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ON THE ROLE OF Fe^{2+} IN BACTERIAL PHOTOSYNTHESIS

THE EFFECT OF BIOSYNTHETIC SUBSTITUTION OF Fe^{2+} BY Mn^{2+} ON THE ELECTRON TRANSFER STEP $Q_1^- Q_2 \rightarrow Q_1 Q_2^-$ IN REACTION CENTERS

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A test of the 'iron-wire' hypothesis for the role of Fe^{2+} in promoting the electron transfer between the primary (Q_1) and secondary (Q_2) quinones in bacterial reaction centers of *Rhodopseudomonas sphaeroides* strain R-26.1 has been conducted. Kinetics of this step, $P^+Q_1^-Q_2 \rightarrow P^+Q_1Q_2^-$, and of recombination with the oxidized donor, $P^+Q_1^- \rightarrow PQ_1$ and $P^+Q_2^- \rightarrow PQ_2$, were followed optically at 4°C in normal iron-containing reaction centers and in reaction centers having 58% Mn^{2+}, replacing Fe^{2+}. This significant replacement is accomplished biosynthetically by control of the growth conditions, and so should preserve the native interactions between the cofactors. There are no significant differences observed in the recombination kinetics of the two types of reaction centers. The electron transfer between the quinones was observed to show apparent biphasic kinetics with major components of approx. 170 μs and 1.5 ms at 4°C and pH = 7.5. There is no statistically significant difference observed between the two types of reaction centers. This major change in the electronic structure of the metal and the unaltered kinetics discount the likelihood of any direct orbital participation of the metal in the electron transfer between the quinones.

Introduction

Bacterial reaction centers contain a single atom of non-heme iron, the function of which has yet to be established. Particular interest has centered on a possible role in coupling the sequential electron transport cofactors Q_1 and Q_2, the primary and secondary quinone electron acceptors, respectively **. There is ample evidence from magnetic susceptibility [1], EPR specteoscopy [2,3] and Mössbauer spectroscopy [4], establishing the presence of a weak interaction between Q_1^- and the Fe^{2+} ion and between Q_2^- and Fe^{2+} by EPR spectroscopy [5–9]. There is sufficient proximity between Fe^{2+} and Q_1^- or Q_2^- to allow for a weak, antiferromagnetic, electron-spin exchange interaction (J). A value of less than 1 cm^{-1} has been estimated for $|J_1|$ from magnetic susceptibility [1], while EPR results indicate $|J_1| \simeq 0.12 \pm 0.03$ cm^{-1} and $|J_2| \simeq 0.056 \pm 0.003$ cm^{-1} [10]. This electron spin exchange coupling establishes the existence of an orbital pathway for interaction between Q_1^- and Q_2^- via the orbitals on Fe^{2+} and gave rise to the 'iron-wire' hypothesis for the naturally occuring electron transfer step $Q_1^-Q_2 \rightarrow Q_1Q_2^-$ [9]. In this model the partially filled orbitals on Fe^{2+} serve as the pathway through which the electron is transferred. No evidence has been reported for

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Abbreviations: DEAE, diethylaminoethane; LDAO, lauryldimethylamine *N*-oxide; PA, phenanthroline.

** Another labelling convention preferred by some authors is Q_A and Q_B.

oxidation-state changes for the Fe^{2+} under any condition. Primary electron transfer to form $P^+Q_1^-$ occurs in reaction centers which are suppressed or devoid of iron [11,2]. This established the iron to be non-essential to the primary charge separation, but left open the possibility that it may mediate the electron transfer between the quinones.

Early attempts to remove the iron without loss of quinones showed that the $Q_1^-Q_2 \rightarrow Q_1Q_2^-$ transfer step is stopped [12]. However, more recent results suggest that this inhibition is caused by disruption of the reaction-center structure rather than specific loss of iron (G. Feher, private communication).

It is interesting that 30% of the Fe^{2+} has been observed to be replaced by Mn^{2+} in reaction centers when the bacteria are grown on an enriched Mn diet [14]. This has no effect on the primary photochemistry or the $P^+Q_1^-$ charge recombination; however, no observations were made on the $Q_1^-Q_2 \rightarrow Q_1Q_2^-$ transfer step.

In this work we report on experiments testing the dependence of the $Q_1^-Q_2 \rightarrow Q_1Q_2^-$ electron-transfer step on the biosynthetic replacement of Fe^{2+} by Mn^{2+} in reaction centers containing 0.58 Mn/reaction center.

Materials and Methods

Cell growth and reaction-center preparation

The carotenoidless mutant of *Rhodopseudomonas sphaeroides* (R-26.1) was grown photrophically as described by Reed and Clayton [14]. Cells were the kind gift of Drs. B.H. Clayton and R. Clayton, Cornell University. Mn-enriched cells were grown on Hutner's medium containing no yeast extract and $1.8 \cdot 10^{-3}$ M $MnSO_4$ (200 × normal) and $7.2 \cdot 10^{-8}$ M $FeSO_4 \cdot 7H_2O$ ($3 \cdot 10^{-3}$ × normal). All chemicals were reagent grade except where analytical grades were available. The principal source of contamination for Fe was the Mn salt. The solutions were prepared using deionized water having an undetectable amount of Mn or Fe as detected by atomic absorption. An aliquot of 0.5 ml of packed normal Fe cells was used to start 250 ml cultures which, when mature, were used to innoculate 2 l bottles. All subsequent innoculations were from the Mn-enriched cultures. The yield of healthy blue-green cells from these large cultures was 85–90% of the yields from normal Fe-grown cells. However, growth to an equivalent cell density usually required 7–10 days instead of the usual 3–5 days with normal Fe media.

Reaction centers were isolated from late log-phase cells as described by Feher and Okamura [9]. The final step of DEAE chromatography was repeated after desalting by dialysis and ultrafiltration against 10 mM Tris (pH 7.5), containing 0.025% lauryldimethylamine *N*-oxide (LDAO, Onyx Chem. Co., Jersey City, NJ). This yielded preparations having an absorbance ratio of 280 nm/803 nm = 1.2–1.4.

Optical kinetics

Laser-flash optical absorbance spectroscopy was performed with an apparatus which has been previously described [15]. Briefly, this consists of a single-beam, monochromatic, xenon light source which is filtered prior to passing through the 5 mm cuvette, passed through a monochromator and filtered again prior to detection by a photomultiplier tube (OP28AV1) or a silicon photodiode (model 500D, United Detector Technologies, Santa Monica, CA). The sample was refrigerated at 4°C. Despite the extensive filtering, fluorescence caused by the laser excitation pulse prohibited absorbance measurements during a period set by the 10 μs time-constant of a buffer amplifier (PAR 215, Princeton, NJ). This signal was recorded by a Biomation 8100 digitizer and transfered to a laboratory computer (North Star Computers, Berkeley, CA) for signal averaging. Typically 36 coadditions were used at a laser repetition period of 15 s. The experiments were performed in a darkened room and the analyzing light source was shuttered when not needed. The measured kinetics were independent of the analyzing beam light intensity. Pulsed laser excitation was provided by a Nd/YAG laser at a wavelength of 532 nm and 15 ns duration (Molectron Corp., Sunnyvale, CA). The laser excitation was perpendicular to the analyzing beam.

Reaction center samples were typically 2.5–5.0 μM in 10 mM Tris plus 0.025% LDAO buffer (pH = 7.5). The reaction center isolation procedure results in the loss of Q_2. However, Q_2 can be reconstituted. Reconstitution of reaction centers with ubiquinone-50 (Q) (Sigma Chemical, St.

Louis, MO) was performed by incubation of a sample with 20-fold excess Q overnight at 0–4°C. Inhibition with 1–5 mM *o*-phenanthroline (*o*-PA) was accomplished by incubation (0°C) for a minimum of 10 min in the dark. The *o*-PA was initially dissolved in a minimal volume of ethanol and diluted in Tris/LDAO buffer prior to addition to the reaction-center sample. The final ethanol concentration was typically 3%. Any undissolved material was then removed by centrifugation to minimize light scattering.

Data analysis was performed using the North Star computer. Digital smoothing on some data was performed by means of a logarithmic smoothing routine [16] to suppress noise at the end of the decay where absorbance changes are small. All data were analyzed graphically as semilog plots and by a non-linear, least-squares computer fit to a biexponential decay function (Groth, E., Princeton University, personal communication) given by $A = A_1 \exp(-\tau/\tau_1) + A_2 \exp(-\tau/\tau_2)$.

Results

Determination of Mn and Fe

A quantitative measurement of the Mn and Fe content was performed by flameless atomic absorption using a Perkin Elmer model 305B and a model HGA-2000 graphite furnace. Consistently reproducible linear calibration curves using five standardized solutions of $FeCl_3$ and $MnCl_2$ were obtained. The results, summarized in Table I, show that 58% replacement of Fe by Mn occurs and that the total Mn + Fe content equals 0.92/reaction center. This represents a significant and stoichiometric replacement which is sufficient to reveal if different spectroscopic and kinetic properties are conferred. The total (Fe + Mn)/reaction center radio is consistently lower than unity (0.92 ± 0.02), yet within the 5–10% error estimated for the extinction coefficient.

EPR

The presence of Mn^{2+} in reaction centers is detectable by EPR spectroscopy at low temperatures [13]. We observe broad EPR resonances at 9 K in dark Mn-enriched reaction centers which are not found in the normal Fe reaction centers (data not shown). These occur near 500, 1500, 2500 and 3500 G (at 9.4 Ghz) and are diagnostic for low-symmetry Mn^{2+}. A photoinducible signal due to $P\text{-}865^+$ is observed at $g = 2.00$. The amplitude of this signal, normalized to total BChl, is not distinguishable in normal vs. Mn-enriched reaction centers.

Electronic spectrum

The optical absorbance spectrum of the bacteriochlorophylls and bacteriopheophytins in reaction centers exhibit characteristic electrochromic shifts which occur when charge separation takes place. The absorbance band at 760 nm undergoes a red shift related to formation of the charge-separated states $P^+Q_1^-$ and $P^+Q_2^-$. The spectral shifts for each state, as given in Fgi. 1, are sufficiently different in magnitude and wavelength

TABLE I

ATOMIC ABSORPTION ANALYSIS FOR Fe AND Mn IN REACTION CENTERS GROWN IN NORMAL AND Mn-ENRICHED MEDIA

Resonance line (Å; element)	Relative sensitivity [a] (μg/ml)	Normal Fe media [b]		Mn-enriched media [b]	
		Fe/RC	Mn/RC	Fe/RC	Mn/RC
2483 (Fe)	0.5	0.90 ± 0.02	–	0.34 ± 0.1 [c]	–
2795 (Mn)	1.0	–	⩽ 0.02	–	0.58 ± 0.1 [c]
4034 (Mn)	0.5				

[a] Concentration giving 1% absorption.

[b] Using $4.38 \cdot 10^{-4}$ M reaction centers determined by an extinction coefficient of $\varepsilon^{1\,cm}_{800\,nm} = 2.88 \cdot 10^5\ M^{-1} \cdot cm^{-1}$ [9].

[c] The value given here refers to the range of metal content observed from several preparations rather than the measured precision of a single measurement which is 0.02.

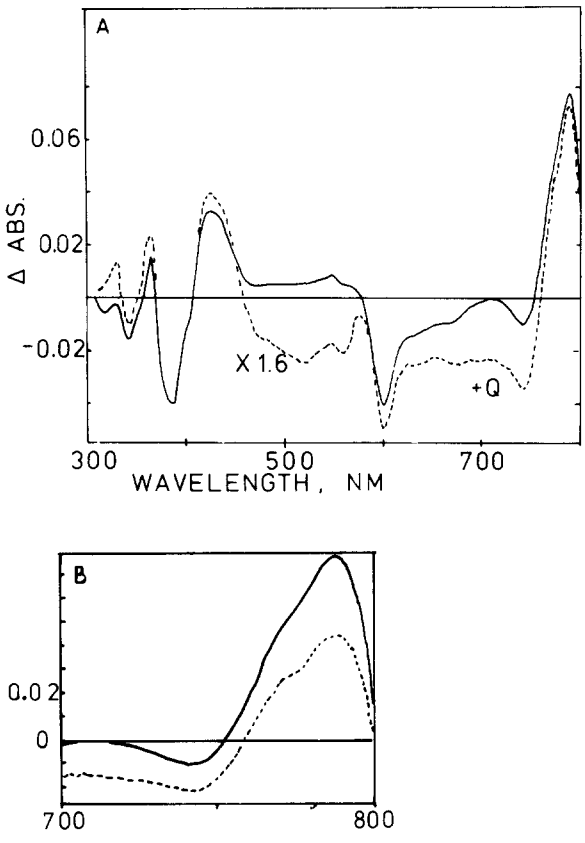

Fig. 1. Light-dark difference spectra for reaction centers ($1.76 \cdot 10^{-6}$ M) with no additions (———) and with 20-fold excess ubiquinone-50 (------). The sample was continuously illuminated with a tungsten lamp; pH = 7.5, $T \approx 295$ K, 1 cm cell path-length.

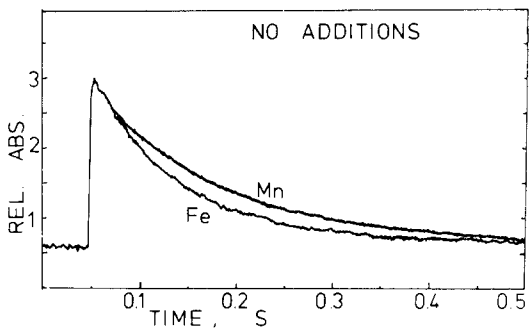

Fig. 2. Kinetics of recombination monitored at 785 nm for normal Fe reaction centers (+) and Mn-enriched reaction centers (○) containing no additions; $T = 4°C$, pH = 7.5, nine coadditions in 15 s. Solid curves represent fits to an exponential function.

that they can be used to monitor the kinetics of electron transfer between Q_1^- and Q_2 [24]. In all measurements reported here, kinetics were followed by the absorbance at 785 nm where the state $P^+Q_1^-$ has a higher absorptivity.

Kinetics

The relative amplitude for formation of P-865$^+$ Q_1^- per reaction center in normal Fe reaction centers was compared to that in Mn-enriched reaction centers by measurement of the extent of the flash-induced absorbance change at 785 nm. No difference was observed, indicating that in the Mn-enriched reaction centers all reaction centers contribute to the signal, not just the population containing Fe.

The kinetics of the absorbance change for both normal and Mn-enriched reaction centers containing no additions are given in Fig. 2. The kinetics are independent of reaction center concentration and exhibit a single exponential decay over the entire 95% of the decay that was monitored. The initial 1/e-lifetimes for decay obtained by a least-squares fitting routine are 99 ± 9 ms for Fe reaction centers and 134 ± 36 ms for Mn-enriched reaction centers. Reconstitution of Q_2 by incubation in 20-fold excess ubiquinone-50 causes a significant slowing down of the kinetics of decay, as shown in Fig. 3. The decay is biphasic with ap-

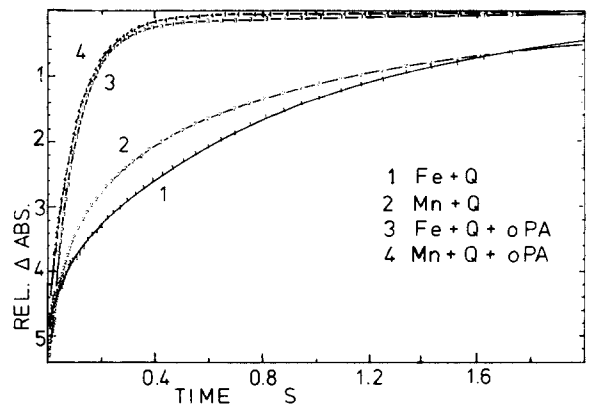

Fig. 3. Kinetics of recombination monitored at 785 nm for normal Fe reaction centers (1) and Mn-enriched reaction centers (2), containing 20-fold excess ubiquinone-50; experiments (3) and (4) are the same as in (1) and (2) but also include 1–5 mM *o*-phenanthroline; $T = 4°C$, pH = 7.5.

TABLE II

RECOMBINATION KINETICS OF 785 NM ABSORBANCE CHANGE IN REACTION CENTERS OF *RPS. SPHAEROIDES* (R-26.1)

Reaction-center sample	Additions [a]	τ-lifetime [b]	Relative amplitude	Fig.	Assignment
Fe	–	99 ± 9	1.0	2	$P^+Q_1^- \rightarrow PQ_1$
Mn	–	134 ± 36	1.0	2	$P^+Q_1^- \rightarrow PQ_1$
Fe	+Q	72 ± 9	0.2	3	$P^+Q_1^- \rightarrow PQ_1$
		910 ± 90	0.8		$P^+Q_2^- \rightarrow PQ_2$
Mn	+Q	96 ± 9	0.4	3	$P^+Q_1^- \rightarrow PQ_1$
		1040 ± 100	0.6		$P^+Q_2^- \rightarrow PQ_2$
Fe	+Q+ *o*-PA	91 ± 9	0.7	3	$P^+Q_1^- \rightarrow PQ_1$
		1310 ± 130	0.3		$P^+Q_2^- \rightarrow PQ_2$
Mn	+Q+ *o*-PA	108 ± 11	1.0	3	$P^+Q_1^- \rightarrow PQ_1$
					$P^+Q_2 \rightarrow PQ_2$
Fe	+ *o*-PA	98 ± 9	1.0		$P^+Q_1^- \rightarrow PQ_1$
Mn	+ *o*-pA	104 ± 10	1.0		$P^+Q_1^- \rightarrow PQ_1$

[a] 20-fold excess ubiquinone-50/reaction centers; *o*-phenanthroline at 1–5 mM (pH = 7.5) in 10 mM Tris and 0.025% LDAO.
[b] 1/e-lifetime in ms, determined by a non-linear least-squares fit to a biexponential decay law.

parent contributions from a small fraction recombining with the same kinetics as the unreconstituted samples ($P^+Q_1^-$ recombination), and a larger fraction recombining more slowly with an apparent exponential decay. A time window of 2 s allows 90% of the decay to be followed. The lifetime of the slow component of recombination ($P^+Q_2^-$) was 910 ± 90 ms for Fe reaction centers and 1040 ± 100 ms for Mn-enriched reaction centers.

Confirmation that the slowly decaying component was due to $P^+Q_2^-$ recombination was obtained by blocking the $Q_1^- \rightarrow Q_2$ electron transfer step in reconstituted reaction centers with *o*-phenanthroline. The decay kinetics given in Fig. 3 show that the fast recombination kinetics observed in reaction centers containing no Q_2 is restored by addition of *o*-phenanthroline. The initial lifetimes are 91 ± 9 ms (70%) for Fe reaction centers and 108 ± 11 ms (100%) for Mn-enriched reaction centers. The difference in the lifetimes is considered insignificant, and disappears if both data sets are forced to fit to a two-component decay. A fraction of 30% or less of the reaction centers recombines by a slow 1.3 s lifetime. This is due to unblocked reaction centers recombining from the state $P^+Q_2^-$ as was proven by the absence of this slow kinetic component in *o*-phenanthroline-inhibited reaction centers that had not been reconstituted with excess Q. All data on the recombination kinetics are summarized in Table II.

The kinetics of electron transfer between Q_1^- and Q_2 in reconstituted reaction centers were followed by increasing the response time of the detection system to 10 μs. Fig. 4 shows the absorbance change at 785 nm for the initial 2 ms after the laser pulse for Q-reconstituted reaction centers with and without *o*-phenanthroline for both Fe and Mn-enriched reaction centers. A rapidly decaying component is present in both Fe and Mn-enriched reaction centers only in the absence of *o*-phenanthroline where the Q_1^- to Q_2 electron transfer is permitted. The amplitude of this transient is the same for both Fe and Mn-enriched reaction centers when identical reaction-center concentrations and flash intensities are used. This transient is shown more clearly in the difference kinetics between samples with and without *o*-phenanthroline given in Fig. 4B. This rapid component does not fit a single exponential decay plot, as noted by the fit to a biexponential decay law having lifetimes and amplitudes as noted in Table III. The normal Fe reaction centers exhibit kinetic components of 180 ± 84 μs (42%) and 1800 ± 200 μs (58%), while the Mn-enriched reaction centers have components of 158 ± 62 μs (33%) and

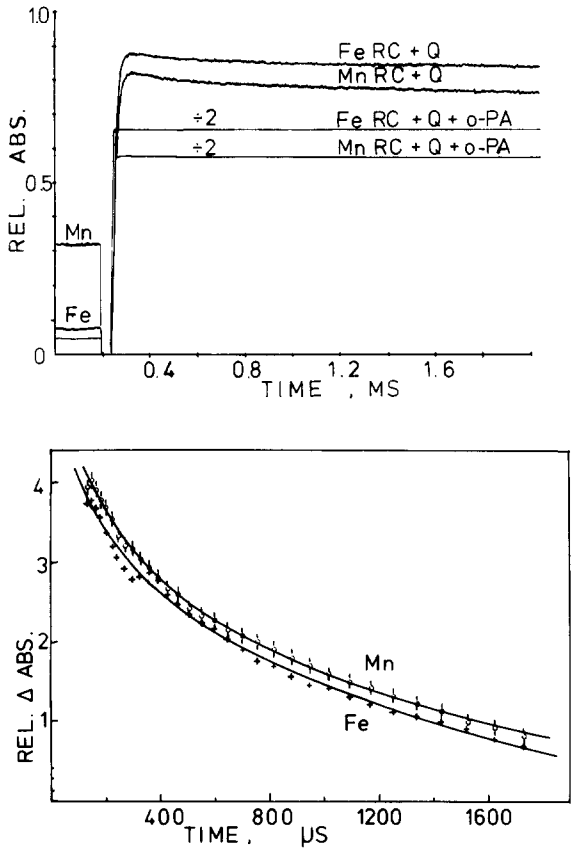

Fig. 4. (A) Kinetics of absorbance changes at 785 nm for normal Fe and Mn-enriched reaction center, both with 20-fold excess ubiquinone-50, and either with or without 1–5 mM *o*-phenanthroline, as noted; pH = 7.5, $T = 4°C$. (B) Difference kinetics for samples without *o*-PA minus sample with *o*-PA.

1200 ± 200 μs (67%). There is no statistically significant difference in the rapid component in the two samples, while the slower component appears to be relatively more rapid in the Mn-enriched reaction centers. However, satisfactory fits were also observed when the two samples were forced to have the same biphasic decay components.

Discussion

The kinetic results summarized in Table II indicate that there is no apparent difference in the recombination rate attributed to $P^+Q_1^- \rightarrow PQ_1$ in normal Fe vs. Mn-enriched reaction centers. With no externally added Q or *o*-PA, there is a 26% slower recombination rate for the latter. However, this difference is abolished in samples incubated with *o*-PA either with or without added Q. This difference probably reflects the retention of a fraction of endogenous Q_2 in the Mn-enriched reaction centers. A fit to two exponentials improved agreement between the kinetics for the two samples, in further support of this interpretation. These data are in agreement with the results observed in chromatophores of *Rhodospirillum rubrum*, for which the dominant decay component is ca. 100 ms, although a faster component of 33 ms (20%) is also claimed [18]. The absence of a difference in recombination kinetics between normal Fe and Mn-enriched (30% Mn-enriched) reaction centers has been observed between 1.5 and 100 K [13].

The recombination kinetics for the reaction $P^+Q_2^- \rightarrow PQ_2$ are found to be the same within experimental error in normal Fe and Mn-enriched

TABLE III

MICROSECOND KINETICS OF 785 nm ABSORBANCE CHANGE IN REACTION CENTERS OF *RPS. SPHAEROIDES* (R-26.1). $P^+Q_1^-Q_2 \rightarrow P^+Q_1Q_2^-$

Reaction-center samples	Additions [a]	τ-lifetime [b]	Relative amplitude	Fig.
Fe	+Q	180 ± 84	0.42	4
		1800 ± 200	0.58	
Fe	+Q + *o*-PA	–	–	4
Mn	+Q	158 ± 62	0.33	4
		1200 ± 200	0.67	
Mn	+Q + *o*-PA	–	–	4

[a] 20-fold excess ubiquinone-50 reaction center 10 mM Tris and 0.025% LDAO at 4°C (pH 7.5).

[b] 1/e-lifetime in μs determined by non-linear least-squares fit to a biexponential decay law.

reaction centers. Since the pathway for recombination may involve the equilibrium $Q_1Q_2^- \rightleftarrows Q_1^-Q_2$ [12,17,19], these kinetics should directly be influenced by factors which affect the relative free energies of these states. The absence of altered kinetics can therefore be interpreted to mean that Mn^{2+} substitution for Fe^{2+} has no discernable effect on the relative free energies of these two states. This is consistent with the very weak electron spin exchange interaction between Fe^{2+} and both Q_1^- and Q_2^- [10]. The average ionic radius for Fe^{2+} is 0.74 and for Mn^{2+} 0.80 Å [20]. Therefore, the charge density difference is very small. The difference in potential energy which this represents at a distance of 7.5 Å, where Q_1^- is located [10], is approx. 200 cm^{-1}, assuming a static dielectric constant of 40 and a point charge for the metal. This energy is merely comparable to the available thermal energy of these experiments and so should be insufficient for influencing the kinetics. Of course this analysis is simplistic and ignores possible charges on the ligands which could either enhance or reduce this effect.

Direct measurement of the kinetics for the forward electron transfer following a flash shows an apparent biphasic decay for which the rapid component ($\tau = 160$–180 μs) exhibits no statistically significant difference between normal Fe- and Mn-enriched reaction centers (Table III). A slower component of 1.2–1.8 ms may be slightly more rapid in Mn-enriched reaction centers than in normal Fe-reaction centers, but the fitting routine yields a satisfactory fit even when identical parameters are chosen for the two types of samples. Chamorovsky et al. [21] measured initial lifetimes for this same transfer in chromatophores of *R. rubrum* at 298 K of 370 ± 100 μs and 4 s in reaction centers [22]. Parson measured approximately 220 μs at pH 7.7 in chromatophores of *R. rubrum* at 4°C [23]. Vermeglio and Clayton estimated a transfer lifetime of 280 μs at pH 7.5 and ambient temperature in reaction centers of *Rps. sphaeroides* (R-26) [24]. These latter results are in close agreement with our results for the overall decay lifetime when corrected for differences in temperature.

Our results show that even under conditions of direct kinetic control of the forward electron transfer reaction there is no appreciable effect of Mn substitution. Evidently, these metals exert no different influence on the free energy of the transition state, which is passed through along the reaction coordinate. If the partially filled metal orbitals were to actively participate in this transfer via orbital overlap with both Q_1^- and Q_2, then there should exist an appreciable difference in the rates for the Mn vs. Fe reaction centers. This can be judged from the ionization potentials which are a direct measurement of the orbital energies. For Mn^{2+} it is 24 500 cm^{-1} larger than for Fe^{2+} in the free ions, owing largely to the additional electron repulsion present in Fe^{2+} ($3d^6$) compared to Mn^{2+} ($3d^5$) [25]. Such a large energy offset should influence the kinetics if orbital coupling is important. These data indicate that the hypothesis of the 'iron-wire' serving as an orbital bridge between the two quinones is not applicable. Alternative roles should be tested. This is also suggested by preliminary experiments which show that a non-redox metal such as Zn^{2+} can be biosynthetically incorporated up to 57% in reaction centers (Ferris, Upadrashta and Dismukes, unpublished data).

We have suggested another role based upon an observed trapping of the charge transfer state, $P^+Q_2^-$, upon simultaneous illumination and cooling [26]. The virtually complete suppression of the recombination reaction observed at -100°C in such preilluminated samples might be attributed to stabilization of the π^* anion radical of the 'free' semiquinone by the Coulomb field of the metal to yield a vibronically trapped, oxygen-centered quinone radical. Such an electrostatic interaction has also been suggested to play a role in determining the redox potential of the primary quinone [27].

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