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CELL BIOPHYSICS

The Effect of Electromagnetic Radiation at Frequencies of 51.8 and 53.0 GHz on Growth, Pigment Content, Hydrogen Photoemission, and F_0F_1-ATPase Activity in the Purple Bacterium *Rhodobacter sphaeroides*

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Abstract—Exposure of the purple bacteria *Rhodobacter sphaeroides* MDC6522 isolated from Jermuk mineral springs (Armenia) to extremely high-frequency electromagnetic radiation (51.8 and 53.0 GHz) for 15 min resulted in a pronounced increase in the specific growth rate and H_2 photoemission. However, a significant decrease in the specific growth rate (1.6–2.0 times) was observed when the duration of irradiation was prolonged to 1 h. The maximum effect was at a frequency of 53.0 GHz. During irradiation for 1 h, absorption maxima typical of carotenoids gradually disappeared, and the level of bacteriochlorophyll *a* complexes decreased. Prolonged irradiation also inhibited the H_2 production during bacterial growth for 72 h, although it was restored after 96 h of growth. The activity of *N,N'*-dicyclohexylcarbodiimide-sensitive proton F_0F_1-ATPase also decreased in *Rh. sphaeroides*. These results indicate that the membrane-bound F_0F_1-ATPase may be the main target of action of extremely-high-frequency electromagnetic radiation. The data we obtained can be used in biotechnology for control of growth and hydrogen metabolism of phototrophic bacteria.

Keywords: Rhodobacter sphaeroides, electromagnetic irradiation of extremely high frequency, growth of bacteria, oxidation-reduction potential, H_2 production, F_0F_1-ATPase

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The study of the effect of electromagnetic radiation of extremely high frequencies (EHF EMR) on living organisms is of current importance in biophysics. Despite the fact that EHF EMR (the range of 40–100 GHz) is weak and extremely weak radiation it has a pronounced biological efficiency (from microorganisms to mammals), with both stimulatory and inhibitory effects, which are already observed in small doses at a power density below 0.005 mW cm^{-2} [1–3].

The study of the effect of EHF EMR on microorganisms is of great interest [2–4]. EHF radiation can have both a stimulatory and inhibitory effect on bacterial growth.

EHF radiation was shown to stimulate the growth and biomass yield of various cyanobacteria [5, 6]. EHF EMR of low intensity was shown to have a pronounced bactericidal effect as well. The effect of EMR on different bacteria (*Escherichia coli*, *Enterococcus hirae*, *Lactobacillus acidophilus*, etc.) was dependent on the frequency and duration of irradiation, aerobic or anaerobic conditions of bacterial cultivation, composition and pH of the growth medium, and metabolism characteristics of the studied strains [7–10].

Specific mechanisms may be the basis of the EHF EMR effect on bacteria. These mechanisms may be changes in water structure and properties (since the water content in living organisms is rather high and bacteria mainly occur in the water medium), as well as changes in membrane proteins and DNA, which may be possible targets at the cellular level [1–3]. The most probable target of the EHF radiation is the plasmatic membrane of the cell [2, 3]. Membrane-acting changes, which are related to the structure and surface properties of membranes, ion transport, and energy transformation processes, were shown to occur during the EHF EMR irradiation [8, 10]. A membrane-bound proton F_0F_1-ATPase is suggested to be one of the targets of the EHF radiation [2, 3]. These changes may be the basis of the bactericidal effects of EHF EMR. The study of the influence of EHF EMR on the

Abbreviations: EHF EMR, electromagnetic radiation of extremely high frequency; ORP, oxidation-reduction potential; BCHL *a*, bacteriochlorophyll *a*; DCCD, *N,N'*-dicyclohexylcarbodiimide.

vital activities of bacteria makes it possible to use these effects in biotechnology and medicine.

However, the mechanisms of the effect of the EHF radiation on bacteria, especially phototrophic bacteria that produce molecular hydrogen and, therefore, are of interest in biotechnology, have been poorly studied. The EMR effects on various bacteria differ from each other. The study of the effect of the EHF radiation on the purple bacteria *Rhodobacter sphaeroides* is of interest. These bacteria differ from the previously studied bacteria in the composition and structure of the plasmatic membrane and metabolic characteristics. The molecular and cellular mechanisms of the EHF EMR effect on bacteria should be studied in detail. The study of the effect of EHF radiation on the components and activity of the cell membrane, including the functioning of the proton ATPase, which plays an important role in the bacterial activity, is especially relevant.

This work reports the parameters of growth, the change in the ambient oxidation-reduction potential (ORP), the content of bacteriochlorophyll *a*, the activity of F_0F_1-ATPase, and H_2 production in *Rh. sphaeroides*. These parameters have been studied for the first time in response to low-intensity EMR at frequencies of 51.8 and 53.0 GHz. Moreover, changes in the bacterial growth and ORP after irradiation were observed for a long period of time (96 h), which may indicate the nature of the changes and has an important applied significance.

MATERIALS AND METHODS

Bacteria and their growth. A purple bacteria *Rh. sphaeroides*, strain MDC6522, isolated from the mineral water springs of Jermuk in the Republic of Armenia (Center for Depositing Microorganisms of NAS of Armenia, Yerevan, Armenia, WDCM803) was used in the present work.

The bacterium was grown under anaerobic conditions on the Ormerod medium in the thermostat at pH 7.5 ± 0.1, a temperature of 30 ± 0.2°C, and illumination of 2000 lx [11, 12]. Halogen lamps with a power of 60 W were used for illumination. Light intensity was measured using a LM37 luxmeter (Carl Roth, Germany).

The growth of *Rh. sphaeroides* was monitored by measuring the optical density of the suspension on a Spectro UV-Vis Auto spectrophotometer (Labomed, United States) at a wavelength of 660 nm [11, 12]. The values of optical density were calibrated taking the dry weight of the bacterium into consideration. The specific growth rate (μ) was determined as the quotient of the division of 0.693 (ln2) by the time of doubling of the optical density within the interval when the change in the optical density in time was linear. The specific growth rate was expressed as h^{-1}: $\mu = 0.693/\tau$, where τ was the time of doubling of the optical density of the bacterial suspension [11, 12]. The duration of the lag phase was determined graphically as the time before the start of the log phase. The dry biomass of bacterial cells was determined as described earlier [11]. The ambient pH was measured using a sensitive pH meter with a selective electrode of the HJ1131B type (Hanna Instruments, United States) and adjusted with NaOH and HCl (0.1 M solutions) [11, 12].

Electromagnetic irradiation of bacteria. Irradiation of bacteria was carried out using a G4-141 EHF EMR generator with a conical antenna (Istok, Fryazino, Moscow oblast, Russia) as described earlier [5–8]. The generator emits coherent electromagnetic waves at a frequency of 45–53 GHz. Bacteria were collected by centrifugation at 6000 rpm for 20 min and suspended in distilled water. The volume of the bacterial suspension was 10 mL, the suspension thickness was 1 mm, and the cell density was approximately 10^7 cells/mL. The suspension was irradiated with EMR at 51.8 and 53.0 GHz in the mode of amplitude modulation at a frequency of 1 Hz (the stability of the frequency signal was 0.05%; the power density was 0.06 mW/cm^2) in sterilized plastic Petri dishes at room temperature under conditions of natural illumination (~1000 lx) [10]. Amplitude modulation was provided by a G3-118 generator of low-frequency signals (Istok, Fryazino, Moscow oblast, Russia). EMR at such a power density has no significant effect on the temperature of the bacterial suspension, which has been shown previously [10]. The irradiated object was at a 20-cm distance from the antenna; irradiation was carried out in the farthest zone of the antenna, while the level of the homogeneity of the distribution of the electromagnetic field was quite high. Bacteria were transferred to fresh cultivation medium immediately after irradiation of the suspension for 15 min and 1 h.

Determination of the membrane-bound activity of bacteria. A Spectro UV-Vis Auto spectrophotometer (Labomed, United States) was used to obtain absorption spectra of the suspension of *Rh. sphaeroides* in the wavelength range of 400–1000 nm [13]. The intracellular concentration of bacteriochlorophyll *a* (BCHL *a*) was determined spectrophotometrically in the ethanol extract at 774 nm [13, 14].

The ORP value was determined using I-160 MP digital ion meters (Gomel Plant of Measuring Devices, Gomel, Belarus) with platinum (EPV-01) and titanium–silicate (EO-21) electrodes as described in [11, 12]. The potential of these electrodes (relative to the comparison electrode) in a control solution containing a mixture of potassium ferrocyanides and ferricyanides was 254 ± 5 mV at a temperature of 25°C. The titanium-silicate electrode is not sensitive to molecular hydrogen and oxygen; it is not able to catalyze redox reactions, which determines the advantage of this electrode in comparison to the platinum one. Therefore, the titanium–silicate electrode is successfully used to evaluate the redox state of the bacterial

suspension, while the platinum electrode is used to determine the presence of O_2 or H_2 in the medium. The difference in the indications of these electrodes makes it possible to measure the H_2 production by bacteria under anaerobic conditions [8, 11, 12]. H_2 production was calculated according to the change in the ORP value and expressed as mmol H_2 per g dry biomass, as described [12]. In some experiments, H_2 production was confirmed by the chemical method, which is based on the reaction of decoloration of the solution of potassium permanganate in sulfuric acid during the reaction with H_2 [11, 12, 15].

ATPase activity was determined by the release of inorganic phosphorus (P_i) after the reaction of membrane vesicles with ATP, as previously described [11]. Membrane vesicles were obtained by the Konings and Cabac method, while the amount of P_i was determined using the Tausk and Shore colorimetric method [11]. Membrane vesicles were preliminarily incubated in the DCCD solution (0.5 M) for 10 min, when using the *N,N'*-dicyclohexylcarbodiimide (DCCD) inhibitor of the F_0F_1-ATPase.

Reagents. Reagents of analytical purity (Carl Roth GmbH, Germany; Sigma Aldrich, United States) were used in the work.

Processing of data. An Excel 2010 software program was used for statistical processing of data. Average arithmetical values from at least three independent experiments with the standard deviation of the measurement results and with the value of the Student's reliability test (p) for the difference between the results of different series of experiments are presented [10, 12].

RESULTS AND DISCUSSION

The effect of electromagnetic radiation on the growth of bacteria. We studied the influence of the EHF radiation at a frequency of 51.8 and 53.0 GHz on the parameters of the growth of the purple bacterium *Rh. sphaeroides* MDC6522. Irradiation of *Rh. sphaeroides* with EHF EMR at a frequency of 51.8 GHz for 15 min resulted in a pronounced increase in the specific growth rate (Fig. 1), while a frequency of 53.0 GHz did not produce a significant effect. An increase in the duration of irradiation up to 1 h caused a considerable decrease in the specific growth rate (1.6–2.0 times) (Fig. 1). In addition, irradiation of the bacteria with EHF EMR for 1 h resulted in a pronounced increase in the duration of the latent phase of growth or lag phase (not shown). The maximum effect was observed at 53.0 GHz, which agrees with the idea that these frequencies may be resonant frequencies for a number of bacteria [3, 8], although this requires further investigations.

The process of phototrophic growth of purple bacteria is known to include synthesis of the photosynthetic apparatus, which consists of two light-harvesting complexes (BCHL800–850 and BCHL875) surrounding the photochemical reaction center [12, 16]. Light-harvesting complexes are composed of proteins and pigments, such as BCHL *a* and carotenoids.

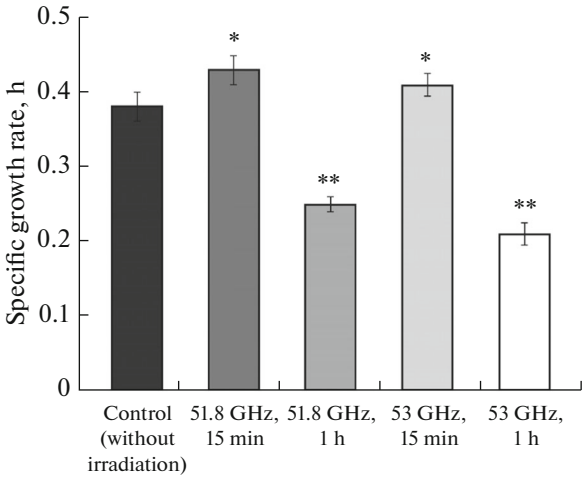

Fig. 1. The change in the specific growth rate of *Rh. sphaeroides* after exposure to EHF radiation (51.8 and 53.0 GHz) for 15 min and 1 h. * The difference from the control is significant, $p < 0.05$; ** the difference is significant, $p < 0.01$.

The absorption spectra of Rh. sphaeroides cells were obtained to study the effect of the EHF radiation on the photosynthetic apparatus (Fig. 2). Several maxima typical for purple bacteria are observed in the absorption spectrum of the control cells in the wavelength range of 400–1000 nm [12, 16]. These maxima indicate the presence of carotenoids (450, 478, and 510 nm) and BCHL a (590, 800, and 850 nm). These pigments that compose Rh. sphaeroides proved to be sensitive to the EHF radiation effect. Irradiation with EMR at a frequency of 51.8 GHz for 1 h resulted in gradual disappearance of the absorption maxima typical for carotenoids (Fig. 2); a decrease in the level of the BCHL800–850 complexes was observed as well. These complexes are proposed to participate in the accumulation and transmission of light energy to the reaction center [12]. After irradiation with EHF EMR for 1 h, the content of BCHL a decreased two times on average compared to the control sample (Table 1), while irradiation for 15 min almost did not affect the concentration of BCHL a. A decrease in the concentration of the main light-harvesting pigment indicates inhibition of the growth of Rh. sphaeroides as well.

Mechanisms of action of electromagnetic radiation on bacteria. The change in ORP and H_2 production by intact cells of bacteria, and ATPase activity of membrane vesicles after irradiation at 51.8 and 53.0 GHz for 15 min and 1 h were determined in order to elucidate the mechanisms of action of EHF radiation on *Rh. sphaeroides*.

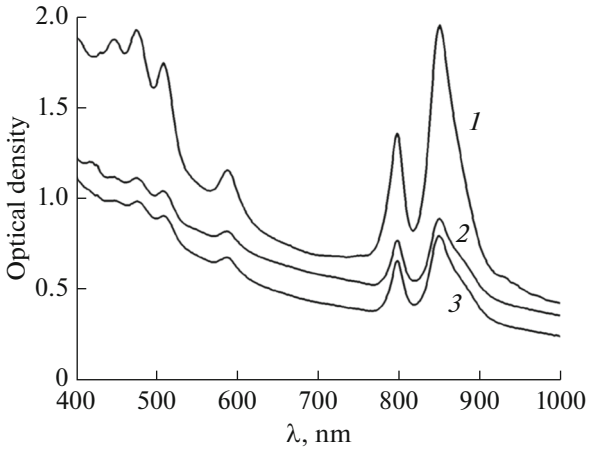

Fig. 2. The effect of EHF radiation on the absorption spectra of intact cells of the *Rh. sphaeroides* culture. (*1*) Control cells (without irradiation); (*2*) during irradiation at a frequency of 51.8 GHz for 1 h; (*3*) during irradiation at a frequency of 53.0 GHz for 1 h.

ORP is an important factor that determines the anaerobic growth of bacteria, which occurs at a high rate and is accompanied by a decrease in ORP from positive values to negative ones [11, 17, 18]. A decrease in ORP indicates an increase in the intensity of the reduction processes associated with the formation of the final products of fermentation, the production of amino acids, and the synthesis of proteins and other compounds, which may be typical for metabolic processes during cell growth under anaerobic conditions [17, 18].

The connection between a decrease in the ORP and photoemission of H_2 was shown for *Rh. sphaeroides* [18, 19]. The photosynthesis process is known to be the basis of light-induced H_2 production by purple bacteria [20]. The process of H_2 photoemission is catalyzed by nitrogenase, while hydrogenase is responsible for the uptake (oxidation) of H_2 [11, 20]. H_2 production catalyzed by nitrogenase requires electrons provided by reduced ferredoxin, as well as large amounts of ATP, i.e., it is an energy-dependent process [20]. Reduction of protons to H_2 is observed under strictly reduction conditions. The involvement of hydrogenase is essential for H_2 production under certain conditions [18, 19], which requires further investigation.

Growth of the control cells of *Rh. sphaeroides* for 72 h was accompanied by a decrease in the ORP value, which was measured using a platinum electrode. The decrease was from positive values (100 ± 10 mV) at the beginning of the lag phase of growth to low negative values (−620 ± 15 mV) (Fig. 3). Changes in the indications of the titanium–silicate electrode were insignificant (not shown). When irradiated at 51.8 and 53.0 GHz for 15 min, a decrease in ORP, which was determined with platinum electrode (72 h of growth), was more intense, reaching the values of (−710 ± 10 mV) and (−700 ± 20 mV), respectively (Fig. 3). Such a decrease in ORP may indicate not only an increase in the intensity of the reduction processes associated with the production of different products of photofermentation, but also H_2 photoemission [17, 18]. The exposure to EHF radiation for 1 h did not cause pronounced changes in the ambient ORP (Fig. 3). Irradiation of bacteria resulted in the slowdown of the ORP decrease. The ORP decreased to (−390 ± 15 mV) at a frequency of 51.8 GHz and to (−330 ± 10 mV) at 53.0 GHz. These data indicate that the slowdown of the decrease in ORP can cause inhibition of bacterial growth.

Calculations showed that H_2 production by *Rh. sphaeroides* (after EMR irradiation at a frequency of 51.8 GHz for 15 min) was two times higher (48–72 h of growth) than that in the control sample (without irradiation) (Table 1), while the H_2 production after irradiation at a frequency of 53.0 GHz increased 1.6 times in comparison to the H_2 production in the control sample. The fact that no H_2 production was observed in the course of anaerobic growth for a relatively long time (48–72 h) after the EMR irradiation at a frequency of 51.8 and 53.0 GHz for 1 h is of interest. This indicates complete inhibition of the process.

Table 1. The effect of EHF radiation on the concentration of BCHL *a* and H_2 photoemission in *Rh. sphaeroides* during anaerobic growth

	H_2 production, mmol per g dry biomass			BCHL *a*, mg per g dry biomass
	48 h	72 h	96 h	
Control (without irradiation)	1.73 ± 0.10	5.58 ± 0.30	6.04 ± 0.30	14.60 ± 1.00
51.8 GHz (15 min)	3.00 ± 0.50	10.74 ± 0.30*	7.53 ± 0.30*	16.06 ± 1.00*
51.8 GHz (1 h)	–	–	2.03 ± 0.10**	7.65 ± 0.50*
53.0 GHz (15 min)	2.85 ± 0.20	8.82 ± 0.30*	7.23 ± 0.25*	15.70 ± 1.00*
53.0 GHz (1 h)	–	–	1.80 ± 0.10**	6.14 ± 0.50*

The (–) sign indicates the absence of H_2 production. *, Difference from the control is significant, $p < 0.05$; **, difference is significant, $p < 0.01$.

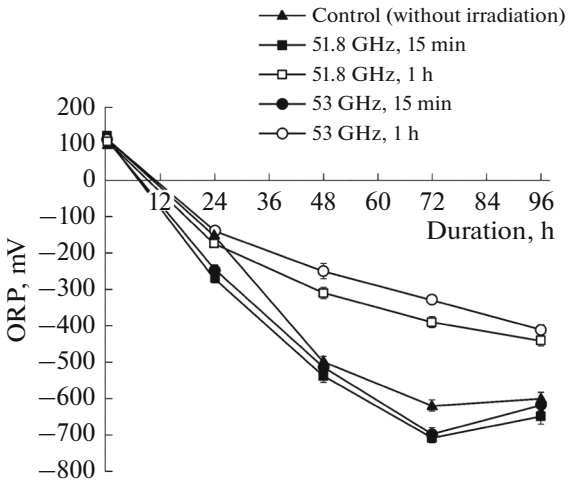

Fig. 3. The kinetics of ORP in *Rh. sphaeroides* after exposure to EHF EMR: (*1*) the values of the platinum electrode in control cells; the values of the platinum electrode during irradiation at a frequency of 51.8 GHz for 15 min (*2*) and 1 h (*3*); the values of the platinum electrode during irradiation at a frequency of 53.0 GHz for 15 min (*4*) and 1 h (*5*).

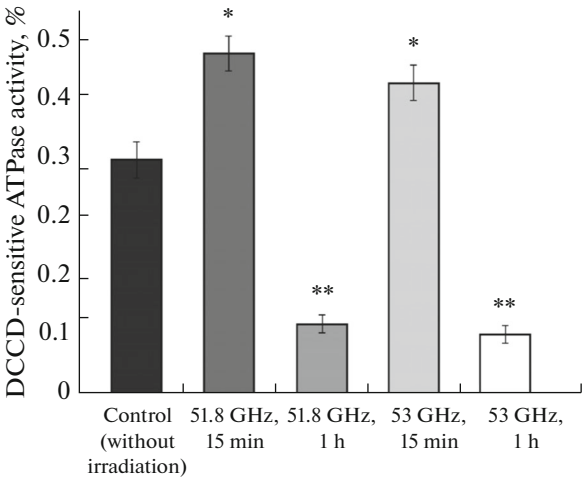

Fig. 4. The effect of EHF radiation (51.8 and 53.0 GHz) on the DCCD-sensitive ATPase activity of membrane vesicles of *Rh. sphaeroides*. *, Difference from the control is significant, $p < 0.05$; **, difference is significant, $p < 0.01$.

However, the H_2 production by *Rh. sphaeroides* was restored after 96 h (see Table 1), which may indicate the presence of defensive or repair mechanisms in the studied bacterium. In contrast to the control sample, the level of H_2 emission was approximately three times lower, which indicates inhibition of the nitrogenase activity. The frequency of 53.0 GHz had the highest inhibitory effect. Similar data were obtained for other bacteria, e.g., *E. coli* and *E. hirae* [5, 6]. *Rh. sphaeroides* MDC6521 isolated from the mineral springs of Arzni proved to be more sensitive to the effect of the EHF radiation. Thus, the H_2 production after irradiation at a frequency of 53.0 GHz for 1 h was inhibited by approximately seven times [21]. This may be associated with the physicochemical characteristics of the sources from which these strains were isolated. The water of the Arzni mineral springs (1250 m above sea level) is of a sodium-chloride type with a temperature of 12.0–22.0°C and pH 6.3–6.6, while the water of the Jermuk springs (2100 m above sea level) is of the sulfate-chloride type with a temperature of 57–64°C and pH 6.5–8.5 [11]. The chemical compositions of these springs also differ. Jermuk springs contain sodium, potassium, chlorine, calcium, magnesium, iron, and other microelements essential for the growth and metabolism of most phototrophic bacteria [22].

Since the photoemission of H_2 is carried out *via* various membrane mechanisms that involve the ATP-dependent nitrogenase enzyme and, probably, proton ATPase (F_0F_1-ATPase), the EHF radiation may affect the particular membrane components that are responsible for this process, the activity of the proton ATPase, in particular. The DCCD-sensitive ATPase activity increased by 1.3 times after irradiation of *Rh. sphaeroides* with EMR at a frequency of 53.0 GHz for 15 min, while the ATPase activity after EMR irradiation of bacteria at a frequency of 51.8 GHz was 1.5 times higher than that of the control sample (Fig. 4). The ATPase activity of the membrane vesicles of *Rh. sphaeroides* exposed to irradiation for 1 h was approximately four times lower than the activity of the control sample (Fig. 4).

These results indicate that the proton F_0F_1-ATPase of these bacteria may play a key role in the bacterial effects of EHF EMR. This ATPase may be the primary target of EHF EMR and determine its membrane-acting effect on bacteria [2, 3].

Thus, the data we obtained indicate that the effect of EHF EMR on *Rh. sphaeroides* depends on the duration of irradiation. A short-term irradiation (15 min) results in stimulation of the parameters of growth of these bacteria, which correlates with an increase in the photoemission of H_2. Short-term irradiation may stimulate photosynthetic activity of the purple bacteria and, therefore, H_2 emission. These results agree with the data obtained for some cyanobacteria [9, 10]. An increase in the duration of irradiation up to 1 h causes inhibition of the growth of bacteria, their photosynthetic activity, production of H_2, and the F_0F_1-ATPase activity.

These results indicate the membrane-acting mechanisms of the EHF radiation. The basis of these mechanisms is probably the resonant (informational) interaction of EHF EMR [1–3], which is associated with changes in the properties of the cell membrane and its components, e.g., the proton ATPase. It should be noted that water molecules may be a target of the EHF radiation as well. The water structure can change during irradiation, resulting in an increase in its chemical activity. Therefore, this should effect the struc-

ture, properties, and functions of the cell membrane [2, 3, 23].

Considering the above, EHF EMR can be used in medicine and biotechnology to control metabolism, including hydrogen metabolism, in phototrophic purple bacteria.

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