seems quite reasonable for photosynthesis.

Our results on whole cells in growth medium deviate considerably from those obtained earlier with membrane fragments of *H. chlorum* [9,12,14]. In such fragments cytochrome *c*-553 oxidation and the corresponding P-798$^+$ rereduction occurs in about 5 ms and to a much smaller extent: at most in about 50% of the reaction centers. This suggests that in membrane fragments cytochrome *c*-553 is less well bound to the reaction center. Kinetics similar to those in membrane fragments were observed in spheroplasts and in whole cells that had been stored at $-20\,^\circ$C: slow oxidation of cytochrome *c*-553 and decrease or absence of electroluminescence. This suggests that electron-transport properties both at the donor and the acceptor side are changed.

The presence of spheroplasts in a batch, which occurred especially in older batches, was associated with a lack of cytochrome *c*-553 reduction in the whole batch. This may indicate that the appearance of spheroplasts is associated with the exhaustion of an electron donor in the medium.

In our preparations the minor part of P-798$^+$, which did not oxidize cytochrome *c*-553, was rereduced in about 20 ms. This time is roughly in the same range as the reported times for the slow component of P-798$^+$ decay in membrane fragments of 30 ms ($1/e$ time) [14] and 26 ms (half-time) [12], indicating that the same process, presumably charge recombination with a reduced acceptor, is involved.

The absorbance changes in freshly harvested cells in the low-ion medium (1 mM Tris) display rather different kinetics (Fig. 7), although the fast submillisecond phases of cytochrome *c*-553 oxidation by P-798$^+$ are still intact. Here oxidized cytochrome *c*-553 is not rereduced within seconds after the flash, i.e., a donor of cytochrome *c*-553 is missing or inactive in this medium. Most of the flash-formed P-798$^+$ which is not rereduced by cytochrome *c*-553 remains oxidized. A minor part is rereduced in another way with a half-time of 2.4 ms.

The decay of the precursor of electroluminescence as determined in the same medium (Fig. 5) can be fitted with the same fast phases (0.11 and 0.7 ms, equal amplitudes) and a slower 2.2 ms phase with an amplitude of 25% of the total electroluminescence directly after the flash. This percentage corresponds to the sum of the amplitudes of the irreversible and the 2.2 ms phases in absorbance change at 800 nm (Fig. 7A). For this reason we ascribe this phase to a combination of forward electron-transport and back-reaction from a reduced acceptor. From the observed amplitude ratio of the 2.2 ms and the irreversible phase of about 1 : 2 it can be calculated that the forward transport time and the back-reaction time should then be 3.5 and 7 ms, respectively. The latter time is somewhat shorter then the back-reaction time directly measured in growth medium (20 ms). This discrepancy may be due to the difference in medium used and/or the accuracy in fitting the amplitude of the 2.2 ms phase.

The dependency on the number of preflashes of the absorbance kinetics at 800 nm and at 553 nm, and of the electroluminescence amplitude as a function of time after a flash was rather complicated (insets Figs. 5 and 7) and could not be described by a simple model. However, the following general features may be noted. (1) The fast submillisecond phases of cytochrome *c*-553 oxidation by P-798$^+$ completely disappear after three flashes, whereas the amplitude of the 2.2 ms phase decreases less quickly. This supports the assumption that a different process is involved. (2) The electroluminescence directly after the flash is higher after the second flash than after one flash and decreases after further flashes. As the amount of available reduced P-798 diminishes upon every flash, this implies that the luminescence yield is higher upon subsequent flashes. This may be due to a change in the energy levels involved in back-reaction caused by charge accumulation at the donor and/or acceptor side.

Summarizing, this investigation has not only revealed the first electroluminescence signals from a bacterial photosystem, but has also shown that electron-transfer kinetics in *H. chlorum* differ markedly from those previously reported. The intact system efficiently photooxidizes cytochrome *c*-553 in two phases of 0.11 and 0.7 ms half-time. Rereduction of the cytochrome takes place in about 20 ms, apparently by an electron donor in the growth medium which is exhausted in cultures containing significant numbers of spheroplasts. When no reduced cytochrome *c*-553 is available, P-798$^+$ decays by back-reaction in 20 ms with an unidentified reduced acceptor.

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