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COMPARATIVE AND ONTOGENIC PHYSIOLOGY

Electrical Responses of *Lymnaea stagnalis* to Light Stimulation: Effect of Divalent Cations

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Abstract—The effects of Ca^{2+}, Mg^{2+} and Mn^{2+} on light-evoked electrical responses, ERG and action potentials of optic nerve fibers, were studied in an isolated eye of *Lymnaea stagnalis*. Signals of both types persisted with minor changes when Mg^{2+} concentration in the bath solution was increased up to 15 mM. This finding suggests that action potentials of photoreceptor cells are transmitted via their axons directly to central ganglia without a relay in chemical synapses on interneurons. At the same time, the changed spiking pattern may indicate chemical interactions between photoreceptors cells themselves. In the presence of 4 mM EDTA or 10 mM Mn^{2+}, both ERG waves and spiking activity were considerably depressed, probably, as a result of impaired phototransduction in photoreceptor cells.

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Key words: *Lymnaea stagnalis*, eye, optic nerve, electroretinogram (ERG), spiking activity, divalent cations.

INTRODUCTION

Electrical responses of the *Lymnaea stagnalis* eye to light stimulation, including slow ERG waves and bursts of optic nerve spiking activity, were scrutinized in several studies [1—3]. However, both types of electrical activity were analyzed separately, so that the link between them remains obscure. Accordingly, it is still unclear whether the ERG components are generated by photoreceptor cells while spiking in the optic nerve owes interneurons, or both types of electrical activity rely on photoreceptor cells. Moreover, the conclusion about photoreceptor cell signaling via second-order neurons, made previously on the basis of the suppression of light-evoked responses in the optic nerve by manganese ions [2], is poorly consistent with the possibility of direct retrograde staining of retinal photoreceptors through optic nerve fibers [4]. Spiking activity, at least, in photoreceptors would have persisted under conditions of impaired chemical mechanism of synaptic transmission.

In the present work, we attempted to elucidate this issue by studying the effect of suppressed chemical synaptic transmission on ERG and optic nerve spiking activity in the pond snail.

MATERIALS AND METHODS

Object. Experiments were carried out on adult pond snail *Lymnaea stagnalis* (shell height: 2.5—3 cm) collected in reservoirs around the city of

Concentration of chemical components (mmol/L) and total osmotic concentration (C_{osm}, mOsmol/L) of solutions used in experiments

Solution	NaCl	KCl	$CaCl_2$	$MgCl_2$	EDTA-2Na	$MnCl_2$	$C_6H_{12}O_6$	C_{osm}
Physiological solution								
PhS	40	3	3	1	–	–	–	98
Experimental solutions								
ES1	40	3	3	1	–	–	33	131
ES2	40	3	0	15	–	–	–	131
ES3	40	3	0	0	–	–	12	98
ES4	40	3	–	–	1	–	9	98
ES5	40	3	–	–	4	–	–	98
ES6	44	3	0.5	1	–	–	–	98.5
ES7	29	3	0.5	1	–	10	–	98.5
ES8	29	3	3	1	–	–	22	98

Kaliningrad. Isolated eye preparations with an optic nerve stump, were made in physiological solution under a binocular microscope with red and heat filters on the microscope lamp.

Electrical signal recordings were performed by a sucking Ag/AgCl electrode with the use of the A–M Systems Model 1800 AC amplifier. ERG recordings were carried out in the frequency bandwidth from 0.1 to 500 Hz. Spiking activity was recorded from the same preparations by narrowing the bandwidth to 10–500 Hz, thus filtering out the slow ERG wave.

Amplified (100-fold) signal was fed to the Digidata 1440A low-noise data acquisition system. Recording and processing of a signal, digitalized with a sample time increment of 1 ms, was carried out using the computer pClamp 8 software package.

Light stimulation was performed in an intermittent mode by a light emitting diode (LED) ARL2-5213PGC (λ_{max} = 525 nm). LED-generated current impulses were fed from the Digidata 1440A output run by pClamp 8 means. Illumination, as created by the LED at the experimental bath level and measured by a luxmeter TKA-PKM (31), was 4500 lx. In most experiments, stimulation was dosed out by changing the stimulus duration as it can be precisely regulated. In some experiments, absorbing neutral grey filters were used to change the intensity of the light stimulus.

The course of experiments. The preparation of the isolated eye was placed into the experimental bath with an inbuilt tip of the sucking electrode, into which a stump of the optic nerve was sucked. The bath with the preparation was put into the experimental setup and left in the dark for 1–2 h, with electrical responses recorded periodically to light flashes of constant intensity and duration until the ERG amplitude stability is attained. Then followed the block of stimulation by light impulses with an increasing duration to obtain the appropriate ERG amplitude dependence. The same block of stimulation was repeated 30–40 min after each change of the solution.

The composition of experimental solutions is presented in Table.

Physiological (PS) and experimental (ES) solutions were applied in different experiments in the following sequences:

(a) PS–ES1–ES2–PS
(b) PS–ES3–ES4–PS
(c) PS–ES3–ES5–PS
(d) PS–ES6–ES7–PS
(e) PS–ES8–PS

The “a” sequence aimed at elucidating the effect of a high Mg^{2+} concentration on electrical responses. In this case, pre-application of the ES1 was supposed to reveal the contribution of the elevated osmotic pressure to this effect.

The “b” and “c” variants of solution changes

aimed at revealing the effect of the divalent cation removal by the introduction of the disodium salt of ethylenediaminetetraacetic acid (EDTA-2Na$^+$) at concentrations of 1 and 4 mM. In this case, the application of ES4 and ES5 was supposed to show the contribution of the removal of these cations to the overall effect.

The "d" variant of solution changes reproduced the experiment by Stoll and Bijlsma [2] with the exception that the effect of a reduced Ca^{2+} concentration in the solution (ES6) was recorded prior to the application of the Mn^{2+}-containing solution.

The "e" variant was applied to check the degree of the effect on electrical responses of the Na^+ concentration reduced to that in the ES7.

Identification of characteristic frequencies of neuronal signal oscillations was conducted using the continuous wavelet transform with the Morlet wavelet in the amplitude norm [5]:

$$w(t,a) = \int_{-\infty}^{+\infty} U(t') e^{i\omega_0(t-t')/a} e^{-[(t-t')^2/2a^2]} \frac{dt'}{\sqrt{2\pi a}}, \quad (1)$$

where ω_0 is a central frequency and a is a scale variable. Their combination is closely associated with the periods of the original signal harmonic components, because the wavelet transform of the simple periodic signal $U(t) = \exp[i(2\pi/T)t]$ with the period T has the appearance

$$w(t,a) = e^{i\frac{2\pi}{T}} e^{-a\frac{\omega_0 T}{2\pi}^2 / \frac{T^2}{8\pi^2}}, \quad (2)$$

i.e. the scale $a = a_{max}$, which corresponds to the maximum of this wavelet transform modulus, allows the characteristic period to be identified as $T = 2\pi a_{max}/\omega_0$.

Previously, it was shown [6] that the wavelet transform modulus (1) is equivalent to the local (corresponding to the t time moment) modulus of the spectral Fourier transform from the signal smoothed by Gaussian filtering with the sliding window width being proportional to the local period of oscillations:

$$|w(t,T)| = \int_{-\infty}^{+\infty} \left[U(t') \frac{e^{-[(t-t')^2/(2[\omega_0 T/2\pi]^2)}}{\sqrt{2\pi[\omega_0 T/2\pi]^2}} \right] e^{-i\frac{2\pi}{T}t'} dt'. \quad (3)$$

Such an approach has an advantage before standard Gaussian filtering, which precedes spectral analysis, since the application of the Morlet wavelet retains the characteristic number of oscillation periods at the smoothing window width uniform irrespective of the magnitude of the identifiable period. Thereby, this allows avoiding the introduction of additional artificial errors caused by inhomogeneity of the smoothing (averaging) interval.

At the same time, since it is the global spectral distribution that is in the focus of our analysis while the analyzed system, following initial excitation, enters a regime of stable oscillations, we consider the wavelet spectrum averaged over a full observation time interval (Δt)

$$W(T) = \frac{\int_0^{\Delta t} |w(t,T)|}{\Delta t} dt, \quad (4)$$

which represents a spectrogram of the smoothed signal at the filtration level determined by the center frequency ω_0. The choice of its numerical value relies on the properties of the Morlet wavelet localization on the time-period plane: a smaller value allows the discrimination of individual spikes, preventing thereby the appearance of peaks of the "parasitic periods", which represent higher harmonics divisible by the main period magnitude [7]. That is why the value $\omega_0 = \pi$ was chosen for use.

Wavelet transformation of experimental data samples was practically realized using a complex of computer programs written in the MATLAB language (for algorithm description and software key see [8]). We analyzed the records of electrical activity within a 2-s interval, made in the dark, beginning from the moment of 300-ms light stimulus presentation.

Data processing was implemented by means of Microsoft Excel and MathCad. To average the ERG amplitudes obtained in different experiments, they were normalized relative to a maximum value recorded from the given preparation.

RESULTS

Electrical signals in the isolated eye. In response to light stimulation of the isolated eye, two types of electrical signals were recorded: slow waves of the electrical potential (ERG) and spiking activity (Fig. 1a). The maximum ERG amplitude

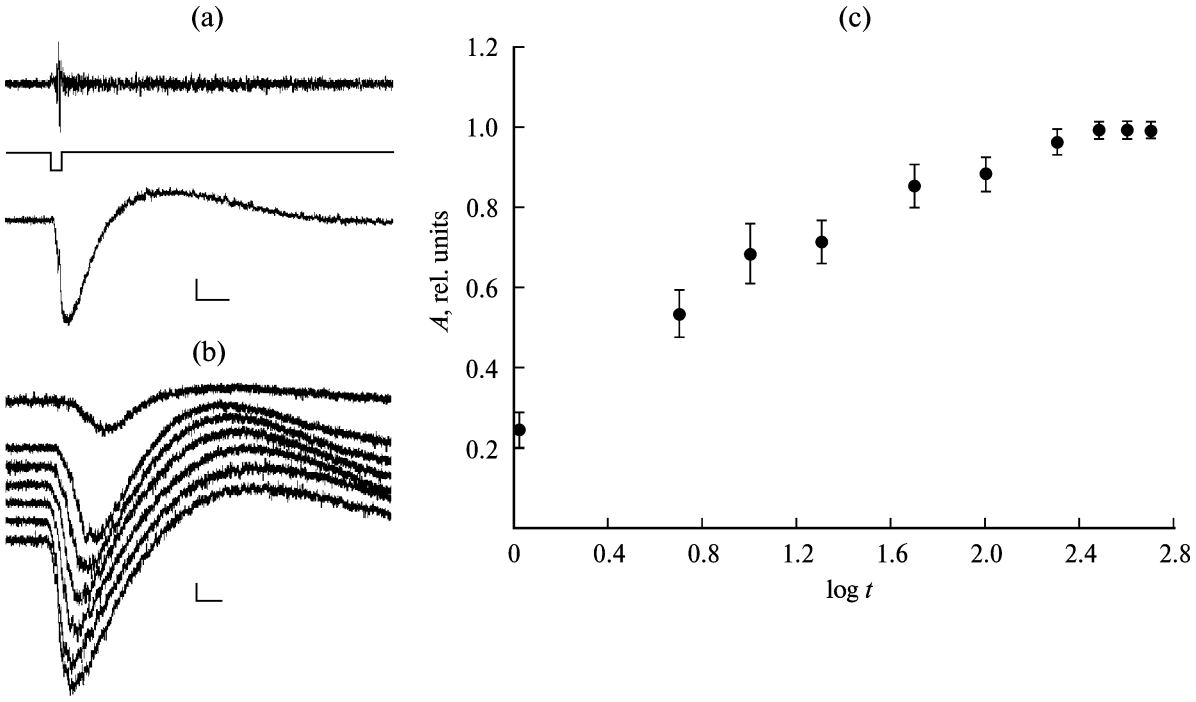

Fig. 1. Electric signals in the isolated *Lymnaea stagnalis* eye to light stimulation. (a) Spike (*above*) and electroretinogram (ERG) (*bottom*) recorded in response to the 300-ms light stimulus (depicted under the record). Calibration: 20 μV, 500 ms (for spike) and 100 μV, 500 ms (for ERG). (b) ERG in response to light flashes of different duration (*downward*): 1, 5, 10, 20, 50, 100 and 300 ms. Calibration: 100 μV, 500 ms. (c) Dependence of normalized ERG amplitude (*ordinate, A*) on common logarithm of stimulus duration (*abscissa*); extrapolation of dependencies yields a threshold value of the threshold stimulus intensity about 0.1 ms. *Vertcal bars*—standard deviations. The number of measurements of each point $n = 24$.

in our experiments reached 5 mV and that of spikes—80 μV. Signals of both types did not occur in records obtained in the dark and reflected light activation of photoreceptors. When the tip of the sucking electrode was removed from the eye cup, spiking activity could be recorded without appreciable changes, whereas the ERG amplitude decreased sharply. The dependence of the ERG wave amplitude on the position of the recording electrode tip reflects a passive character of signal propagation and allows likening it to receptor potentials of retinal cell. At the same time, relative independence of the spiking activity amplitude from the site of its recording allows identifying spikes as action potentials of the optic nerve fibers, propagating without attenuation. In the absence of light stimulation, the maximum amplitude of recorded electrical signals was about 20–25 μV. Noises generated by the "idle" electrode were about the same magnitude, and this does not allow us to assert categorically the absence or presence of the dark background of low-amplitude electrical activity.

Durations of ERG and spiking activity generated in response to light stimulation did not coincide completely. Most high-amplitude spikes in the light response arose approximately in the middle part of the rising phase of the ERG response. After the completion of repolarization, spiking activity could be observed during several seconds. In the studied interval of light stimulus durations, the ERG amplitude depended on the flash duration (Fig. 1b), reaching saturation at 300 ms (Fig. 1c).

The distribution spectra of the total average amplitude of wavelet components, corresponding to the main interspike period of the light response, differ noticeably from the spectra of background records obtained in the dark and the spectrum of the "idle" electrode (Fig. 2). In the spectra of light responses, there are maxima corresponding to the characteristic interspike intervals (frequencies). The height and position of these maxima are individual, but nevertheless it is possible to notice a permanently occurring maximum that corresponds to the periods within the interval 0.04–

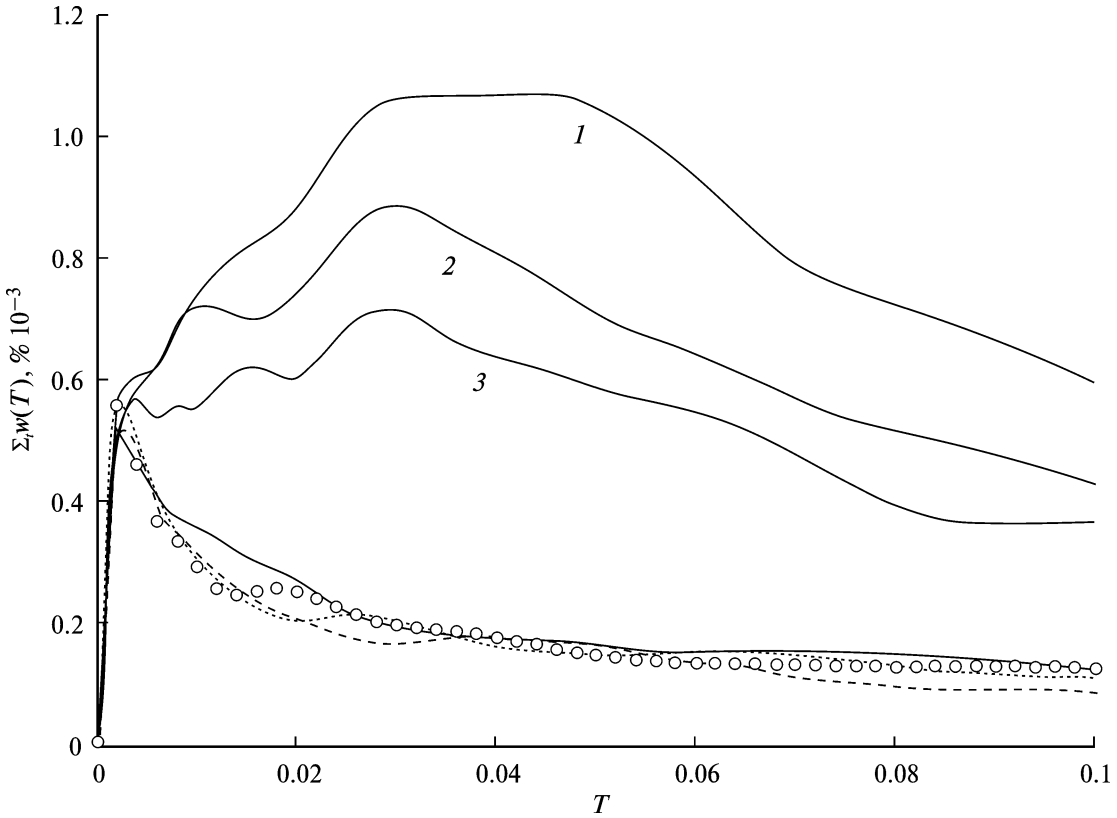

Fig. 2. Spectrum of main spike periods in the response of *Lymnaea stagnalis* eye to light stimulation. *Ordinate*: sum of all wavelet components with a fixed period; *abscissa*: main spike periods. *Solid grey enumerated lines*—spike spectrum in response to light flash in physiological solution, PS (*1*), experimental solution ES2 (*2*) and after return to PS (*3*). *Dotted lines and round-marker line* denote background signal spectra in the dark: *black dotted line*—signal spectrum in PS, *round-marker line*—same in ES2, *dotted grey line*—same after return to PS. *Black solid line*—"idle" electrode signal spectrum.

0.05 s. It should be pointed out that the spectral peak height corresponds to the relative signal amplitude, i.e. the higher the spectral peak, the more "apparent" the local signal.

Introduction of glucose into solutions. Changes in the osmotic pressure of the solutions caused by changes in their chemical repertoire were compensated by the addition of glucose. In all experiments, glucose introduced at concentrations up to 33 mM did not affect appreciably the parameters of electrical responses.

The effect of changes in Mg^{2+} and Ca^{2+} concentrations in the bath solution on light responses. In these experiments ($n = 6$), the solutions replaced one another in the following order: PS–ES1–ES2–PS. The removal of Ca^{2+} and simultaneous elevation of Mg^{2+} was applied to suppress the chemical mechanism of synaptic transmission. It was expected that if electrical signals of the considerable part of photoreceptors are transmitted to the central ganglia via chemical synapses on interneurons, then a disruption of this connection would be supposed to affect, first of all, spiking activity, leaving ERG almost intact. The glucose-added solution (ES1) was applied as a control of the possible effect of increased osmotic pressure on EGR.

The elevation of Mg^{2+} with simultaneous removal of Ca^{2+} had no unequivocal effect of the ERG amplitude. Only in two experiments, the ERG amplitude was observed to decline, while in other experiments it either remained intact or even rose. At the same time, light response was always accompanied by spiking, although its pattern changes appreciably. In the experiment presented in Fig. 3, the burst of spiking became longer, but the high-amplitude potentials disappeared, corresponding to a decrease (relative to the control)

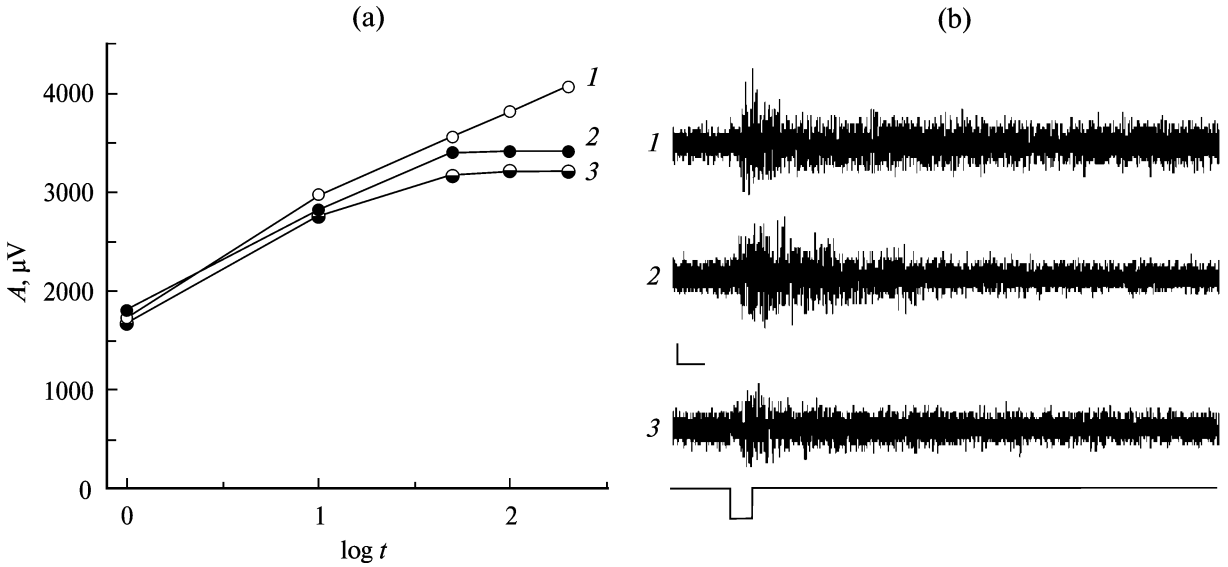

Fig. 3. Dependence of ERG amplitude on light stimulus duration, and records of spiking activity of the isolated *Lymnaea stagnalis* eye obtained in the experiment with Ca^{2+} removal and Mg^{2+} elevation up to 15 mM in the bath solution (ES2). (a) *Ordinate*: ERG amplitude (*A*, μV), *abscissa*: decimal algorithm of light flash duration in ms; (b) records of spiking activity to light flash with a duration of 400 ms. Numeration of graphs and records: *1*—physiological solution (PS), *2*—experimental solution ES2, *3*—return to PS. Calibration: 20 μV, 500 ms.

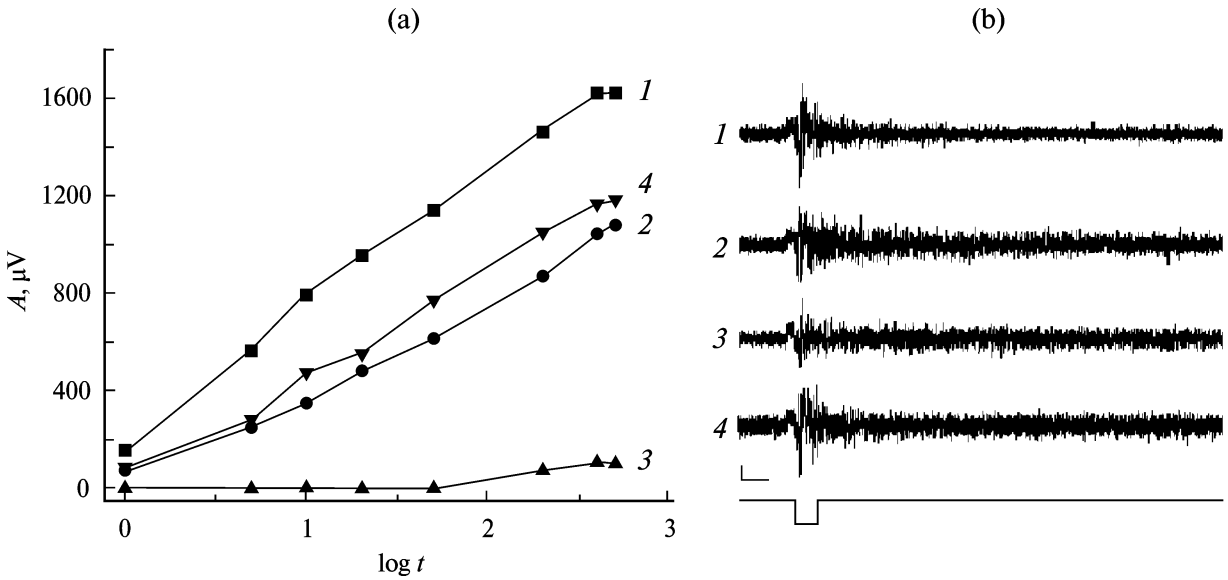

Fig. 4. Dependence of ERG amplitude on light stimulus duration, and records of spiking activity of the isolated *Lymnaea stagnalis* eye obtained in the experiment with Ca^{2+} and Mg^{2+} removal from the bath solution. (a) *Ordinate*: ERG amplitude (*A*, μV), *abscissa*: decimal algorithm of light flash duration in ms; (b) records of spiking activity to light flash with a duration of 400 ms. Numeration of graphs and records: *1*—physiological solution (PS), *2*—experimental solution ES3, *3*—return to PS. Calibration: 25 μV, 500 ms.

in the ERG amplitude for this stimulus duration (400 ms). The height of interspike intervals as well as the maximum of the characteristic period shifted relative to initial values, indicative of a change in the frequency pattern of spike discharges. Pattern deformations persisted, as a rule, after the reapplication of PS, reflecting the degree of incompleteness of the electrical response restoration in

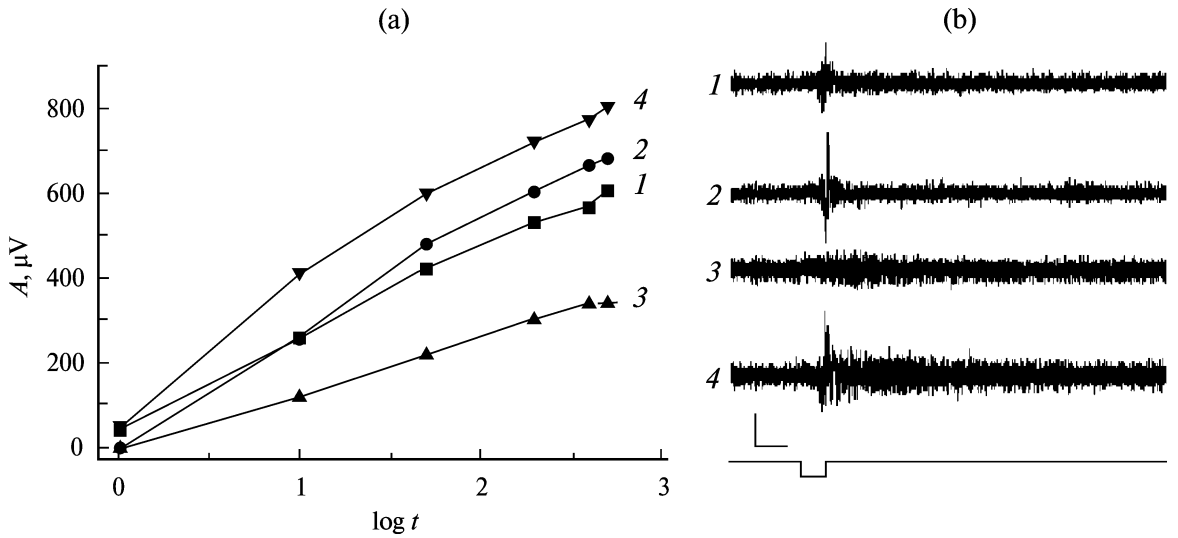

Fig. 5. Dependence of ERG amplitude on light stimulus duration, and records of spiking activity of the isolated *Lymnaea stagnalis* eye obtained in the experiment with increased Na^+ concentration (ES6) and introduction of 10 mM Mn^{2+} (ES7) in the bath solution. (a) *Ordinate*: ERG amplitude (*A*, μV), *abscissa*: decimal algorithm of light flash duration in ms; (b) records of spiking activity to light flash with a duration of 400 ms. Numeration of graphs and records: *1*—physiological solution (PS), *2*—experimental solution ES6, *3*—experimental solution ES7, *4*—return to PS. Calibration: 50 μV, 500 ms.

this particular experiment (Fig. 2).

The effect of Ca^{2+} and Mg^{2+} chelation of light responses. The major purpose of the EDTA-2Na^+ introduction was a complete removal of free Ca^{2+} from the solution. Since this reagent binds both Ca^{2+} and Mg^{2+}, both these cations were preliminarily removed from the solution, with a decrease in the osmotic pressure compensated by glucose. The solutions were changes in the following order: PS–ES3–ES4 (or ES5)–PS.

The removal of divalent cations from the solution (ES3) in all the experiments ($n = 6$) led to decrease the ERG amplitude and change the spiking pattern similar to what was observed in the solution with a high Mg^{2+} concentration (Fig. 4, record 2).

The introduction EDTA-2Na^+ at a concentration of 1 mM (ES4) led to a greater decrease in the ERG amplitude (up to 40–50% from that in PS). The elevation of the EDTA concentration up to 4 mM (ES5) resulted in an almost complete suppression of the ERG amplitude. At the same time, there was observed a slight decrease in the impulse response duration and amplitude of action potentials (Fig. 4, record 3). After the return to PS, the ERG amplitude and impulse response were largely restored in all cases.

The effect of Mn^{2+} on light responses (Fig. 5). This variant of experiments ($n = 5$) was carried out to supplement the previous data on the Mn^{2+}-induced suppression of optic nerve spiking [2] by observations of ERG changes. For this reason, the composition of the applied solution (ES7) was analogous to that in the above-mentioned study. Since the addition of Mn^{2+} was accompanied by a decrease in Na^+ and Ca^{2+} concentrations, this factor was also taken into account. The preliminary trial of the solution with decreased Na^+ and Ca^{2+} concentrations revealed a slight decrease in the ERG amplitude (about 10%). At the same time, an increase in the Na^+ concentration was accompanied by an increase in the ERG amplitude and spiking rate.

The introduction of 10 mM Mn^{2+} always led to a conspicuous decrease in ERG and the amplitude of action potentials in the spike component of the light response. At the same time, low-amplitude spikes could persist, and the duration of their discharge could even increase, as shown in Fig. 5. In some experiments, there was observed an almost complete suppression of the response. The return to PS was accompanied by an increase both in the ERG amplitude and spike component of the light response.

DISCUSSION

The single-layered retina in most gastropod molluscs studied contains hundreds and even thousands of photoreceptors [9]. In the retina of the same species, along with cells responding to light by a gradual receptor potential, there can be present cells generating spikes at the background of depolarization. This dualism of the light response was described in *Aplysia californica* [10], *Achatina fulica* [11], *Helix lucorum* [12], *Lymnaea stagnalis* [13].

Using intracellular dye injections, it was shown that photoreceptors in the retina of *A. californica* and *L. stagnalis* can direct its axons to the optic nerve without an interneuronal delay [10, 13]. Along with photoreceptors, neurons were found in the retina of these molluscs that could be involved in the signal transmission chain from photoreceptors to the central nervous system (CNS) [14, 15]. Thus, spiking activity recorded in the *L. stagnalis* optic nerve can result from activation both of photoreceptors themselves and interneurons. Quite obviously, it is difficult to make an unequivocal idea of the preferential pathway of visual signal transmission to the central ganglia based solely on intracellular staining. The *L. stagnalis* retina contains about 2,000 photoreceptors [9], and only one of them is known to form direct connections with statocyst neurons [16]. Practically nothing is known about the projections of other photoreceptors, although the possibility of their retrograde staining through the optic nerve may indicate the existence of direct neural pathways from the retina to cerebral ganglia [4].

We believe that the presence of chemical synapses on the way of visual signal transmission to central ganglia could be evidenced by the suppression of the spike component of the light response with simultaneous persistence of ERG waves. The use of solutions with increased Mg^{2+} concentration serves as a widespread tool to reduce vesicular endocytosis and suppress transmission in chemical synapses [17, 18]. At a concentration of 15 mM, Mg^{2+} suppresses neuromuscular transmission in *L. stagnalis* [19]. However, we failed in our experiments to attain detectable suppression of the spike component of the light response. Based on this result, we believe that at least a major part of photoreceptor cell axons in the pond snail are projected to the CNS directly, without a delay in chemical synapses on interneurons, Theoretically, of course, signal transmission via electric synapses cannot be ruled out completely. However, no morphological evidence for these contacts in the pond snail eye has been obtained so far.

The slight decrease in the maxima of spectral components of the optic nerve spiking in the "magnesium solution" as well as the change in its frequency spectrum could be interpreted as being indicative of the fact that a part of signals can still be transmitted to the CNS via chemical synapses. However, more plausible is the suggestion that the "magnesium" solution suppresses the performance of synaptic contacts that interlink A- and T-type photoreceptors [13]. It is quite imaginable that the disruption of the cell–cell interaction in the retina is a real reason of the observed changes in the spiking pattern.

The removal of Ca^{2+} and Mg^{2+} from the solution led only to a partial suppression of the ERG amplitude and some changes in the spiking pattern. These changes can result both from impaired chemical interactions between retinal photoreceptors and kinetic changes in receptor potentials. Specifically, intracellular recording showed that in a Ca^{2+}-free solution developmental kinetics of light-evoked depolarization in T-type photoreceptors that send their axons to the cerebral ganglion [13]. Suppression of electric signals is more pronounced in the EDTA-containing solution than in that deprived of divalent cations. The possible reason of this effect is a chelation of divalent cations, remaining in tissues after their mere removal from the solution.

Manganese ions are well known to efficiently suppress transmission in chemical synapses [20]. This is why their blocking effect on the spike component of the light response in *L. stagnalis* led to conclude that the light signal is transmitted from photoreceptors to relay interneurons [2]. However, since this effect is accompanied by suppression of ERG, its reason is, most likely, to be sought for in defects of photoreceptor depolarization in response to light. More reasonable interpretation of the effect of Mn^{2+} on phototransduction can hardly be offered now for want

of clear insight into the molecular mechanisms of this process in gastropod molluscs. As far as the change in the spiking pattern in the presence of Mn^{2+} is concerned, impaired chemical mechanisms of the interaction between photoreceptors can contribute to this effect.

CONCLUSION

Our studies of the effect of Ca^{2+}, Mg^{2+} and Mn^{2+} allow us to maintain that the electric response recorded in the *L. stagnalis* optic nerve in response to light is formed mainly by spiking activity of photoreceptors, whose axons travel to the cerebral ganglia directly, without a relay in chemical synapses on interneurons. At the same time, we suggest that interphotoreceptor contacts have a chemical mechanism of transmission. Apparently, these horizontal links provide synchronization of photoreceptor excitation during light stimulation. Suppression of all the response components after the introduction of Mn^{2+} to a solution appears to be due to impairments both of phototransduction and the interaction between photoreceptor cells.

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