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Electron Transfer between Exogenous Electron Donors and Reaction Center of Photosystem 2

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Abstract—Transfer of electrons between artificial electron donors diphenylcarbazide (DPC) and hydroxylamine (NH_2OH) and reaction center of manganese-depleted photosystem 2 (PS2) complexes was studied using the direct electrometrical method. For the first time it was shown that reduction of redox-active amino acid tyrosine $Y_Z^{\cdot}$ by DPC is coupled with generation of transmembrane electric potential difference ($\Delta\Psi$). The amplitude of this phase comprised ~17% of that of the $\Delta\Psi$ phase due to electron transfer between Y_Z and the primary quinone acceptor Q_A. This phase is associated with vectorial intraprotein electron transfer between the DPC binding site on the protein–water interface and the tyrosine $Y_Z^{\cdot}$. The slowing of $\Delta\Psi$ decay in the presence of NH_2OH indicates effective electron transfer between the artificial electron donor and reaction center of PS2. It is suggested that NH_2OH is able to diffuse through channels with diameter of 2.0-3.0 Å visible in PS2 structure and leading from the protein–water interface to the Mn_4Ca cluster binding site with the concomitant electron donation to $Y_Z^{\cdot}$. Because the dielectrically-weighted distance between the NH_2OH binding site and $Y_Z^{\cdot}$ is not determined, the transfer of electrons from NH_2OH to $Y_Z^{\cdot}$ could be either electrically silent or contribute negligibly to the observed electrogenicity in comparison with hydrophobic donors.

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Key words: reaction center, photosystem 2, proteoliposomes, photopotential, diphenylcarbazide, hydroxylamine, channels

Thylakoid membrane of cyanobacteria, green algae, and higher plants is the place of localization of photosystems 2 and 1 (PS2 and PS1), which are photoactive pigment–protein complexes. PS2 complex mediates photoinduced oxidation of water to molecular oxygen at the lumenal side and reduction of plastoquinone to plastohydroquinone on the stromal side of the membrane [1, 2]. The core complex of PS2 contains two antenna proteins (CP47 and CP43), reaction center (RC) (D1D2-cyt b_{559}), and a few low-molecular-weight proteins. The structure of core complex of PS2 has been resolved with atomic resolution 3.4 and 2.9 Å using X-ray diffraction analysis of protein crystals from thermophilic cyanobacteria [3, 4]. Basic PS2 components (chlorophyll *a* dimer P_{680}, chlorophyll *a* monomer, pheophytin *a*, primary Q_A and secondary Q_B quinone acceptors, redox-active amino acid residue tyrosine Y_Z and Mn_4Ca cluster) contribute to transmembrane electron transfer, and they are associated with RC proteins D1 and D2. Charge separation in RC is induced by a light quantum giving rise to P_{680} oxidation and reduction of Q_A. This is followed by reduction of cation-radical P_{680}^+ by the electron from Y_Z. Reduction of radical $Y_Z^{\cdot}$ is mediated by manganese ions and includes electron transfer from a water molecule. One O_2 molecule is formed from two water molecules in four photochemical acts of the RC.

It was demonstrated earlier that both native and Mn_4Ca depleted PS2 complexes (PS2(–Mn)) contain high-affinity Mn-binding sites [5-10]. Not only manganese but also artificial donors were found to be capable of donating electron to endogenous $Y_Z^{\cdot}$ in PS2(–Mn) samples [5, 8, 9, 11-18].

Earlier, it was demonstrated in our experiments with bacterial RC (BRC) and PS1 complexes that photoin-

Abbreviations: (B)RC, (bacterial) reaction center; DCPIP, 2,6-dichlorophenolindophenol; DPC, diphenylcarbazide; NH_2OH, hydroxylamine; OEC, oxygen-evolving complex; P_{680}, primary electron donor; PS2(–Mn), PS2 preparations depleted of Mn; Q_A (Q_B), primary (secondary) plastoquinone electron acceptor; TMPD, N,N,N′N′-tetramethyl-*p*-phenylenediamine; τ, time constant; Y_Z, redox-active tyrosine of D1 polypeptide; $\Delta\Psi$, electric potential difference.

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duced reduction of photooxidized primary electron donors P_{870}^+ and P_{700}^+ is electrogenic when natural and artificial secondary electron donors are used [19-22]. Based on similarity of amplitudes of electrogenic reactions observed in the presence of cytochrome *c* and redox-mediators N,N,N′N′-tetramethyl-*p*-phenylenediamine (TMPD) and phenazine methosulfate in photosynthetic RC preparations isolated from photosynthetic bacteria [19, 20], as well as in the presence of plastocyanin, TMPD, and 2,6-dichlorophenolindophenol (DCPIP) in PS1 complexes isolated from cyanobacteria [21, 22], it was concluded that electrogenesis associated with reduction of primary electron donor was due to vectorial electron transfer within complexes BRC and PS1, respectively.

Recently the direct electrometrical method revealed that electron transfer from reduced exogenous donors TMPD and DCPIP to the tyrosine $Y_Z^{\cdot}$ in proteoliposomes containing PS2(−Mn) complexes was electrogenic, constituting ~30% of fast rise phase ΔΨ. This fast phase is due to generation of the ion-radical pair $Y_Z^{\cdot}Q_A^-$ [17]. Similar electrogenic phase amplitude was observed in PS2(−Mn) preparations in the presence of synthetic trinuclear manganese complex [15].

In contrast to BRC and PS1 complexes, native PS2 complexes besides Mn_4Ca cluster lack natural electron donors capable of reducing $Y_Z^{\cdot}$. It follows from the 3D structure of PS2 complex [3, 4] and polarity profile of PS2 donor side that the Mn_4Ca cluster is localized far from the protein/water interface. The Mn_4Ca cluster is surrounded by hydrophobic amino acid residues [23]. Comparative analysis of relative amplitude of electrogenic stages corresponding to reduction of $Y_Z^{\cdot}$ from artificial donors with distance projection between protein complex border and Y_Z to membrane plane normal revealed that mean dielectric permittivity ε at this site was ~10 [23]. By analogy with BRC and PS1 complexes, we suggested that electrogenesis observed in PS2(−Mn) preparations during $Y_Z^{\cdot}$ reduction from artificial electron donors was also due to vectorial electron transfer within the protein complex.

The donor side of PS2 is most frequently studied using artificial electron donors 1,5-diphenylcarbazide (DPC) and hydroxylamine (NH_2OH). However, the possible electrogenic character of photooxidized PS2 RC reduction from these donors remains insufficiently understood. If DPC in PS2(−Mn) preparations is oxidized from tyrosine $Y_Z^{\cdot}$ radical, the nature of the NH_2OH oxidizer remains obscure [9, 10]. The goal of this work was to study electron transfer from DPC and NH_2OH to RC in proteoliposomes with core PS2(−Mn) complexes using the direct electrometric method.

MATERIALS AND METHODS

PS2 complexes with functionally active oxygen-evolving complex (OEC) were isolated from membrane fragments enriched with PS2 [24], as described in [25] with minor modification. The isolation medium for membrane fragments contained 1 M glycinbetaine. PS2 preparations devoid of Mn cluster were prepared from PS2 core complex (0.5 mg chlorophyll *a*/ml) incubated in medium containing 0.9 M Tris-HCl buffer (pH 9.0) for 30 min at 23°C. The resulting preparations were twice washed using 25 mM Hepes (pH 7.5) buffer containing 20 mM NaCl and 300 mM sucrose [17]. The preparations were concentrated using ultrafiltration to 1.5-2.0 mg chlorophyll *a*/ml, frozen in liquid nitrogen, and stored in a freezer at −80°C.

Proteoliposomes with PS2 core complexes were prepared as follows [26]: azolectin suspension (lecithin, type IIS) (40 mg/ml) in buffer solution (50 mM Hepes, pH 7.5, 200 mM sucrose, and 2% sodium cholate) was sonicated (10 sec, 30 sec interval) until clarification using a UZDN-2T generator (22 kHz, 50 mA). The resulting suspension was centrifuged for 10 min at 15,000*g*. The supernatant was collected. Transparent phospholipids solution was mixed with PS2 core complexes (lipid/protein ratio = 50 : 1 w/w), incubated for 60 min, and applied to a Sephadex G-25 column equilibrated with 20 mM Hepes (pH 7.5) buffer. The same buffer was used for elution.

ΔΨ generation kinetics was measured using the direct electrometric method. The proteoliposomes were immobilized on the surface of a nitrocellulose film impregnated with azolectin solution in *n*-decane. Electric potential was detected using an Ag/AgCl pair of macroelectrodes [27]. Time resolution of the detector was 100 nsec. A Quantel Nd-YAG laser (France) (emission wavelength, 532 nm; half-width, 15 nsec) was used as the source of light pulses.

Kinetic signals were analyzed using program packages Pluk [28] and Origin (OriginLab Corporation, USA).

RESULTS

Photoinduced electron transfer in RC is accompanied by generation of transmembrane electric potential difference [23]. Vectorial electron transfer from Y_Z to Q_A provides the major contribution to ΔΨ generation in PS2 RC. The ΔΨ component associated with $Y_Z^{\cdot}$ reduction mediated by electron transfer from Mn in response to the first light pulse ($S_1 \rightarrow S_2$ transition of OEC) constitutes ~3.5-5% of the $Y_Z^{\cdot}Q_A^-$ phase. This component was observed in thylakoids using electrochromic carotenoid absorption shift detection [29] and in proteoliposomes with PS2 containing active OEC [23, 29] using the direct electrometrical method. Similar result was also observed in the presence of exogenous manganese in PS2(−Mn) preparations [15]. Additional electrogenesis associated with vectorial electron transfer from TMPD-reduced and from trinuclear Mn complexes in PS2(−Mn) prepara-

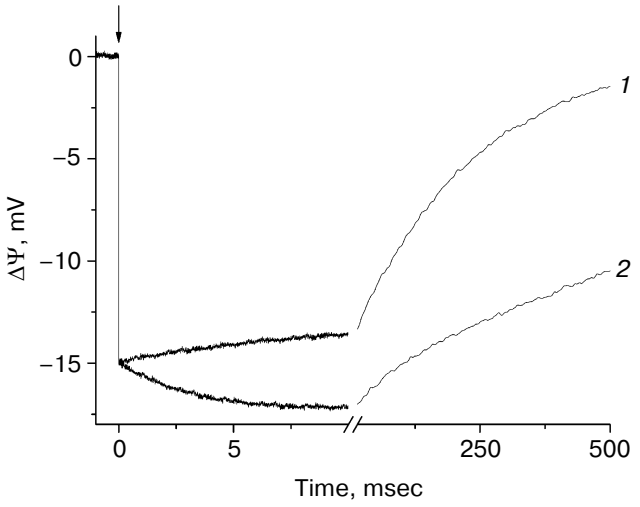


Fig. 1. Photoelectric response of proteoliposomes containing PS2(−Mn) core complexes from spinach in the absence (*1*) and in the presence of 50 μM DPC (*2*). Incubation medium contained 50 mM Hepes (pH 7.5), 15 mM NaCl, and 300 mM sucrose. Here and further the arrow indicates the time of incidence of the laser pulse.

tions constituted ~25-30% of fast phase associated with formation of $Y_Z^{\cdot}Q_A^-$ [15, 17].

Photoelectric response induced by a single laser pulse in proteoliposomes containing PS2(−Mn) core complexes from spinach in the absence of (curve *1*) and in the presence of DPC (artificial donor for $Y_Z^{\cdot}$) (curve *2*) is shown in Fig. 1. The maximal fast phase with rise time shorter than the instrumental resolution (<100 nsec) corresponded to charge separation in PS2 RC between P_{680} and Q_A with further reduction of P_{680}^+ by electron transfer from the tyrosine Y_Z.

In these samples in the absence of exogenous manganese, the OEC is inactive. Therefore, ΔΨ decay under these conditions is due to electron recombination between Q_A^- and the $Y_Z^{\cdot}$ radical. This suggestion is supported by results of kinetic analysis. Kinetics of ΔΨ decay was reasonably approximated by two exponential components with $\tau_1 \sim 5$ msec (relative amplitude $A_1 \sim 6\%$) and $\tau_2 \sim 230$ msec ($A_2 \sim 94\%$). Perhaps, this biphasic decay kinetics is due to two hypothetical conformational states of PS2 RC [30]. Similar biphasic decay kinetics was earlier observed in our experiments [15].

It follows from curve *2* that addition of 50 μM DPC slows ΔΨ decay and results in the appearance of additional electrogenesis on the millisecond time scale. The DPC effect depends on DPC concentration, 50 μM being saturating with respect to both amplitude and ΔΨ rise kinetics (not shown in Fig. 1).

Kinetics of ΔΨ decay is biexponential (Fig. 1, curve *2*) ($\tau_1 \sim 10$ msec ($A_1 \sim 9\%$) and $\tau_2 \sim 930$ msec ($A_2 \sim 91\%$)). It is safe to suggest that the fast component of the decay kinetics (τ_1) is due to electron recombination between Q_A^- and $Y_Z^{\cdot}$, whereas slow component of the decay kinetics (τ_2) represents passive permeability of the proteoliposomal membrane. The characteristic time τ of the additional component of ΔΨ rise is ~3 msec and its amplitude is ~17% of the amplitude corresponding to ΔΨ generation induced by electron transfer from Y_Z to Q_A. It was suggested that the additional phase of ΔΨ generation observed in the presence of DPC on the millisecond time scale is due to electrogenic reaction between DPC and tyrosine $Y_Z^{\cdot}$.

It should be noted that generation of ΔΨ additional phase amplitude in the presence of DPC (~17%) is less than in the presence of TMPD and synthetic trinuclear complex (25-30%) [15, 17]. However, the kinetics of the ΔΨ decay fast component observed in the absence of DPC ($\tau_1 \sim 5$ msec, $A_1 \sim 6\%$) was comparable with the kinetics of ΔΨ rise phase in the presence of DPC. This circumstance may lead to underestimation of the real ΔΨ rise amplitude.

In contrast to DPC, TMPD and DCPIP mediate additional electrogenic activity only at high concentration (1-8 mM) [17]. At lower concentration of redox mediators, reduction of the $Y_Z^{\cdot}$ tyrosine does not contribute to photopotential generation (not shown), which is due to low rate of ΔΨ increase masked by the decay of the potential.

Similar amplitude of photoelectric response of proteoliposomes with PS2(−Mn) induced by the first and second light pulses in the presence of DPC (not shown) is evidence of generation of a stable DPC form in response to each light pulse.

The effect of the low-molecular-weight donor NH_2OH on kinetics of ΔΨ generation in proteoliposomes with core PS2(−Mn) complexes was also studied under conditions of photoactivation with single laser pulses. In PS2 membrane fragments devoid of Mn cluster, it was shown that NH_2OH at micromolar concentration served as effective electron donor for RC [31].

Photoelectric response of proteoliposomes containing PS2(−Mn) core complexes in the absence (curve *1*) and in the presence of (curve *2*) 100 μM NH_2OH is shown in Fig. 2 using two time scales. ΔΨ generation was induced by single laser pulses. Deceleration of decay kinetics in the presence of NH_2OH (($\tau_1 \sim 25$ msec ($A_1 \sim 5\%$), $\tau_2 \sim 720$ msec ($A_2 \sim 95\%$)) as compared to control (($\tau_1 \sim 3.5$ msec ($A_1 \sim 5\%$), $\tau_2 \sim 230$ msec ($A_2 \sim 95\%$)) is evidence of prevention of charge recombination in PS2 RC mediated by effective electron transfer between NH_2OH and PS2 RC. In contrast to experiments with DPC, no additional phase of ΔΨ generation was observed.

DISCUSSION

Such low-molecular-weight compounds as NH_3 and CH_3OH, the latter being an analog of H_2O, contain at

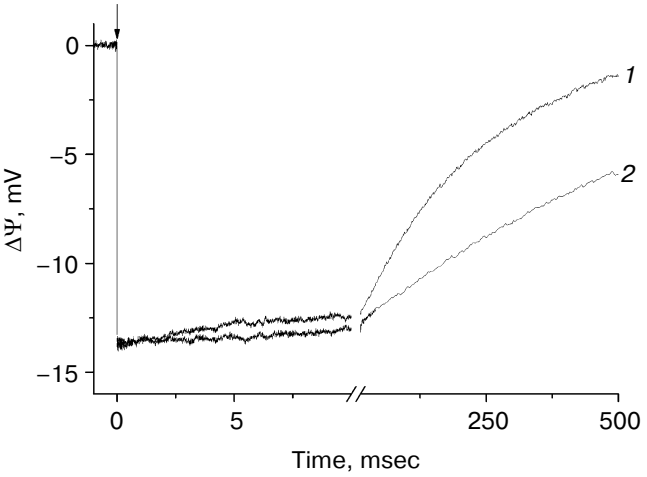


Fig. 2. Photoelectric response of proteoliposomes containing PS2(−Mn) core complexes in the absence (*1*) and in the presence of 100 μM NH_2OH (*2*). Conditions as in Fig. 1.

least one common binding site in the Mn_4Ca cluster [32]. Structural and spectroscopic data provided a basis for the suggestion that methanol binds the same Mn ion (perhaps, Mn^3) in all S-states of the Mn_4Ca cluster [33]. Other structural analogs of the water molecule (H_2O_2, N_2H_4, NH_2OH) are redox active and mediate reduction of the Mn cluster in PS2 preparations [33].

X-Ray diffraction analysis of PS2 crystals revealed several channels connecting the protein–water interface at donor site with the Mn_4Ca cluster [4, 34]. Three channels have minimal Van der Waals diameter ~2.7 Å. It was suggested that these channels served for oxygen and water transport between the catalytic site of the OEC and the lumen.

As noted above, removal of the Mn_4Ca cluster also results in removal of three peripheral PS2 subunits (PsbO, PsbU, and PsbV) [11-15]. We modeled the structure of PS2 donor site in the absence of the three subunits. To provide this modeling, the three subunits were removed from the PS2 monomer structure [4]. The channel structure was simulated using the Caver 2.0 v.0.003 software [35]. Channels were visualized using the PyMOL, v.0.99rc6 software.

The structure of three channels with diameter >2 Å observed at the donor side of RC of PS2 complex is shown in Fig. 3. It follows from Fig. 3 that the three channels originate near the Mn_4Ca cluster and are terminated at the protein/water interface.

Change in the channel diameter along the channel length is shown in Fig. 4. Figure 4 shows that minimal diameter of channel 1 is ~3 Å and the minimal diameter of channels 2 and 3 is ~2 Å. Removal of the three peripheral subunits has virtually no effect on the channels at the donor side [34]. It is obvious that DPC is larger than the diameter of the channels, whereas NH_2OH size allows this molecule to diffuse freely through the channels.

A hypothetical scheme of electron transport at the donor side of PS2(−Mn) complex in the presence of DPC and NH_2OH is shown below. According to this scheme, an electron is donated from DPC to $Y_Z^{\cdot}$ resulting in ΔΨ generation because of intraprotein vectorial electron transfer from the DPC-binding site to Y_Z embedded in the pigment–protein matrix. NH_2OH is able to diffuse through the channel with diameter ~2.0-3.0 Å. The reduction of $Y_Z^{\cdot}$ is mediated by NH_2OH.

It follows from Fig. 2 that addition of hydroxylamine does not result in an additional phase of ΔΨ generation. However, a minor component with characteristic time τ ~ 3.5 msec is decelerated to 25 msec. This finding can be

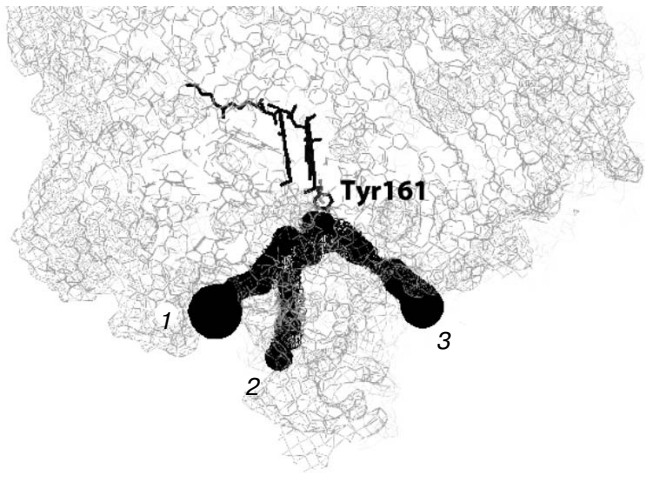


Fig. 3. Structure of three channels with diameter >2 Å observed at the donor side of RC of PS2 complex.

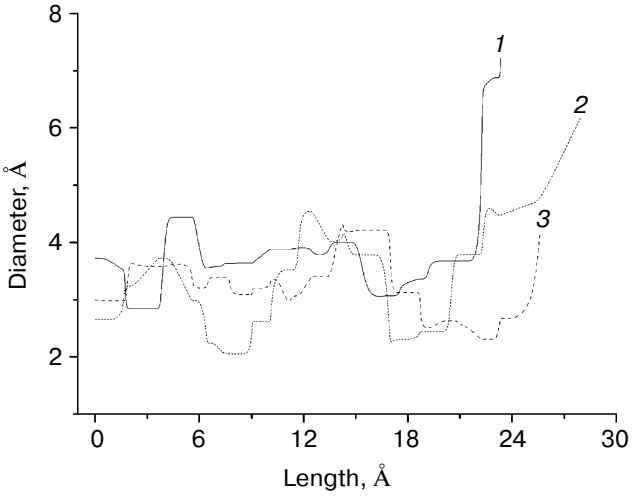
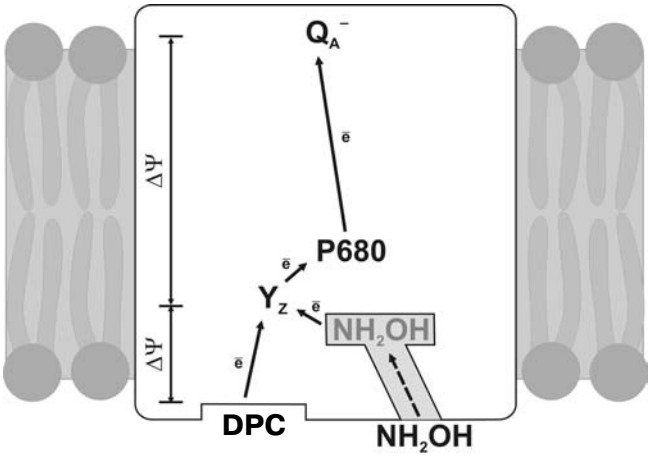


Fig. 4. Change in channel (1, 2, 3) diameter along the channel length.



Scheme of electron transport at the donor side of PS2(–Mn) complex in the presence of DPC and NH_2OH. Solid arrows show electrogenic stages of electron transfer. A dashed arrow shows the hypothetical stage of NH_2OH diffusion through a hydrophilic channel from the protein surface to the Mn_4Ca cluster-binding site

interpreted by either deceleration of charge recombination in a minor fraction of PS2 RC as a result of electroneutral electron donation from NH_2OH or appearance of a minor phase of $\Delta\Psi$ generation caused by electrogenic electron donation from the NH_2OH-binding site to $Y_Z^{\cdot}$ and compensated by $\Delta\Psi$ decay within the same time range. This suggestion was supported by the results reported in our recent work, in which it was demonstrated that addition of exogenous Mn resulted in appearance of an electrogenic phase with similar amplitude and faster kinetics [15]. The NH_2OH-binding site is located close to the binding site of exogenous Mn. This is illustrated by Fig. 3, in which the channels approach each other near the binding site of the Mn_4Ca cluster [4].

These results provide greater insight into mechanisms of membrane potential generation at the donor side of PC2 complexes. Effective reduction of oxidized $Y_Z^{\cdot}$ from artificial electron donors in PS2 RC preparations devoid of the Mn_4Ca cluster was found to be either electrogenic or non-electrogenic. In the first case, hydrophobic donors (DPC) provide electrogenic reduction of $Y_Z^{\cdot}$. The electrogenicity is provided by vectorial electron transfer from the binding site at the protein/water interface. In the second case, low-molecular-weight hydrophilic donors (NH_2OH) can diffuse through the small-diameter (2.0-3.0 Å) channels connecting the Mn_4Ca cluster binding site with the lumenal protein surface. Then, $Y_Z^{\cdot}$ is reduced. Because the dielectrically-weighted distance between the NH_2OH-binding site and $Y_Z^{\cdot}$ is not determined, electron transfer from NH_2OH to $Y_Z^{\cdot}$ is either electrically silent or this reaction contributes insignificantly to observed electrogenesis as compared to hydrophobic donors (DPC, TMPD).

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