Acta Biologica Szeged *18* (1—4), pp. 241—252 (1972)

SPONTANEOUS ELECTRICAL ACTIVITY OF THE HELIX HEART: DIFFERENT CHANGES OF THE ATRIAL AND VENTRICULAR ELECTROCARDIOGRAMS AS A RESULT OF VARIOUS EFFECTS

L. ERDÉLYI

Department of Animal Physiology, Attila József University, Szeged

(Received November 30, 1971)

The isolated atrium and ventricle of the *Helix* heart are each able to function separately, that is they possess the ability to generate independent spontaneous electrical activity. In spite of this the literature data to date refer to the description of the ECG of only the whole heart and to the observed variations of this under different experimental conditions (EVANS, 1912; ARVANITAKI and CARDOT, 1933; SMIRNOV and TURPAYEV, 1948).

More recent experiments carried out with suction electrodes and microelectrodes were limited mainly only to the isolated ventricle, or to the study of the action potential of the in situ heart (KISS, and S.-RÓZSA, 1971; S.-RÓZSA and VERÓ, 1971).

The present paper presents results obtained on the basis of the different effects exerted on the generation of the atrial and ventricular action potentials by various ions and drugs.

Materials and Methods

Recording of the spontaneous electrical activity: In one of the experimental series the action potentials were led off from the isolated atrium and ventricle of the *Helix* herat. In the other series the lead-off was from the atrial end of the isolated whole heart. In all cases the lead-off was unipolar and extracellular. The lead-off electrodes were Ag/AgCl non-polarizable electrodes. A DISA Universal Indicator DC amplifier was used to observe the biopotentials, and the photographs were taken with a COSSOR camera. The different electrode was always attached to the appropriate heart-part (pulmonary vein or aorta), while the indifferent electrode was immersed in the bath-fluid and was connected to a common earth point. During the lead-off the intact hearts and heart-parts were stretched with a 0.5 g weight (isolated ventricle or whole heart) or with a 0.1 g weight (isolated atrium) at the end opposite to the electrode. During the recording the hearts or heart-parts were raised a little above the liquid level at the attachment of the electrode.

Materials: After preparation the isolated hearts or heart-parts were made to function for 20 minutes in physiological solution (at 20—22 °C, under oxygenated conditions), and the effects of various ions and drugs were then investigated.

The effect of the barium ion was examined, partly independently in a physiological solution of defective composition (112.4 mM NaCl, 4 mM $BaCl_2$), and partly after pretreatment with the studied drugs, but always in an identical dose and in a solution of the given composition.

The effect of the lanthanum ion was studied only independently, in the following solution: 114.4 mM NaCl, 2 mM $LaCl_3$.

The following drugs were examined in physiological solution: ouabain (10^{-4} M), cocaine-HCl (10^{-3} M), procaine-HCl (10^{-3} M) and tetraethylammonium iodide (TEA—I) (10^{-3} M).

The *Helix pomatia* L. hearts used in the studies were prepared from active animals collected during the summer and early autumn.

Results

In all lead-offs, monophase action potentials were recorded, similarly to those reported by HILL and IRISAWA (1967) for the *Rapana* heart, and to those obtained with suction electrodes by S.-RÓZSA and VERÓ (1971) for the in situ *Helix* heart.

In the case of the isolated atrium the lead-off was from the pulmonary vein and the heart was stretched with a 0.1 g weight. The atrium and the atrio-ventricular junction were intact, and the weight was attached to a small ventricular piece cut into the atrium. The fixing of the lead-off electrode was similarly assisted by a small piece of tissue cut into the pulmonary vein. The action potentials obtained are shown in Plate I, Figure 1. The protracted, slow depolarization is striking in the appearance of the action potential; this attains the level of the peak potential only in several steps. Meanwhile, the slow depolarization increases up to 1—2 mV, and the spike amplitude maximum to 5 mV. At 20 °C the total duration of the spike potential is 2—3 sec.

Characteristic pacemaker potentials of completely uniform appearance can be led off from the aortic ends of the isolated whole heart and the isolated ventricle. The pacemaker nature of this region is dealt with in the review by KRIJGSMAN and DIVARIS (1955). The action potentials obtained are shown in Plate I, Figures 2 and 3, recorded at two different film-speeds. The prepotential, the spike and the repolarization stage on the action potentials exhibit completely regular appearances. The duration of the spike potential was found to be 1 sec (20 °C), while the depolarization of the prepotential was 2—4 mV, and the amplitude of the peak potential was 12—20 mV.

If the lead-off is performed from the atrial end (pulmonary vein) of the isolated whole heart, then, depending on how high the heart is raised above the fluid level, recordings can be made of the atrial action potentials, or of the ventricular and atrial action potentials together. This is shown in Plate I, Figures 4—7. In Figure 4 only the atrial action potential can be seen, since the lead-off here was performed on the atrium just as it left the solution. If the preparation is lifted above the liquid level to the height of the atrio-ventricular junction, then the more rapid ventricular action potentials are superimposed on the atrial action potentials (Figure 5). If the raising is continued further, then the size and width of the ventricular action potentials increase, while the size of the atrial action potential decreases somewhat. If a ligature is placed on the lower third of the ventricle, the ventricular action potential becomes split and appears as shown in Figure 6, but the atrial action potential does not change substantially. If the atrium is isolated completely from the ventricle by a new ligature on the atrio-ventricular junction, again only the atrial action potentials

are apparent (Figure 7). Thus, this lead-off method also provides a possibility for the observation of the joint changes of the two potentials.

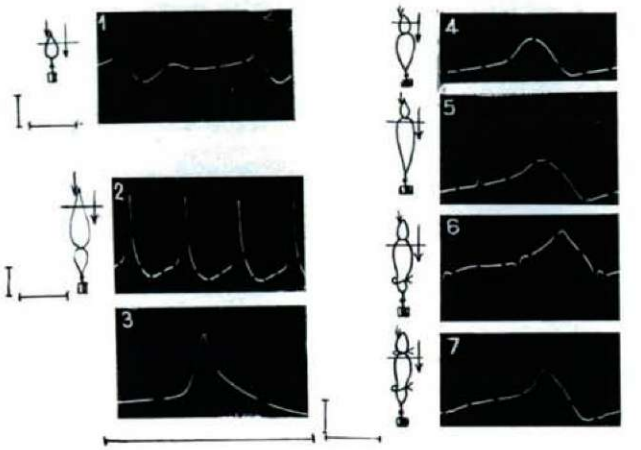

Plate I. 1. Spontaneous action potential of the isolated atrium.
2 and 3. Spontaneous pacemaker potential of the ventricle recorded at two different film speeds, 145 sec/m and 33 sec/m.
4. Atrial ECG on a photograph prepared from the atrial end of the isolated whole heart.
5. Atrial and ventricular action potentials in a common lead-off.
6. Change observed after ligation of the lower third of the ventricle. The ventricular action potential changes its course, becomes split and is synchronized.
7. A new ligature on the atrio-ventricular junction completely separates the ventricular potentials.
Calibration: 1.: 1 mV, 1 sec; 2., 3.: 5 mV, 1 sec; 4.—7.: 2 mV, 1 sec.

On the basis of lead-offs prepared from the hearts of many individual snails it proved possible to establish that under isolated conditions the snail-hearts function in three types of rhythm. The term „synchronized rhythm" can be applied in the case of those hearts in which the two significant phenomena (atrial and ventricular action potenial generation) always appear simultaneously. Plate II, Figure 1 shows the rhythm pattern of a heart functioning in synchronization, where the atrial and ventricular action potentials are formed simultaneously in a 1 : 1 ratio. The characteristic of a heart with „harmonized rhythm" is that a definite period (T_1) for one of the related phenomena corresponds to a certain number of periods (T_2) for the other phenomenon. Plate II, Figure 2 was prepared from a heart functioning in harmonized rhythm. The atrial and ventricular action potential generation ratios here were 1 : 2 and 1 : 3, but only every fifth atrial action potential is repeated with an identical ventricular potential pattern. Finally, Plate II, Figure 3 shows an „asynchronized rhythm" pattern. Here no regularly repeating or coinciding periods can be recognized at all in the appearances of the atrial and ventricular action potentials.

Following this, experiments were carried out both on isolated heart-parts and on the whole heart by the joint study of the two types of action potential.

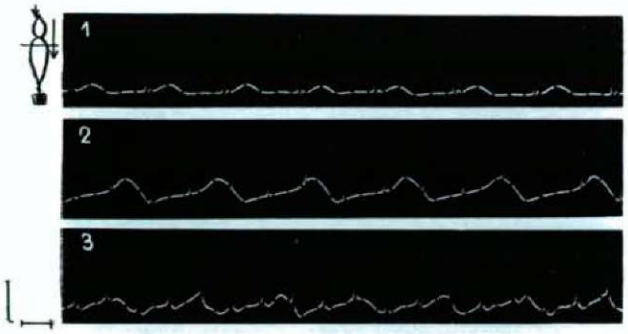

Plate II, Rhythm patterns in a lead-off prepared from the atrium of the whole heart. The prominent spikes correspond to the ventricular action potentials.

1. ECG of a heart functioning in synchronized rhythm by repeating ventricular and atrial action potential generation.
2. ECG of a heart functioning in harmonized rhythm. Every fifth atrial action potential repeats with the same ventricular potential pattern.
3. ECG of a heart funcioning desynchronizedly.

Calibration: 5 mV, 1 sec.

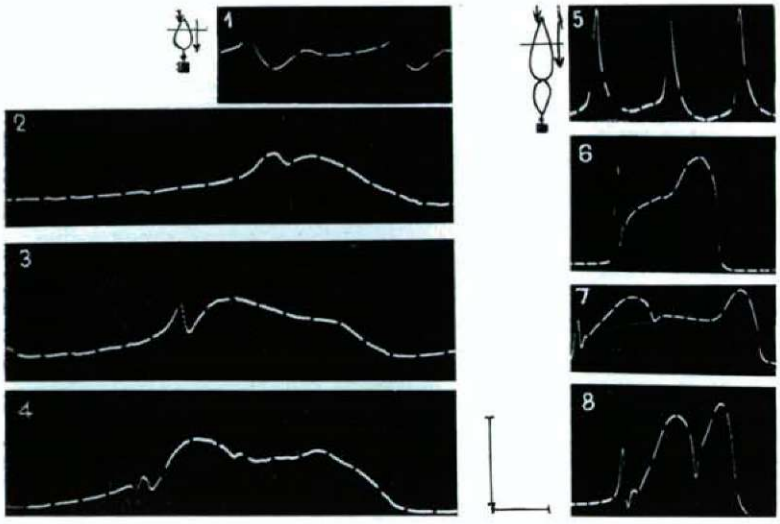

Plate III, Effect of 4 mM $BaCl_2$ on atrial and ventricular action potentials.

1. Control prepared from the isolated atrium in physiological solution.
2—4. Changes of the atrial action potential on the action of the barium ion in the 3rd, 6th and 9th minutes.
5. Control prepared from the ventricular potentials in physiological solution.
6—8. Changes of the ventricular action potentials on the action of the barium ion in the 3rd, 6th and 9th minutes.

Calibration: 1.—4.: 2 mV, 1 sec; 5.—8.: 10 mV, 1 sec.

Plate III, Figures 1—8 show the changes of the atrial and the ventricular action potentials on the action of 4 mM $BaCl_2$. It can readily be seen from the Figures that the barium ion increases the duration of the spike potential for both action potentials, while it decreases the peak potential, and generates a strongly negative after-potential or after-potential series. At the same time, the effects of the barium ion on the slow depolarization stages of the two action potentials differ strikingly. In a barium-containing medium the prepotential of the ventricular action potential does not appear, but the slow depolarization of the atrial action potential does not change substantially. A further conspicuous difference can be seen in Plate IV, Figures 1—4, where the two types of action potential were recorded in a common lead-off from the pulmonary vein of an isolated whole heart. Figure 1 shows the control action potentials in physiological solution. Figures 2, 3 and 4 depict the effects of 4 mM $BaCl_2$ in the 3rd, 6th and 9th minutes, respectively. The individual action potentials in the Figures compare well in form with the action potentials to be seen in Plate III. It is striking that as a result of the barium treatment the frequencies of the ventricular action potentials (the larger prominent potentials in the Figure), which are otherwise generated at a much faster rate, are strongly decreased, while the generation of the atrial action potential is slowed down to only an extremely small extent. In the end, therefore, a reversal ensues. The originally slower atrial action potential generation becomes the faster as a result of the effect of the barium.

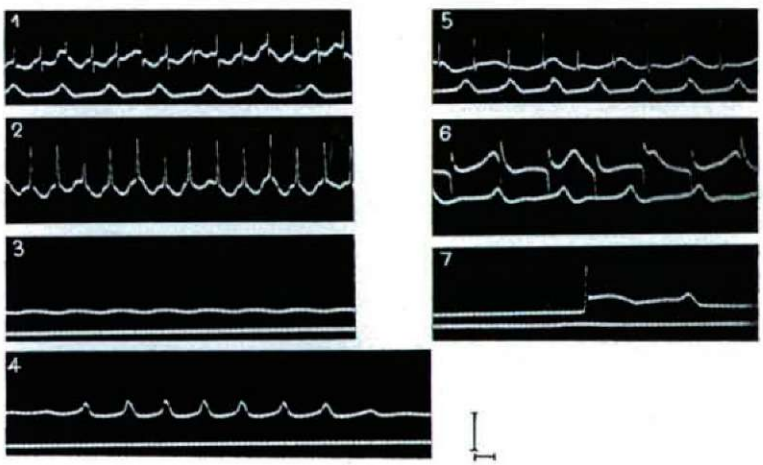

Plate IV. Effects of barium and lanthanum ions on the atrial and the ventricular action potentials.

1. Control prepared in physiological solution. The two types of action potential appear in a common lead-off.

2—4. Effects of 4 mM $BaCl_2$ on the atrial and ventricular action potentials in a joint lead-off in the 4th, 8th and 15th minutes.

5. Control prepared in physiological solution.

6 and 7. Effects of 2 mM $LaCl_3$ in the 4th and 8th minutes, leading to the suspension of the ventricular action potential generation.

Calibration: 5 mV, 1 sec.

The other ion studied was lanthanum. Plate IV, Figures 5—7 show the effects of 2 mM $LaCl_3$ on the two action potentials. The control action potentials are seen here too, in Figure 5, while Figures 6 and 7 show the changes due to the lanthanum ion which occur in the 4th and 8th minutes, respectively. The striking change here is the blocking of the ventricular action potential generation, while the atrial action potential generation remains practically completely unchanged in the lanthanum-containing medium. The potential-change to be seen in the Figures can not be regarded as a specific effect of the lanthanum ion, because it can also be observed sometimes after the ligation of a part of the ventricle and in potentials led off in physiological solution. It appears from these investigations that together with the lead-off methods described the lanthanum ion too is suitable for the distinguishing of the two types of action potential.

In more recent experiments a study was made of the effects of the cardiac glycoside ouabain, the local anaesthetics cocaine and procaine, and TEA—I which blocks the K-channels; these were used either independently, or in conjunction with the barium ion.

Plate V, Figures 1—4 show recordings obtained after pretreatment with ouabain. Figure 1 gives the control here. The lower recording in the Figure depicts the atrial potentials, and the upper one the common atrio-ventricular lead-off. Figure 2 is a recording prepared in the first minute of the effect of 10^{-4} M ouabain; the atrial and ventricular action potentials can be seen in a common lead-off. Figure 3 shows that 10^{-4} M ouabain totally suspends the atrial action

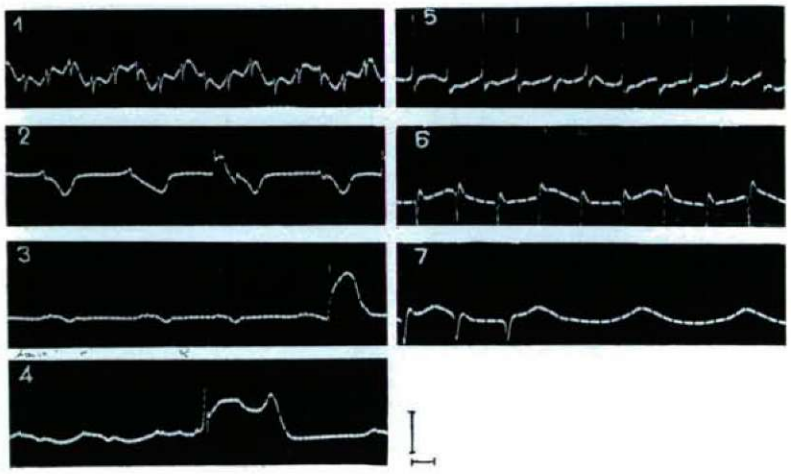

Plate V. Effects of ouabain (10^{-4} M) and cocaine-HCl (10^{-3} M) on the atrial and ventricular action potential formations.

1 and 5. Controls prepared in physiological solution. Upper recording: atrial and ventricular potentials in a common lead-off. Lower recording: atrial action potentials.

2 and 3. Effects of ouabain in the 1st and 10th minutes.

4. A rhythmic potential series is generated from the 4th minute in the ventricle on the action of 4 mM $BaCl_2$ after ouabain pretreatment.

6. Change observed in the 8th minute on the action of 10^{-3} M cocaine-HCl.

7. The atrial action potential formation is completely eliminated on the action of 4 mM $BaCl_2$ following cocaine pretreatment (lower recording).

Calibration: 5 mV, 1 sec.

potential generation (lower line) from the 10th minute, and the ventricular one too is reduced almost to zero. Figure 4 shows the effect of 4 mM $BaCl_2$ following the exchange of the ouabain medium in the 4th minute. It can be well seen that the complete inhibition of the atrial action potentials further continues even under such conditions. In the ventricle, on the other hand, similarly to the results described by SPERELAKIS and LEHMKUHL (1968) for chicken embryo myocardial cells kept in tissue culture, a series of rhythmic action potentials consisting of 8—10 individual potentials is generated on the action of the barium ion. The barium potentials after the ouabain pretreatment differ essentially in form from that produced by the action of the barium ion alone. The absence of the after-potential and the presence of the prepotential are apparent in the excited action potentials in question. At the same time, the duration of the spike potential is also smaller, and the size of the peak potential too is decreased.

The heart did not prove very sensitive to cocaine applied in a concentration of 10^{-3} M. Plate V, Figures 5—7 show the observed changes, Figure 5 being the control. The atrial and the atrio-ventricular action potentials are each depicted separately. Figure 6 shows the effect of cocaine in the 8th minute, as a result of which the cells have not substantially lost their sensitivity and potential generation. Figure 7 shows the effect of 4 mM $BaCl_2$ in the 8th minute. It can readily be seen from the Figure that the atrial action potential generation does not occur on barium treatment, while the ventricular action potential exhibits a regular appearance. The duration of the spike potential may perhaps be a little longer, and the size of the after-potential may be less than when the barium ion acts without a cocaine pretreatment. Cocaine in the applied concentration, combined with the $BaCl_2$ treatment, likewise proved suitable for the confirmation of the different susceptibilities of the two heart-parts.

TEA—I in the applied concentration of 10^{-3} M proved to be very effective towards snail hearts. These changes are depicted in the Figures of Plate VI. Figure 1 shows the usual control lead-offs. Figure 2 gives the effect of 10^{-3} M TEA—I in the 5th minute. The action potentials can be seen in the Figure in a common lead-off, in such a way that the consecutive stages of the continuous recording are photographed one under the other. It can be well seen that the original rhythm pattern changes on the action of the TEA—I, and the individual ventricular action potentials too are modified. The changes are repeated with a certain regular periodicity. This can be seen from a comparison of the two stages photographed one under the other. If, as a result of the repeating succession in the regular changes, the original signal is considered to be oscillating, then according to the irregularly repeating stages the new signal has become fluctuating. Figure 3 shows the atrial action potentials ,and reflects the fact that the change in this initial stage affects primarily the ventricular action potentials. Later, however, the atrial action potential generation too is modified. This can be seen in the photographs prepared in the 10th minute (Figure 4), wehere the synchronization of the spike generation can be observed in a slow ventricular rhythm. The atrial-ventricular action potential generation ratio is 2 : 1. The ventricular action potentials always appear at the end of the second atrial potential. On the action of 4 mM $BaCl_2$, from the 6th minute the atrial action potential generation can be observed with a strongly decreasing amplitude, but there is no striking change in the rhythm. The ventricular action potentials, on the other hand, very striking and known

action potential forms are obtained (Figure 5), which are quite characteristic of the vertebrate myocardium. This means that the original pacemaker potentials can be transformed by TEA—I treatment and subsequent barium ion treatment into the action potential form characteristic of the vertebrate mechanical heart musculature.

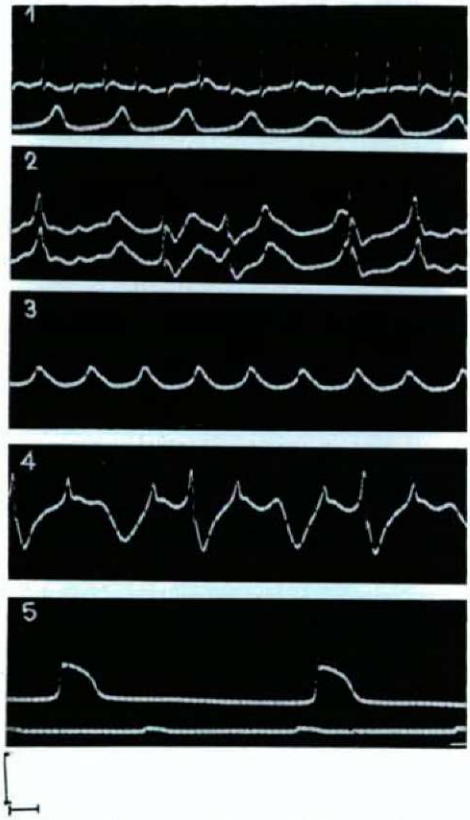

Plate VI. Effect of 10^{-3} M TEA—I on the action potential formation.

1. Control prepared in physiological solution. Upper recording: the action potentials in a common lead-off. Lower recording: atrial action potentials.
2. Change in the 5th minute on the action of 10^{-3} M TEA—I. Two consecutive stages of the recording are shown one under the other.
3. Up to the 5th minute the atrial action potentials are little changed.
4. Effect of 10^{-3} M TEA—I in the 10th minute. In the heart with synchronized rhythm the ventricular action potentials always appear at the end of the second atrial action potential.
5. From the 6th minute during the after-treatment with 4 mM $BaCl_2$ the characteristic formation of potentials reminiscent of action potentials of the vertebrate myocardium can be observed.

Calibration: 5 mV, 1 sec.

The effect of procaine applied in a concentration of 10^{-3} M is very similar to that of TEA—I. In spite of this, the same changes could not be produced in the form of the action potential with the barium treatment, as those following

the TEA—I pretreatment, and this indicates the specificity of the phenomenon. After procaine pretreatment the full after-potential generating ability of the barium ion always remains.

Discussion of the results

The heart of the edible snail generates two types of action potential. The spontaneous activity of the ventricle is maintained by true pacemaker potentials, and that of the atrium by somewhat modified pacemaker potentials. Our experiments reveal that the different changes of the two types of action potential on the action of various ions and drugs are very striking. From this point of view the effect of the barium ion, which had already been studied earlier (ERDÉLYI, 1971), is primarily considered to be of importance; this was now studied partly independently, and partly in conjunction with various drugs possessing a membrane-effect.

One of the reasons why the barium ion is worthy of attention and has been extensively studied is that some of its physical constants, for example the radius of the non-hydrated ion (1.35 Å), are very close to those of the potassium ion (1.33 Å). In addition, its chemical properties, such as its bonding to oxygen ligands and its coordination number of 8, make it similar to the Ca ion. Indeed, it is a physiological fact that some of the known and general effects of the barium ion have been related with K- or Ca-dependent processes. Among these, its effects increasing the duration of the action potential and delaying the repolarization in the atrial and ventricular action potentials of the edible snail heart are very striking. In their experiments on chicken embryo myocardial cells among others, SPERELAKIS and LEHMKUHL (1968) succeeded in connecting this property with the effect of the barium ion in decreasing the K-conductivity (g_k). It is probable that an essentially similar effect also takes place, on the basis of the same mechanism, in the snail heart.

Another known effect of the barium ion on various biological objects is its potential-generating ability. This property can also be observed with snail hearts. The barium ion is capable of restoring the ventricular action potentials even after the ouabain inhibition. Probably the same ability is reflected in the after-potential generation too. The increase of the susceptibility is in part explained here too by the decrease of the K-conductivity (g_k). Besides this, however, the phenomenon may be understood best if a charge-carrying role is attributed to it, and in this respect it is likened at least in part to Ca. The studies of WERMAN, MCCANN and GRUNDFEST (1961) on the neuromuscular system of Romalea, and of KOKETSU and NISHI (1969) on the sympathetic ganglion cells of the frog, confirm the participation of the barium ion in such a charge-carrying function. These results at the same time show that the barium ion can exert its potential-generating effect on the object in this case too on the basis of the same mechanism.

The question of why the barium ion affects the action potentials of the two heart-parts, and the frequencies of formation of the action potentials, in different ways, is at present not understood. It is hoped that newer studies in this field too will provide more profound results.

The experiments with the local anaesthetics similarly indicate that the barium ion exerts its effect in part according to the Ca and perhaps the K-Na

pump-mechanism. The different changes of the action potentials of the two heart-parts here can be explained by the differing sensitivities of the Ca binding-sites. The change itself may be brought about by the complicated interaction of the Ca-binding site and the local anaesthetic, as well as of the barium ion, which possesses a higher bonding-strength than the Ca. According to the studies of BLAUSTEIN and GOLDMAN (1966) and KWANT and SEEMAN (1969), the local anaesthetics can compete with calcium, or can replace it at the membrane binding-sites.

The results obtained with the lanthanum ion also indicate the different sensitivities of the muscular systems of the two heart-parts with respect to the ion regarded as replacing calcium in the individual processes.

The most interesting change was obtained after TEA—I treatment and subsequent barium treatment. In this case the original ventricular pacemaker potentials were transformed into the action potential form characteristic of the mechanical muculature of the vertebrate heart. It seems that a decisive role is played in this change by the effect of the TEA—I in blocking the K-channels. The role of the TEA ion in this respect is confirmed by the examinations of many authors on numerous objects (HILLE, 1967; and others). One of the essential processes of the transformation, the development of the plateau stage, may be a result of the properties of the barium ion in decreasing the K-conductivity and of the TEA—I in blocking the K-channels, because of the delayed repolarization. The negative after-potential generation characteristic of the barium ion does not occur as a result of TEA—I pretreatment. The decisive part in this is probably not played by the permeability of the K-channels. This is shown by the procaine pretreatment: this drug also has an effect on the conductivity of the membrane connected to the K-channels, as proved by the studies of NARAHASHI and MOORE (1968), and others. Even so the procaine is not able to eliminate the after-potential generating effect of the barium ion. In this respect the TEA undoubtedly may interact as a charge-carrying ion with the barium ion and may bring about the disappearance of the after-potential by preventing the charge-transfer. Finally, in repressing the prepotential and in the establishment of the frequency of the action potential, a primary role may presumably be attributed to the barium ion, by means of some unknown mechanism. This transformability of the original pacemaker potentials is also considered interesting from the point of view that in such a model-like system a possibility is provided for the systematic and evolutionary elucidation of functional connections on objects remote from each other, by the recognition of interconnected mechanisms.

Summary

The spontaneous electrical activities of the atrium and ventricle of the heart of the edible snail (*Helix pomatia* L.) were studied on two types of preparation, in an extracellular, unipolar lead-off. In one of the preparations the ECG's of the isolated heart-parts were examined separately, while the atrial and ventricular electrical activities could be studied jointly in a lead-off from the pulmonary vein of the isolated intact heart. The use of this latter lead-off method also offered a possibility for the analysis of the rhythm patterns of the isolated hearts.

In the further experiments the effects of barium and lanthanum ions, and of ouabain, cocaine, procaine and TEA—I on the two types of action potential generation were studied. These experiments provide data on the different natures and different susceptibilities of the two types of action potential, which may be explained in all porbability by the different sensitivities of the muscular structures of the two heart-parts. The different changes of the action potentials could be observed in among others the combination of the barium effect with ouabain, which inhibits the K-Na pump-mechanism, with the local anaesthetics cocaine and procaine, and with the TEA ion, which blocks the K-channels.

The spontaneous electrical activity suspended with ouabain could be re-established with the barium ion in the ventricle, but not in the atrium. The pretreatment completely eliminated the effects of the barium ion repressing the prepotential and generating the after-potential, while its effect increasing the duration of the spike potential was considerably reduced.

The effects of the barium ion increasing the duration of the spike potential and generating the after-potential were only slightly modified in hearts pretreated with cocaine and procaine. The different susceptibilities of the two types of action potential could be observed however.

Pretreatment with TEA—I completely suspended the after-potential generating ability of the barium ion in the ventricular action potentials, but the prepotential-eliminating effect remained, while the effect increasing the duration of the spike potential was moderated. By this means the original pacemaker potential changed to an action potential form characteristic of the mechanical musculature of the vertebrate heart.

References

ARVANITAKI, A.—CARDOT, H. (1933): Des modifications d'un électrocardiogramme sous l'action des ions alcalino-terreux. — Arch. Int. Physiol. *36*, 28—40.

BLAUSTEIN, M. P.—GOLDMAN, D. E. (1966): Competitive action of calcium and procaine on lobster axon. — J. gen. Physiol. *49*, 1043—1063.

ERDÉLYI, L. (1971): Effect of ion milieu and barium ions on the ventricular electrocardiogram of the edible snail (*Helix pomatia* L.). — Acta Biol. Szeged. *17*, 171—184.

EVANS, C. L. (1912): Toxikologische Untersuchungen an bioelektrischen Strömen III. Vergleichend-toxikologische Spezifität des chemischen Alterationsstromes, zugleich ein Beitrag zur vergleichenden Physiologie und Toxikologie des Herzens der *Helix pomatia*. — Ztschr. Biol. *59*, 397—414.

HILL, R. B.—IRISAWA, H. (1967): The immediate effect of changed perfusion pressure and the subsequent adaptation in the isolated ventricle of the marine Gastropod *Rapana thomasiana (Prosobranchia)*. — Life Sci. *6*, 1691—1696.

HILLE, B. (1967): The selective inhibition of delayed potassium currents in nerve by tetraethylammonium ion. — J. gen. Physiol. *50*, 1287—1302.

KISS, T.—S.-RÓZSA, K. (1971): Effect of ions on the resting and action potentials of the myocardial fibers of *Helix pomatia* L. — Acta Physiol. Acad. Sci. Hung. *40*, 27—35.

KOKETSU, K.—NISHI, S. (1969): Calcium and action potentials of bullfrog sympathetic ganglion cells. — J. gen. Physiol. *53*, 608—623.

KRIJGSMAN, B. J.—DIVARIS, G. A. (1955): Contractile and pacemaker mechanisms of the heart of *Molluscs*. — Biol. Rev. *30*, 1—39.

KWANT, W. O.—SEEMAN, P. (1969): The displacement of membrane calcium by a local anaesthetic. — Biochim. biophys. Acta *193*, 338—349.

NARAHASHI, T.—MOORE, J. W. (1968): Neuroactive agents and nerve membrane conductances. — J. gen. Physiol. *51*, 93—101.

S.-RÓZSA, K.—VERÓ, M. (1971): Electrocardiograms in insecta and gastropoda and their changes under experimental conditions. — Anal. Biol. Tihany *38*, 79—86.

SPERELAKIS, N.—LEHMKUHL, D. (1968): Ba^{2+} and Sr^{2+} reversal of the inhibition produced by ouabain and local anaesthetics on membrane potentials of cultured heart cells. — Exper. Cell Res. *49*, 396—410.

SMIRNOV, G. D.—TURPAYEV, T. M. (1948): Osobennosti elektrogramm serdtsa bespozvonochnykh zhivotnykh (vinogradnaya ulitka). — Doklady Akad. Nauk. SSSR *60*, 525—527.

WERMAN, R.—MCCANN, F. V.—GRUNDFEST, H. (1961): Graded and all-or-none electrogenesis in *Arthropod* muscle I. The effects of alkali-earth cations on the neuromuscular system of *Romalea microptera*. — J. gen. Physiol. *44*, 979—995.

Addres of the author:
Dr. L. ERDÉLYI
Department of Animal Physiology,
A. J. University, 6701 Szeged,
Hungary