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All-Optical Switching in *Pharaonis* Phoborhodopsin Protein Molecules

Sukhdev Roy*, Takashi Kikukawa, Parag Sharma, Student Member, IEEE, and Naoki Kamo

**Abstract**—Low-power all-optical switching with *pharaonis* phoborhodopsin (pR) protein is demonstrated based on nonlinear excited-state absorption at different wavelengths. A modulating pulsed 532-nm laser beam is shown to switch the transmission of a continuous-wave signal light beam at: 1) 390 nm; 2) 500 nm; 3) 560 nm; and 4) 600 nm, respectively. Simulations based on the rate equation approach considering all seven states in the ppR photocycle are in good agreement with experimental results. It is shown that the switching characteristics at 560 and 600 nm, respectively, can exhibit negative to positive switching. The switching characteristics at 500 nm can be inverted by increasing the signal beam intensity. The profile of switched signal beam is also sensitive to the modulating pulse frequency and signal beam intensity and wavelength. The switching characteristics are also shown to be sensitive to the lifetimes of ppR<sub>R</sub>, ppR<sub>M</sub>, and ppR<sub>O</sub> intermediates. The results show the applicability of ppR as a low-power wavelength tunable all-optical switch.

**Index Terms**—Bacteriorhodopsin, optical modulation, optical switching.

I. INTRODUCTION

Recent developments in nanophotonics have given impetus to synthesize novel photosensitive molecules for all-optical information processing [1], [2]. The possibility of tailoring the nonlinear optical response at the molecular level coupled with advantages of small size and weight, low propagation delay, and power dissipation make interesting prospects for optimized device applications [1], [2].

The naturally occurring photosensitive biological molecules optimized over centuries of evolution offer exciting possibilities for device applications. The photochromic bacteriorhodopsin (bR) protein found in the purple membrane of *Halobacterium halobium* has by far received the most attention for a wide range of biomolecular photonic applications [3]–[7].

A switch is the basic building block of information processing systems. Recently, there has been considerable research interest in using the photochromic properties of bR to design an all-optical switch [8]–[16]. All-optical switching in bacteriorhodopsin has been reported using multiple-laser geometries involving holograms [8], [9], refractive index modulation [10], enhanced photinduced anisotropy, and excited-state absorption [11]–[16]. Most of these studies are based on the pump-probe technique in which a continuous-wave (cw) probe beam is switched by a pulsed pump beam. Our analysis of all-optical light modulation in bR shows that longer lifetimes of the intermediate states lead to low-power operation [13], [14].

Recently, a new photoreceptor sensory rhodopsin II (sRII) or phoborhodopsin (pR) like protein, synthesized from *Natriobacterium pharaonis*, a halophilic alkaliphilic bacterium termed *pharaonis* phoborhodopsin (ppR), has received much attention due to its good stability and recent structural elucidation [17]–[21]. Among the archaean sensory rhodopsins, ppR has the most robust properties and is able to function during photosignaling in *N. pharaonis*, *H. salinarium*, and *Escherichia coli*. NpSRII or ppR remains stable both in the dark and under prolonged illumination, and it retains its native absorption spectrum and photocycle in different membranes; in a range of detergents; in salt concentrations from 25 to 4 M; and
over a broad range of pH. These exceptional properties have made it the prototypical sensory rhodopsin for crystallography and structure/function studies [17]. It exhibits a blue-shifted photocycle similar to bR as shown in Fig. 1 [21]. After excitation with 498-nm wavelength light, the molecule gets excited from the initial ppR state to the ppR$^K$ state and transforms to the ppR$^{KL}$ state within 50 ns. From there it transforms in 990 ns into the ppR$^L$ state. From the ppR$^L$ state, the molecules transform to the ppR$_M$ state in about 32 μs. The species in the ppR$_M$ state relax to the ppR$_O$ intermediate state in 1.7 s, from which it finally relaxes to the initial ppR state in 770 ms. The intermediates are named in analogy to those in the photocycle of bR.

The ppR photocycle exhibits longer lifetimes of the ppR$_M$ and the ppR$_O$ intermediate states even in its native state, i.e., the wild-type (WT) form, and hence leads to all-optical light modulation at considerably lower modulating pump powers in comparison to bR. Recently, we have reported theoretical designs of low-power all-optical spatial light modulators and logic gates with WT-ppR and its mutants [22]–[24].

For all-optical information processing, it is important to have the capability to effectively control the switching characteristics. Moreover, for digital operation, it is necessary to perform all-optical switching with a train of modulating pulses. All-optical switching based on the principle of excited-state absorption, using a pump-probe configuration, is a simple, flexible, and convenient technique for practical applications compared to other methods, for instance, those based on phase conjugation and interference phenomena. The switching characteristics using the pump-probe configuration, with pulse train excitation, would be similar to the single modulating pulse excitation, provided the period of the modulating pulse train is greater than the switching time of the switched signal beam due to single modulating pulse excitation. An increase in modulating pulse frequency would affect the nature and contrast of switching characteristics. Thus, it is important to study the effect of the modulating pulse frequency on the switching characteristics. In addition to this, the existence of different intermediates that exhibit respective absorption spectra spanning the entire visible range, provides interesting opportunity to switch the transmission of probe (signal) beams at different wavelengths. Hence, it would be interesting to investigate the all-optical control of: 1) the switching characteristics to realize positive or negative switching and 2) the switched signal beam pulse profile that have not been reported as yet.

The aim of this paper is to experimentally investigate: 1) all-optical switching in this new ppR protein based on excited-state absorption; 2) the effect of modulating pulse frequency; 3) the effect of signal beam wavelength at 390, 500, and 560 nm, which correspond to the peak absorption of the ppR$_M$, ppR$^L$, and ppR$_O$ states, respectively, and also at 600 nm; 4) the effect of modulating beam and signal beam intensity, on the apparent phase shifting of the switched signal beam with respect to pulsed modulating beam; and 5) to explain the experimental results theoretically. We demonstrate a simple, mirrorless all-optical switch with ppR. We show that the switching characteristics, i.e., the apparent shifting of the switched signal beam with respect to modulating pulses and the profile of the switched pulses, are sensitive to the modulating pulse frequency, signal beam intensity, and wavelength. Theoretical simulations using the rate equation approach are in good agreement with experimental results.

II. EXPERIMENTAL SETUP AND MATERIAL CHARACTERIZATION

The WT-ppR sample was prepared by following the procedure reported earlier [20]. The concentration of ppR in the sample was 53 μM. Fig. 2 shows the experimental setup. A vertically polarized second harmonic of Nd-YAG laser beam.
(532 nm) at 5 mW of 5 mm diameter was used as the modulating beam. Signal light beams at different wavelengths, respectively, were taken from a monochromator which was illuminated by a 150-W Xenon lamp. The depolarized signal beam had a diameter of 3 mm. The modulating beam overlapped with the signal beam over a 5-mm length in the sample placed in a quartz cuvette. To select the measuring signal wavelength and exclude the scattered modulating light from the sample, another monochromator was placed in front of the photomultiplier tube (PMT). The output of the PMT was connected to a digital storage oscilloscope.

The ppR sample was characterized using computer-controlled flash photolysis [20]. Interestingly, an additional ppR' intermediate state after the ppR$_O$ state, having absorption spectrum similar to the initial ppR state, was observed, due to three exponential global fitting for the absorbance changes at 390-, 500-, and 560-nm wavelengths, as shown in Fig. 3. The lifetimes of the three long lifetime ppR$_{M}$, ppR$_{O}$ and ppR’ intermediate states in the photocycle, were measured to be 112 ms, 323 ms, and 6.773 s, respectively, which are considerably lower than typical values due to the presence of imidazole, which accelerates the decay of ppR$_{M}$ and ppR$_{O}$ intermediates.

III. THEORETICAL MODEL

We introduce a simplified level diagram shown in Fig. 4 to represent the photocycle of ppR molecules of the sample, which enables the adoption of the simple rate equation approach for the population densities in the various intermediates. To simulate the effect of the intensities of both the modulating and signal beams, we consider the ppR molecules exposed to light beams of intensities $I'_m$ and $I'_s$, which modulate the population densities of different intermediate states through the excitation and de-excitation processes. These can be described by the rate equations in the following form [14], [22]–[24]:

$$\frac{dN_i(t)}{dt} = \left[ (I_m\sigma_{1i} + I_s\sigma_{is})N_i(t) \right. - \left. (k_2 + I_m\sigma_2 + I_s\sigma_{2s})N_i(t) \right]$$

where $N_i$, $i = 1$ to 7 represents the population densities of ppR, ppR$_K$, ppR$_{KL}$, ppR$_L$, ppR$_M$, ppR$_O$, and ppR’ states, respectively; $\sigma_i$ and $k_i$ are the absorption cross sections and rate constants of respective states; subscript $s$ denotes the value at signal wavelength; and $\psi = 0.51$ is the quantum efficiency for the ppR → ppR$_K$ transition [19]. $I_m$ and $I_s$ are the photon density fluxes of the modulating laser and signal beams, respectively, i.e., ratio of the intensity to the photon energy $h\nu$ at respective wavelengths.

The modulating laser beam pulses are considered to have a super-Gaussian pulse profile given by

$$I'_m = I'_m_0\exp \left( -\frac{(t - t_m)^2}{\Delta t^2} \right)$$

IV. RESULTS AND DISCUSSION

The all-optical switching characteristics of the ppR sample were studied for different signal beam wavelengths (390, 500, 560, and 600 nm), for modulating pulses at 532 nm, over a wide range of modulating pulse frequencies (0.05–20 Hz). Fig. 5 shows the experimental curves for ppR$_O$ state dynamics, i.e., variation of TSI at 560 nm that corresponds to peak absorption
of $ppR_O$ intermediate state, switched by a modulating pulse train at 532 nm, for different modulating pulse frequencies. The switched signal beam exhibits out-of-phase characteristics with respect to modulating pulse (negative switching), for single pulse excitation or for a pulse train at low frequencies as shown in Fig. 5(a). Initially, in the absence of the modulating pulse, all protein molecules stay in the initial $ppR$ state, hence, the TSI is high (ON state) due to less linear absorption of signal beam by initial $ppR$ state only. As the modulating pulse excites the $ppR$ molecules, the population of longer lived $ppR_O$ intermediate increases, which leads to increased absorption of the signal beam and hence switching OFF of the TSI. This results in the basic all-optical switching mechanism, as shown in Fig. 5(a).

Increase in modulating pulse frequency to larger values results in an apparent phase shift of TSI with respect to the modulating pulse as shown in Fig. 5(d)–(k). For a modulating pulse train, the presence of a second successive pulse at a time interval less than the relaxation time of the photocycle, results in the TSI not reaching the steady-state OFF-ON values. This results in a decrease in contrast and an asymmetric switched signal profile, while maintaining out-of-phase switching behavior, as is evident from Fig. 5(b). Increasing the frequency further results in a symmetric triangular profile, Fig. 5(c). This apparent phase shift of TSI saturates after a certain value, maintaining the switched signal profile and exhibits a continuous decrease in contrast.

Fig. 5. Measured TSI at 560 nm (solid lines) and input modulating beam at 532 nm (dashed lines) for modulating pulse frequency: (a) 0.05 Hz; (b) 0.42 Hz; (c) 1.53 Hz; (d) 2.86 Hz; (e) 5 Hz; (f) 5.42 Hz; (g) 6.42 Hz; (h) 6.86 Hz; (i) 8.57 Hz; (j) 10.55 Hz; and (k) 19.52 Hz.
As the modulating pulse appears, the TSI switches off after a certain time lag. This time lag appears due to the time taken by the molecules to relax from the long lifetime ppR intermediate that does not absorb the signal beam at 560 nm, to the probed ppR state. This time lag appears to be significant at higher modulating pulse frequencies, when it becomes comparable to the modulating pulse width, which is evident from Fig. 5(d)-(k).

Theoretical simulations have been carried out by numerically solving the nonlinear time-dependent equations (1)-(5), using the experimentally measured lifetimes of the ppRM, ppRO, and ppR' states and the typical values of other parameters reported in literature as given in Table I [20]-[24].

Fig. 6 shows the corresponding theoretically simulated optical switching curves for ppRO state dynamics, considering the experimental conditions and pulse profile parameter $q = 8$. It is evident from Figs. 5 and 6 that simulated results are in good accord with experimental results. The theoretical results are in good agreement at relatively lower intensity values. This may be attributed to the effective absorption after considering reflection and scattering losses.

To study the switching characteristics at different wavelengths, we carried out experiments with signal beams at 390, 500, and 600 nm also that correspond to the peak absorption wavelengths of ppRM, ppR, and near the peak absorption wavelength of ppRO state, respectively. The experimental results are shown in Fig. 7(a)-(d) at modulating pulse frequency of 5 Hz.

Fig. 7(a) shows the variation of TSI at 390 nm corresponding to the peak absorption of ppRM intermediate state with time. For single modulating pulse excitation, the linear TSI at 390 nm is low due to its high absorption by initial ppR state [20], [21]. As the modulating pulse excites the molecules, the TSI at 500 nm increases due to decrease in the population of initial ppR state. The TSI saturates to its initial value after the passage of the modulating pulse due to relaxation of excited molecules back to the initial state. Thus, the TSI at 500 nm shows positive switching for broad modulating pulses at lower frequencies and also at 5 Hz modulating pulse frequency as shown in Fig. 7(b).

The variation of TSI at 560 nm, corresponding to the peak absorption of ppRO intermediate state with time, is shown in Fig. 7(c), for comparison. The switching characteristics are inverted (positive switching) in comparison to low modulating pulse frequency case [negative switching, Fig. 5(a)], due to apparent phase shift as described earlier.

Fig. 7(d) shows the variation of TSI at 600 nm with time. The switching characteristics in this case also are inverted (positive switching) in comparison to negative switching exhibited at low modulating pulse frequencies. This is due to ppRO state dynamics, as the signal wavelength is nearer to the peak absorption wavelength of ppRO intermediate (560 nm).

The corresponding theoretically simulated optical switching curves for different signal beam wavelengths, considering the experimental conditions, for pulse profile parameter $q = 10$ are shown in Fig. 8. It is evident from Figs. 7 and 8 that simulated results agree well with experimental results.

Thus, the apparent phase shift of TSI with respect to modulating pulses is sensitive to the signal beam wavelength and frequency $f$. Our theoretical simulations show that it can be continuously varied between some specific ranges at different signal beam wavelengths, for a given frequency range.

It is also evident from Figs. 7 and 8 that the profile of the switched TSI is sensitive to the wavelength of the signal beam. For instance, the TSI at 390 and 500 nm has triangular profile, whereas it is like a sinusoid at 560 and 600 nm. The profile of the switched TSI is also sensitive to frequency. For broad pulses, TSI attains steady-state off-on values, and exhibits symmetric

### Table I

Absorption Cross Sections and Rate Constants of Different Intermediates of PPR [20]-[24]

<table>
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<tr>
<th>Rate Constant</th>
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<tr>
<td></td>
<td></td>
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<td>532 nm</td>
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<tr>
<td>$k_2$</td>
<td>$2.0 \times 10^7$</td>
<td>$\sigma_1$</td>
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</tr>
<tr>
<td>$k_3$</td>
<td>$1.0 \times 10^6$</td>
<td>$\sigma_2$</td>
<td>$\tilde{O}$</td>
</tr>
<tr>
<td>$k_4$</td>
<td>$3.1 \times 10^4$</td>
<td>$\sigma_3$</td>
<td>$1.08 \times 10^{-16}$</td>
</tr>
<tr>
<td>$k_5$</td>
<td>$8.93$</td>
<td>$\sigma_4$</td>
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</tr>
<tr>
<td>$k_6$</td>
<td>$3.09$</td>
<td>$\sigma_5$</td>
<td>$1.30 \times 10^{-16}$</td>
</tr>
<tr>
<td>$k_7$</td>
<td>$0.148$</td>
<td>$\sigma_6$</td>
<td>$\tilde{O}$</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$\sigma_7$</td>
<td>$5.60 \times 10^{-17}$</td>
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Fig. 6. Simulated normalized TSI at 560 nm (solid lines), and input modulating beam at 532 nm (dashed lines) for modulating pulse frequency: (a) 0.05 Hz; (b) 0.42 Hz; (c) 1.53 Hz; (d) 2.86 Hz; (e) 5 Hz; (f) 5.42 Hz; (g) 6.42 Hz; (h) 6.86 Hz; (i) 8.57 Hz; (j) 10.55 Hz; and (k) 19.52 Hz, for peak modulating power of 1 mW and signal beam of 0.2 mW.

Profile. On increase in frequency, the TSI is unable to reach the steady state, as the molecules are unable to relax to the initial or probed excited state, which results in lower contrast and an asymmetric profile that becomes symmetric at higher values.

Theoretical simulations for $ppR_M$ state dynamics show that the switching contrast ($TSI_{\text{max}} - TSI_{\text{min}}$) decreases exponentially after a certain frequency value, whereas, apparent phase shift varies monotonically with frequency, in the range $0.05 \leq f \leq 5$ Hz, Fig. 6. The switch OFF and ON times are 1.3 and 1.1 s for $f = 0.42$ Hz; and 59 and 58 ms for $f = 8.57$ Hz, respectively. The switching contrast can be increased by using the modulating beam at 498 nm, which is the peak absorption wavelength of initial $ppR_M$ state.

The apparent phase shift is also sensitive to the kinetic parameters of $ppR$ photocycle. The rate constants of the intermediates, especially $ppR_M$ and $ppR_O$ states can be tailored by various techniques [25]–[29]. For instance, addition of azide affects the $ppR_M$ state life time and replacing the amino acid (Val-108) by methionine (Val-108 mutant of $ppR$) causes three times faster decay of $ppR_M$ state and removes the shoulder of its spectrum [25]–[29].

Theoretical simulations for $ppR_O$ state dynamics at a particular frequency (1.53 Hz) are shown in Fig. 9. At lower $\tau_D$ values, the population of initial $ppR$ state is much greater than the population of the shorter lived $ppR_{O2}$ state. As modulating pulse appears, the TSI at 560 nm increases (positive switching) due to depletion of population of initial $ppR$ state, which has a significant absorption at 560 nm, Fig. 9(a). An increase in $\tau_D$ results in peak TSI shifting towards the peak of modulating pulse with decrease in its contrast. This is due to decrease in contribution of
ppR state to switching in comparison to ppR\(\Omega\) state. At a particular \(\tau_{\Omega}\) value, the TSI becomes completely in-phase and also exhibits a super-gaussian-like profile. Further increase in \(\tau_{\Omega}\) shifts the peak of TSI towards increasing edge of modulating intensity. At particular \(\tau_{\Omega}\) value (15 ms), the TSI becomes out-of-phase with modulating intensity, due to increased absorption of signal beam at 560 nm by highly populated longer lived ppR\(\Omega\) state, as discussed earlier, Fig. 5(a), (b). At higher \(\tau_{\Omega}\) values, the peak of TSI further shifts from increasing edge of modulating intensity towards its peak value, as shown in Fig. 9(b). The contrast of TSI decreases and then increases with increase in \(\tau_{\Omega}\) values. It is clear from Fig. 9 that the profile of TSI is also sensitive to the \(\tau_{\Omega}\) values.

Since the apparent phase shift in switching characteristics appears due to time taken by excited molecules to relax from the long lived ppR\(M\) state to the probed ppR\(\Omega\) state, hence, for a fixed modulating frequency \(f\), increase in ppR\(M\) state lifetime \(\tau_{M}\) would result in a similar variation as in Figs. 5 and 6, as shown in Fig. 10. An increase in \(\tau_{M}\) from 0.001 s–0.7 s, keeping the frequency fixed at 1.53 Hz, results in an apparent phase shift of the peak of the switched signal beam from increasing to decreasing edges of the modulating pulses. Hence, a corresponding increase in \(\tau_{M}\) at constant frequency results in a monotonic variation in apparent phase shift. The lifetime of ppR\(') state appears to have no effect on the switching characteristics.

In general, the apparent phase shift appears when the modulating pulse width \((\sim 1/2f)\) becomes of the order of the rate constant of an earlier longer lifetime intermediate, in the range in which experiments have been conducted. The variation of apparent phase shift in this frequency range depends on the lifetimes of the probed excited state and its earlier intermediates. A theoretical fit of the experimental switching curves at different modulating frequencies would result in the estimation of the lifetimes of ppR\(M\) and ppR\(\Omega\) states.

Fig. 11 shows the switching characteristics at different signal wavelengths at a higher value of \(I'_{m0} = 500\) mW/cm\(^2\). On comparison with Fig. 8, it is clear that the switching contrast increases with increase in \(I'_{m0}\). Our simulations show that it saturates at higher values. Increase in \(I'_{m0}\) leads to the TSI at 390, 560, and 600 nm shifting towards lower values due to increase in the population of the respective probed excited states. The TSI at
500 nm shifts towards higher values due to decrease in the population of the initial \( p_{R} \) state that gets depleted due to increased pumping by the modulating pulse at 532 nm. The switching contrast of TSI at 390, 500, 560 and 600 nm is 25.78%, 33.06%, 55.66% and 31.84%, respectively, as shown in Fig. 11. It can also be increased by using the modulating beam at 498 nm.

The switching characteristics are also sensitive to signal intensity \( I_{s} \). Fig. 12 shows the variation in the switching characteristics with increase in \( I_{s} \). For a weak \( I_{s} \) at 500 nm, the switching characteristics exhibit positive switching as shown in Figs. 7(b) and 8(b). The signal wavelength at 500 nm corresponds to the peak absorption of initial \( p_{R} \) state and the modulating wavelength at 532 nm is nearer to peak absorption wavelength of \( p_{R} \) state \([20], [21]\). Hence, for increased values of \( I_{s} \), initially, in the absence of the modulating pulse, \( I_{s} \) induces the photocycle by exciting the initial \( p_{R} \) state and leads to relatively higher TSI due to the depleted population of the \( p_{R} \) state. The appearance of the modulating pulse at 532 nm switches the \( p_{R} \) state molecules back to initial \( p_{R} \) state. This results in increase in absorption of signal beam at 500 nm by increased population of the initial \( p_{R} \) state and leads to out-of-phase switching characteristics. Thus, for this case, the switching characteristics can be varied from in-phase to out-of-phase by considering the absorption by \( I_{s} \) (\( I_{s0} = 50 \text{ mW/cm}^2 \)) and varying \( I_{s} \) from negligible values to 9 mW/cm², as shown in Fig. 12.
variation in $I'_b$ at 390, 560, and 600 nm in the same range has no effect on the apparent phase shift.

The apparent phase shift and profile of the TSI, which are sensitive to the kinetic and spectral response of the photointermediates, may possibly be useful to characterize ppR like proteins and to generate different forms of pulsed signal beams. Since the initial ppR state exhibits absorption over a broad visible range around 500 nm and the ppR$_M$ intermediate covers UV region around 390 nm and has a long lifetime, UV radiation can be blocked by ppR excited by visible light. The absorption spectra of different intermediates spanning the entire visible spectrum provide possibilities of nonlinear absorption at multiple wavelengths, which can be useful in the design of all-optical devices at different wavelengths.

Since ppR exhibits a blue-shifted photocycle with characteristics such as number of intermediates, overlap of absorption spectra of intermediates, and long lifetime intermediates in the later part of the photocycle similar to that of bR, the qualitative features of all-optical switching based on excited-state absorption are similar. The control of the apparent phase shift between the switched signal and the modulating beams and the profile of TSI currently studied in ppR would therefore also be observed in bR. The existence of longer lifetime states in the native WT form of ppR leads to switching at relatively lower modulating powers than bR, at the expense of slower switching time.

Since the kinetic and spectral properties of ppR can also be tailored by physical, chemical, and genetic engineering techniques, the switching characteristics can be optimized to increase the contrast and obtain faster response time [20]–[29]. Recently, new ppR mutants (T204C, T204S, S/E/T/A, S/E/T/C, S/E/T/S, etc.) with azide have been reported which exhibit the switching, filtering, spatial light modulation, logic operations, etc., based on its photochromic properties.

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REFERENCES


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Prof. Kamo is a Member of the Biophysical Society (USA), Biophysical Society of Japan, Biochemical Society of Japan, and Pharmaceutical Society of Japan.

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