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Bump Latency Distribution and Bump Adaptation of Limulus Ventral Nerve Photoreceptor in Varied Extracellular Calcium Concentrations*

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Abstract. 1) Bumps were recorded as voltage signals following dim flashes of light. Bump amplitude and width did not much depend upon external Ca^{2+}-concentration. However, the distribution of bump latencies was strongly shifted to longer latencies and broadened more than two-fold when the external Ca^{2+}-concentration was lowered from 10 mmol/l to 0.25 mmol/l. Raising the external Ca^{2+}-concentration to 40 mmol/l had the opposite effect. A preadapting light flash caused shortening and narrowing of bump latency distribution similar to the effect of raised external Ca^{2+}-concentration.

2) The bump amplitude is not correlated with the length of the latent period of the bump, indicating that the amplification processes determining the bump size are distinctly different from those which determine the latent period.

3) In a 10 s light/10 s dark cycle, a weak preadapting light flash slightly enlarges, a stronger flash diminishes the average bump amplitude (bump adaptation). The Calcium dependence of bump adaptation which was studied for external Ca^{2+}-concentrations ranging from < 1 nmol/l to 100 mmol/l is relatively weak: Lowering the external Ca^{2+}-concentration to < 1 nmol/l reduces, raising it to 40 mmol/l Ca^{2+} slightly intensifies the diminution of bump size due to light adaptation.

4) The average amplitude of the "light bumps" (recorded during the 10 s light period) is larger than that of the "dark bumps" (recording during the dark period), because the light-evoked bumps are on the average larger than the spontaneously generated bumps.

5) A preadapting light flash increases the rate both of light-evoked, and of spontaneous bumps.

Key words: Limulus photoreceptor – Bump latencies distribution – Bump amplitudes – Light adaptation – Extracellular calcium

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Introduction

A successful absorption of a photon by a rhodopsin molecule in the Limulus ventral nerve photoreceptor evokes a delayed transient conductance increase of the photosensory membrane, a bump. Bumps are the elementary excitatory events; they can be recorded as fluctuations of membrane current or voltage.

The bump latency, i.e., the delay between photon absorption and start of the bump, and the bump amplitude, both vary considerably under constant stimulus conditions. It was an aim of our study to determine whether these variations are correlated.

Light adaptation causes a reduction in bump amplitude and a slight increase in bump frequency. These effects differ in 10 and 40 mmol/l extracellular Ca^{2+}-concentration (Stieve and Bruns 1980). Bump light adaptation was now studied over a range of Ca^{2+}-concentrations between 1 nmol and 100 mmol.

Material and Methods

Bumps were recorded as membrane voltage signals with one intracellular electrode in a ventral nerve photoreceptor cell of Limulus. The method is described in detail by Stieve and Bruns (1980a).

Two types of stimulus conditions were adopted:

1) A dim 10 ms light flash, evoking in about 50% of the cases a bump within 1 s, was repeated every 10 s.

2) A 10 s weak "bump-evoking illumination", evoking a bump about every 1–2 s, was repeated every 20 s.

A 20 ms preadapting light flash, of which intensity was different in different series of measurements, could be presented 2 s before the bump-evoking illumination.

The light intensity I_0 ca. $32 \cdot 10^{12}$ photons $cm^{-2} \cdot s^{-1}$ (λ_{max} 543 ± 40 nm) was attenuated by neutral density filters.

Thus bump responses to identical bump-evoking stimuli of 10 ms or 10 s duration were recorded at different levels of adaptation. The ventral nerve was continuously superfused by salines the Ca^{2+}-concentration of which was varied. In each experiment only one type of test saline was used after reference responses had been measured with the same photoreceptor cell in the physiological, reference saline (Stieve and Bruns 1978). In the experiments in which test salines of lowered Ca^{2+}-concentrations were used, the calcium omitted in the test saline was replaced by sodium, in those with raised calcium concentration, a corresponding amount of sucrose was added to the reference saline to make its osmotic pressure equal to that of the test saline. The < 1 nmol/l Ca^{2+}-saline was prepared by the addition of 1 mmol/l EGTA in a saline without added calcium, but with 55 mmol/l magnesium. All experiments were performed at 15° C.

"Light bumps", the bumps recorded during the 10 s bump-evoking illumination, were evaluated separately from the "dark bumps" recorded during 5 s in the dark, the 13th–17th s of the cycle.

Bump amplitudes A and other bump parameters, latency T LAT, half time T1 of rise and half time T2 of decline were determined with the help of a computer program for all first bumps observed following the bump-evoking flash. For the determination of bump frequency *f* the times of the maxima of all bumps including "riders" (bumps riding on top of a foregoing bump) were used. Bumps with amplitudes $\geq 0.5-1.0$ mV could be recognized.

For Table 2 bump amplitudes and frequencies were determined by eye; in this case bumps > 0.5 mV could be detected. We do not know how many bumps we did not detect in the noise.

In Table 1 the values for the response parameters in each experiment are normalized to a reference value of the parameter obtained without preadaptation while the ventral nerve was superfused by physiological (reference) saline. These normalized values were then averaged for one group of experiments and the scale obtained by averaging all reference values for this parameter.

Results and Discussion

Several parameters of the first voltage bumps following a weak bump-evoking flash were determined for three different external Ca^{2+}-concentrations (0.25, 10, and 40 mmol/l; Table 1A). The average bump amplitude and the width of the bump, characterized by T1 and T2, show only minor changes when the external Ca^{2+}-concentration is altered. The most significant alteration due to changes in external Ca^{2+}-concentration, is observed in the distribution of bump latencies (Table 1A, Fig. 1). The asymmetrical, bell-shaped distribution which is similar to those described by Behbehani and Srebro (1974) can be characterized by the maximum (i.e., the most frequently observed latency) and the lower and the upper half width. The higher, the external Ca^{2+}-concentration becomes, the shorter, the most frequently observed latency and the narrower the latency distribution. Table 1A and Fig. 1 show, for example, that after lowering the external Ca^{2+}-concentration from 10 to 0.25 mmol/l the most frequently observed latency as well as the half width of the latency distribution are more than doubled. In contrast to this, the bump amplitude is not changed and the half width of the bump (T1 + T2) enlarged by only 25%.

Figure 2 shows plots of the bump amplitudes versus the corresponding bump latencies of the same data as Fig. 1. It can be seen that the two parameters are not correlated; at a given latency one finds bump amplitudes over the whole range of variation. This indicates that the processes determining the amplitude of the bump are distinctly different from those determining the length of the delay between photon absorption and starting point of the bump; for instance, the amplification determining the bump size is not a function of the length of the latency.

This observation is in concord with the observation of Wong et al. (1980, 1982) that the temperature dependence of bump latency is stronger than that of

Table 1. A Parameters of voltage bumps depending on the external Ca^{2+}-concentration. First voltage bumps recorded after flash as described in Fig. 1. n = number of experiments. Bump parameters: Amplitude A, latency T LAT, half time T1 of rise and half time T2 of decline. For T LAT, maximum (i.e., the most frequently observed latency), lower (−) und upper (+) half width of distribution is given, since the distribution of latencies is asymmetric. For the other parameters mean ± SEM is given; 15° C. **B** Parameters of linear summated voltage bumps following dim light flashes as in Fig. 3. In the same four experiments of Table 1 A all bumps following dim flashes repeated every 10 s were summed. The resulting curve was treated like a receptor potential, i.e., the parameters: Amplitude H MAX, latency T LAT, time to peak T MAX, half times T1 of rise and T2 of decline were determined. Mean ± SEM are listed. Average number of bumps summed per experiment; 10 mmol/l Ca^{2+}: 177 ± 73; 250 µmol/l Ca^{2+}: 116 ± 11. **A and B:** Values are normalized and scaled with respect to reference values (boldfaced).

A

$[Ca^{2+}]_{ex}$		250 µmol/l $n = 4$	10 mmol/l $n = 7$	40 mmol/l $n = 3$
A [mV]		7.4 ± 1.3	**7.4** ± 0.7	5.9 ± 1.4
T LAT [ms]	−	349 ± 69	109 ± 12	79 ± 15
	max	601 ± 93	**207** ± 20	152 ± 28
	+	365 ± 61	147 ± 23	64 ± 16
T1 [ms]		44 ± 0.4	**39** ± 8.2	39 ± 3.7
T2 [ms]		68 ± 4.3	**53** ± 6.9	71 ± 11

B

$[Ca^{2+}]_{ex}$	250 µmol/l $n = 4$	10 mmol/l $n = 4$
H MAX [mV] per 100 flashes	67 ± 26	**177** ± 34
T LAT [ms]	233 ± 66	**104** ± 21
T MAX [ms]	590 ± 56	**270** ± 17
T1 [ms]	157 ± 38	**60** ± 7
T2 [ms]	330 ± 93	**82** ± 5

bump amplitude (Q_{10} 4 resp. 2.5) and with the above mentioned observation that bump latency has a stronger calcium dependence than bump amplitude, and with the results of Howard (1982).

When voltage bumps of Limulus ventral nerve photoreceptors, evoked by dim flashes as described, are linearly summed, the shape of the resulting sum curve resembles a receptor potential (Fig. 3). Under the same condition as those applying for Figs. 1 and 2, and Table 1A, the determined parameters for such sum-curves of bumps recorded in physiological saline (10 mmol/l Ca^{2+}) are shown in Table 1B. Summation of voltage bumps from the same cells recorded in 250 µmol/l Ca^{2+} resulted in sum-curves with a much slower timescale (Fig. 3, Table 1B). Latency T LAT, time to peak T MAX and half time T1 of rise and T2 of decline of these sum-curves are much prolonged (see Stieve and Bruns 1981;

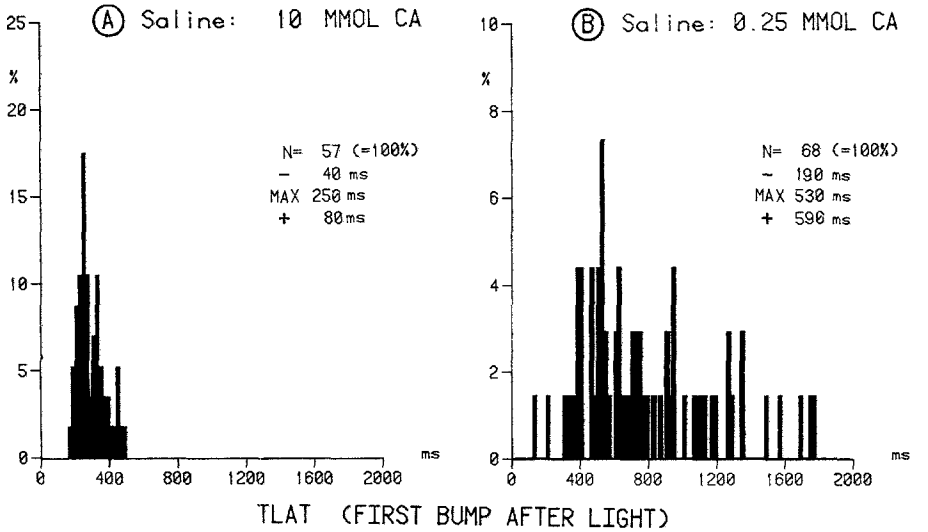


Fig. 1 A and B. Frequency distribution of latencies of first voltage bumps following a dim flash. The latent periods of the first voltage bumps (fluctuations of membrane voltage) following very dim 10 ms light flashes (λ_{max}543 nm; E corresponding to ca. 3×10^8 photons · cm^{-2}) were measured and their frequencies plotted. The frequency distribution is characterized by the maximum MAX (the most frequently observed latency) and by the lower and the upper half width – and +. **A** The photoreceptor was superfused by physiological saline containing 10 mmol/l Ca^{2+}. **B** Same experiment, but during this period the photoreceptor was superfused by a saline in which the calcium concentration was lowered to 250 µmol/l, 15° C. N number of first bumps; the number of stimulating light flashes was 200 (A and B), ca. every 2nd stimulus evoked one bump, JB 256 S

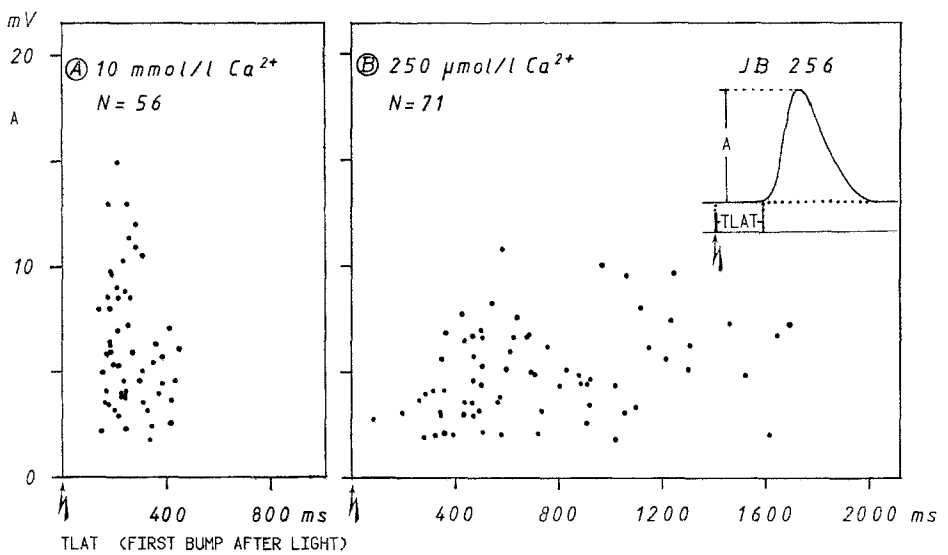


Fig. 2 A and B. Amplitude of first voltage bumps plotted versus their respective latencies in two different Ca^{2+}-concentrations. The first bumps following 10 ms dim flashes were recorded and their amplitudes and latencies plotted. Same experiment and same data as in Fig. 1. **A** Superfusate containing 10 mmol/l Ca^{2+}. **B** Superfusate containing 250 µmol/l Ca^{2+}

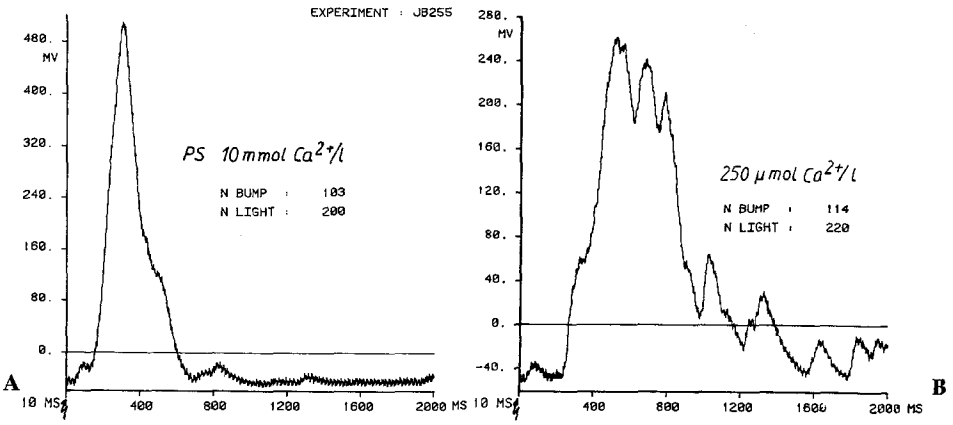


Fig. 3 A and B. Sum-signals resultant of linear summation of voltage bumps, recorded as fluctuations of membrane voltage of dark adapted Limulus ventral nerve photoreceptor. The bumps evoked by very dim 10-ms flashes were linearly summed by computer. The shape of the sum-signal resembles that of a receptor potential. **A** Sum-signal of bumps while the receptor was superfused by physiological, 10 mmol/l Ca^{2+} containing saline and **B** while superfused by a saline in which the Ca^{2+}-concentration was lowered to 250 µmol/l. N BUMP: number of individual bumps which were summed, N LIGHT: number of light stimuli. About every 2nd stimulus is followed by a bump

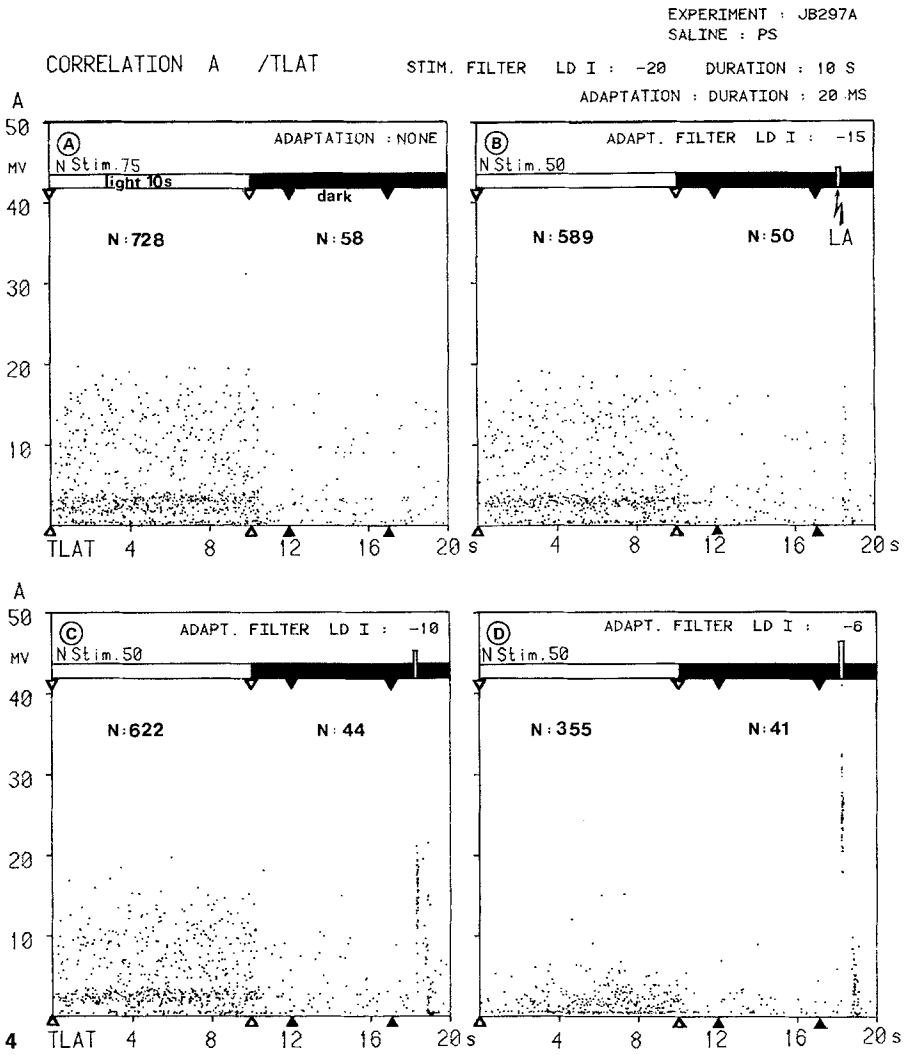
Stieve 1983). These values and their changes due to lowerling of Calcium (except for the response amplitude) are quantitatively similar to those of the receptor potential evoked by much stronger stimuli in consequence of lowering the external Ca^{2+}-concentration.

Light adaptation due to a preadapting light flash, preceding the bump-evoking flash by 2 s, causes a diminution of the average bump amplitude and a

Fig. 4 A–D. Distribution of amplitudes of voltage bumps in the 20 s cycle, consisting of 10 s bump-evoking illumination and 10 s darkness. Individual bump amplitudes are plotted at the cycles time at which the peak of the bump was observed. **A** Dark adapted; **B–D** 2 s before the bump-evoking illumination (18th s of the cycle) a conditioning, light-adapting flash was administered; this had increasing strength from the series B to D. Only single or forrunning bumps (no riding bumps) were plotted. Average bump amplitude $\bar{A}$ of light bumps (recorded during the 10 s bump-evoking illumination) and average bump frequency $\bar{f}$ (including riders) and the corresponding values of dark bumps (recorded during the 13th and 17th s of the cycle) were:

	$\bar{f}$ [s^{-1}]		$\bar{A}$ [mV]	
	Light	Dark	Light	Dark
A	1.06	0.16	5.7 ± 0.2	5.1 ± 0.6
B	1.31	0.20	5.5 ± 0.2	4.3 ± 0.6
C	1.43	0.18	4.8 ± 0.2	3.9 ± 0.5
D	0.82	0.16	3.5 ± 0.1	1.8 ± 0.3

Light intensity I_0 corresponds to 32×10^{12} photons $cm^{-2} \cdot s^{-1}$ at 543 nm. **A** 75 cycles; **B–D** 50 cycles. In **B–D** the response to the preadapting flash is seen in the 18th s. The "church-shaped" frequency distribution of bump amplitudes (described in detail in Stieve and Bruns 1980) can be obtained by projecting the number of points on the ordinate



shortening of the most frequently observed bump latency and a narrowing of the frequency distribution of bump latencies (Stieve and Klomfaß, unpublished); for instance, the bump latency distribution of a dark adapted photoreceptor in physiological saline was characterized by the values 150, +30, −50 ms, which was shortened due to moderate light adapting flashes to 110, +30, −20 ms. This shortening and narrowing of the bump latency distribution does not depend much upon external Ca^{2+}-concentration: In 250 µmol/l Ca^{2+}-concentration the dark adapted value of the same cell was 250, +60, −60 ms, and light adapting flashes, identical to those applied in the reference conditions, caused a shortening to 180, +90, −60 ms. The maximal observed latency is in both cases shortened by the same proportion due to the same light adaptation.

In former publications (Stieve and Bruns 1980b; Stieve 1981) we have shown that the light adaptation of the receptor potential of the Limulus ventral nerve

photoreceptor strongly depends upon external Ca^{2+}-concentration. The simplest assumption is that external Ca^{2+}-concentration determines the magnitude of the light-induced increase in intracellular Ca^{2+}-concentration (Lisman and Brown 1975; Fein and Charlton 1977; Maaz and Stieve 1980), which causes a reduction in bump size in accordance with the adapting bump model proposed by Adolph (1964) and Dodge et al. (1968). In another publication we have studied the diminution of bump size due to moderate light adaptation for two different external Ca^{2+}-concentrations (Stieve and Bruns 1980a). The Calcium dependence of the effect of light adaptation on bump size (bump adaptation) has now been studied over a wider range of Ca^{2+}-concentrations, between 1 nmol/l and 100 mmol/l.

A 10 s light/10 s dark cycle was used. Figure 4 shows an example for the basic findings in physiological saline. The distribution of bump amplitudes and their frequencies is virtually uniform during the 10 s of the bump-evoking illumination (light bumps) and slightly smaller but also uniform during the 13th and 17th s of the cycle in which the dark bumps were collected with no or moderate light adaptation (Figs. 4A–C). This indicates that under these conditions the state of adaptation is quite constant during the 20 s of the cycle. However, when the strongest light adaptation was applied (Fig. 4D), the distribution became time dependent: more and larger bumps are found in the 5th–10th s of the cycle.

Table 2 shows the evaluation of 18 experiments of this kind with different Ca^{2+}-concentrations. In concord with our expectations it can be seen in Fig. 4 and in Table 2 that, while the photoreceptor is superfused by physiological (reference) saline containing 10 mmol/l Ca^{2+}, a relatively strong preadapting light flash causes a diminution of the amplitudes of both light and dark bumps. The effect of external Ca^{2+}-concentration on bump adaptation is remarkably weak under the experimental conditions reported here: Raising the external Ca^{2+}-concentration to 40 mmol/l causes, as already reported (Stieve and Bruns 1980), a slightly stronger diminution of bump size due to light adaptation. Lowering the external Ca^{2+}-concentration to 1 nmol/l results in a reduction in the diminution of bump amplitude due to stronger light adaptation (see also Stieve 1983, Fig. 12) in contrast to the effect of lowering the external Ca^{2+}-concentration to 250 μmol/l.

Besides the reduction in bump size due to light adaptation some other effects could be observed in these experiments (Table 2):

1) The dark bumps, recorded in the 13th–17th s of the cycle, are on the average smaller than the light bumps, recorded during the 10 s bump-evoking illumination. This has already been shown by Yeandle and Spiegler (1973) for voltage bumps and by other experiments of ours for voltage and current bumps recorded under voltage clamp conditions (Stieve, Klomfaß and Bruns, unpublished). Dark bumps are spontaneously generated; the observed light bumps are a mixture of many light-evoked bumps and fewer spontaneously generated bumps. The amplitude distributions of spontaneously generated and of light-evoked bumps overlap.

2) Light adaptation causes an increase in bump rate of both light and dark bumps. The rise in (spontaneous) dark bump frequency is too small to account

Table 2. Dependence of frequency f and amplitude A of voltage bumps upon adaptation and external Ca^{2+}-concentration. Experiments as described in Fig. 4, each consisting of one series in 10 mmol/l Ca^{2+}-containing physiological (reference) saline and one series in a test saline the Ca^{2+}-concentration of which was varied. The absolute strength of the pre-adapting flash varied slightly from experiment to experiment, each of which had at least four different series. The "weak" and "strong" pre-adapting flash intensity were selected as to obtain corresponding data. In all cases light adaptation was moderate in order to allow measurement of bump amplitudes. $\bar{A}$: average bump amplitude, $\bar{f}$: average bump rate, Mean ± SEM

$[Ca^{2+}]_{ex}$	Adaptation	$\bar{f}\,s^{-1}$		$\bar{A}$ [mV]	
		Light	Dark	Light	Dark
< 1 nmol	No	0.29 ± 0.14	0.11 ± 0.06	4.6 ± 0.9	3.6 ± 1.5
$n = 6$	Weak	0.30 ± 0.13	0.12 ± 0.06	5.2 ± 1.2	6.1 ± 2.2
	Strong	0.42 ± 0.01	0.14 ± 0.08	3.5 ± 1.9	1.8 ± 0.4
250 µmol	No	0.63 ± 0.16	0.29 ± 0.21	5.0 ± 2.0	3.6 ± 2.3
$n = 4$	Weak	0.58 ± 0.17	0.25 ± 0.19	3.4 ± 0.7	2.2 ± 0.9
	Strong	0.65 ± 0.36	0.43 ± 0.33	0.8 ± 0.1	0.7 ± 0.2
10 mmol	No	0.57 ± 0.06	0.13 ± 0.04	4.9 ± 0.8	2.7 ± 0.5
$n = 18$	Weak	0.65 ± 0.08	0.14 ± 0.04	5.4 ± 0.7	3.4 ± 0.6
	Strong	0.63 ± 0.09	0.21 ± 0.06	2.0 ± 0.4	1.6 ± 0.3
40 mmol	No	1.06 ± 0.11	0.39 ± 0.08	5.1 ± 1.4	2.8 ± 0.8
$n = 5$	Weak	1.11 ± 0.17	0.45 ± 0.13	5.1 ± 1.1	2.5 ± 0.6
	Strong	0.81 ± 0.15	0.36 ± 0.11	1.4 ± 0.3	1.2 ± 0.3
100 mmol	No	0.47 ± 0.19	0.12 ± 0.08	2.8 ± 0.9	1.2 ± 0.3
$n = 3$	Weak	0.66 ± 0.19	0.13 ± 0.06	4.5 ± 1.0	2.7 ± 0.3
	Strong	0.25 ± 0.08	0.22 ± 0.08	1.2 ± 0.1	0.9 ± 0.1

for the increase in light bump frequency (see also Stieve and Bruns 1980). Preadaptation apparently raises the probability for both light evoked and spontaneous bumps.

3) Besides the increase in bump frequency, weak light adaptation can cause an increase in amplitude of light and dark bumps (facilitation).

These two effects (2 and 3) do not show a systematic Ca^{2+}-dependence and are observed independently from each other and more pronounced in some individual experiments than in others.

Concluding Remarks

1) It is well known that lowering the external Ca^{2+}-concentration greatly changes the shape of the receptor potential of Limulus ventral nerve photoreceptor; it causes mainly a retardation of the decline of the light response (e.g., Stieve 1973, 1981; Lisman and Brown 1975). Our results indicate that this is not caused by changes in the shape of the bumps which build up the receptor potential, but primarily by the strong broadening of the distribution of bump latencies (Stieve and Bruns 1981).

2) Light adaptation, when strong enough, always causes a diminution of bump size in accordance with the adapting bump model (Adolph 1964; Dodge et al. 1968). This "bump adaptation" depends only very little upon extracellular Ca^{2+}-concentration under the experimental conditions applied here (weak light adaptation).

In other experiments of ours (Maaz et al. 1981; Nagy and Stieve 1982; Claßen-Linke and Stieve 1981) we found two phases of recovery of the light response after a strong light adapting flash (which may be identical with the two phases described by Srebro and Behbehani 1974); only the first phase showed a significant dependence upon external Ca^{2+}-concentration and a correlation with the level of intracellular Ca^{2+}-concentration. From these experiments we concluded that there are at least two mechanisms in Limulus ventral nerve photoreceptors responsible for gain control in adaptation (Stieve 1982):

a) The reduction of bump size via a transient increase in intracellular Ca^{2+}-concentration.

b) An additional gain controlling mechanism which is not (or at least not very) calcium dependent. We assume that this second mechanism –which is observed, when the photoreceptor is already fairly dark adapted – governs adaptation when the intracellular Ca^{2+}-concentration is low.

In the experiments reported here we applied only weak light adaptation (including those adaptations which are termed "strong" in Table 2) in order to measure the size of individual bumps. Therefore we conclude that we investigated here mainly that (second) adaptation mechanism, which does not show a pronounced Calcium dependency.

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