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THE MOVEMENT OF SODIUM AND OTHER IONS IN PACINIAN CORPUSCLES

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Alvarez-Buylla & de Arellano (1953) demonstrated potentials, graded to the stimulus strength, in Pacinian corpuscles. Gray & Sato (1953) analysed these receptor potentials and suggested that, on the evidence then available, the most reasonable explanation of their generation was that charge was transferred by one or more ions moving down their electrochemical gradients subsequent to a change in membrane permeability. It was clearly important to investigate the effects on the receptor potential of different concentrations of various ions. Some preliminary experiments suggested that the times taken for ions to enter or leave Pacinian corpuscles might be long, and therefore experiments were done to measure the rate of loss of ^{24}Na from, and its distribution in, these bodies. A few experiments were done on the rate of loss of ^{82}Br and the uptake of ^{42}K.

METHODS

Two methods were employed; in the first the Pacinian corpuscles were allowed to come into equilibrium with the tracer ion *in vivo* and then groups of corpuscles were soaked for varying times; in the other, individual corpuscles were loaded with the tracer ion *in vitro* and then measured at intervals while soaking in an inactive solution; finally the corpuscle was divided for the spatial distribution of the ion to be determined. All *in vitro* procedures were carried out at room temperature.

Method 1. A cat was injected intraperitoneally with 6·5 to 10 ml. of a solution (see below) containing the tracer ion, and about 16 hr later the mesentery was removed under ether anaesthesia. At the time of the operation the animal contained about 2·5 mc of radioactive material.

All available corpuscles were dissected from the mesentery, care being taken to keep them moist. The numbers obtained in thirteen different experiments ranged from 27 to 90 (mean 68); in only two experiments were there less than 50. The corpuscles were then divided at random into groups, usually of 10 corpuscles each; though up to 20 were placed in groups which were to be soaked for 2–3 hr. Sometimes clusters of large or small corpuscles occurred in the mesentery so that if the corpuscles were not randomized some groups had much larger average masses than

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others. The groups were placed in watch-glasses filled with the solution in which the corpuscles were to soak; the time at which the first and last corpuscle of each group was placed in the solution was noted. The process of transferring 10 corpuscles usually took from 1 to 2 min, and the mean was taken as the time soaking began. One group of corpuscles was not placed to soak in the solution, but the corpuscles were rinsed, blotted and placed in a boiling tube. They were then covered with 1 ml. of concentrated nitric acid (NaOH in ^{82}Br experiments); after 15 min, 9 ml. of distilled water was added. The sample was then ready for counting. The groups placed in the solution were soaked in a volume of about 5 ml.; since the volume of 20 corpuscles, the largest group used, was about 2·5 mm^3 the volume ratio was normally greater than 1 in 2000. When a group was due to soak for 2 hr or more the solution was usually changed once. The groups were left for various times ranging from 10 min to 3 hr; each corpuscle was then taken, blotted and transferred to a boiling tube and the times noted at which the first and last corpuscles of a group were transferred; the mean time was taken as the end of soaking. Once the group of corpuscles had been transferred to the boiling tube it was treated in the same way as the unsoaked group.

Samples of 9 ml. were transferred to a 20th Century Electronics M.6 fluid counter and counted for a time sufficient to make the counting errors small compared with the other errors. All the counts were corrected for background, dead time and the decay of the isotope activity.

Method 2. In this method the cat was not injected with a solution containing the tracer element, but corpuscles were dissected from the mesentery and placed in a solution containing about 0·2–0·3 mc/ml. of the radioactive ion; the compositions of the solutions are given below. After soaking for 4–5 hr each corpuscle was rinsed, blotted and placed in a shallow, flat-bottomed basket made of fine silver or stainless steel gauze; one corpuscle to each basket. Each basket fitted, on top of a disk of filter-paper moistened with the solution used for soaking, into a shallow Perspex trough 2·5 cm in diameter, designed to fit under a General Electric G.M. 4 end window counter. The procedure was as follows; as soon as the corpuscle had been placed in the basket the time was noted and the activity counted for either $\frac{1}{2}$ or 1 min; immediately the counting was finished the basket was taken from the trough and placed in a Petri dish containing the solution in which the corpuscle was to soak; the time at which the corpuscle was immersed was noted. After a period, usually 10 min, the basket was lifted out of the solution, the time noted, excess moisture blotted from the basket and the activity again counted; the counting completed, the basket was returned to the solution and the time recorded. The procedure was then repeated at intervals for periods varying between 30 and 90 min.

The majority of the 32 corpuscles treated in this way were then divided in order to estimate the relative concentrations of the tracer at different distances from the centre. The Pacinian corpuscle consists of fibrous tissue lamellae with fluid between each; it is thus possible to cut through a number of the outer lamellae and then shell out the intact centre. It was possible to repeat this procedure a number of times and four parts were normally obtained from each corpuscle. The technique was as follows: immediately after the corpuscle had been counted for the last time in its basket it was transferred to a small drop of solution on a round cover-glass; under a dissecting microscope (magnification $\times 50$) the outer layers were split with needles sharpened into micro-scalpels and the centre was removed as quickly as possible to another cover-glass, where the whole procedure was repeated. It was important that the micro-scalpels should be sharp and free from burrs so that damage to the lamellae of the central part should be minimal; it was also important that once the central part had been exposed to the drop of fluid it should be transferred as rapidly as possible to the next cover-glass in order to reduce the loss of active material from it.

In order to obtain a measure of the volume, the corpuscle was viewed with a microscope fitted with a camera lucida and the profile traced; this was repeated at each stage of the dissection. The axes of the tracing were measured, and the area was obtained by calculation from the hemi-axes on the assumption that the profile was an ellipse; the area was also measured with a planimeter. The mean differences of these two estimates were 6·2% (range 0–25%) regardless of sign, for the 22 corpuscles used in the four complete experiments quoted in this paper. Volumes were then calculated from the areas obtained with the planimeter by assuming that the corpuscles were

prolate spheroids, i.e. by multiplying by $4/3b$, where b is the minor hemi-axis. Sample volumes were obtained by subtracting the successive measurements obtained at each stage of the dissection.

Errors of measurement

Method 1

Counting errors. With this method the counting rate obtained from the unsoaked samples of 10 corpuscles ranged from 140 to 1000 per min. After 2–3 hr soaking the counts were very low and were counted for periods up to 1 hr. The background was counted for a comparable time, and the standard error of the difference was calculated. It was practicable to count all but the samples of lowest activity for long enough for this standard error to be small compared with other experimental errors. To check that the errors of counting were limited to those expected on theoretical grounds, a sample was counted repeatedly, each count being about the same size as the total counts normally reached; the counting rate was slightly higher than those found in the experiments. The observed standard deviation agreed well with that obtained theoretically from the Poisson distribution.

Errors of sample volume. This constituted the main source of error since each group of corpuscles had to be assumed to have the same volume. When groups having different numbers of corpuscles were used in the same experiment it was assumed that the activity was proportional to the number of corpuscles. An estimate of this source of error was obtained in two experiments in which groups of corpuscles were taken without soaking and the variation in activity between the groups observed. In the first of these, in which eight groups were obtained and the corpuscles were not allotted to the groups at random, the overall coefficient of variation was 17·3%; most of the error was accounted for by the result of one sample; excluding this sample, the coefficient of variation was 7·7%. In the second experiment the corpuscles were grouped at random and three groups were obtained; the coefficient of variation was 8·5%. In calculating the errors a coefficient of variation of 8% was taken as the contribution of this source of error.

The results are presented here as a percentage of the initial activity and each point is plotted with lines indicating $\pm$ twice the calculated standard error of the point; the standard error was calculated by summing the variances due to counting and volume errors and including that due to the error in the estimate of the initial activity.

Time. A group of 10 corpuscles was normally transferred into or out of a solution in 1 min; rarely the process took longer than 1·5 min. The time plotted as the soaking time was the difference between the means of two such periods. An error of $\pm$ 1 min has been indicated in the figures.

Method 2

Counting errors. With this method the initial activity had to be very high in order that the final samples, after the corpuscle had been soaked and divided, should have enough activity to count. With the sample in the usual position in relation to the counter window this activity gave counts around 10,000 per min. At these counting rates the error observed between repeated counts was considerably greater than the theoretical error, and the dead time correction became large; in three of the experiments described the counting rate was kept below 5000 per min by increasing the distance between the sample and the counter window. At this counting rate counts could be repeated with the accuracy expected from theory, but in spite of efforts to keep the geometry constant the ratios between the counts obtained with the sample in the two positions varied by more than the expected error; there may be an extra error of about 5% due to this but in nearly all runs it is confined to the measurement of the initial activity. In one experiment initial count rates were kept below 6000 by using a more dilute solution of the tracer and all counts were made with the sample in the normal position. The total number of counts obtained at each test was decided by the time that could be allowed without introducing large timing errors.

Another counting error, when using this technique, was the self absorption of the tissue. The greatest length of pathway through the tissue for a β-particle that could enter the counter was about 0·5 mm. This thickness of tissue could reduce the count of ^{24}Na by about 5%, but as the counts

were made from the whole corpuscle and ionic movement should have been uniform in all directions, the error in the relative counts would have been small.

Time. With this technique the corpuscle could not be soaked when it was counted; none the less ionic movement would continue inside even if the loss at the surface was much reduced. Two times were recorded therefore: the total time from the moment at which the corpuscle was first placed in the soaking solution, and this time less the time during which the corpuscle was out of the solution for purposes of counting. These two times are the limits of the uncertainty and are indicated by the crosses and dots on the appropriate figures.

Errors of sample dimensions. As only one corpuscle was used for each run relating fall of activity to time, this source of error, which was the most important with Method 1, can be regarded as negligible.

Errors in estimating the relative concentrations at different distances from the centre of the corpuscle. The error of these measurements was large. The overall errors can be seen in an experiment in which 6 corpuscles were soaked in a solution containing ^{24}Na for 4–5 hr; the total activity of each corpuscle was then counted and each was divided into 3 or 4 parts; the activity of each part was measured. Volumes were measured at the same time, and the relative concentration of ^{24}Na in each part was calculated. The coefficient of variation of the relative concentration of ^{24}Na in the whole corpuscle was 37% (number = 6), that of the parts 69% (number = 22). If the relative concentrations of the ion in the parts were calculated as proportions of the relative concentration in the whole corpuscle from which they were dissected, then the coefficient of variation of these proportions over the whole 22 samples was 56%; it is this figure which relates most directly to the experimental results. The biggest contribution to these errors was probably in the estimates of volume.

Solutions of tracer ions

^{24}Na *for injection.* 1 g of irradiated Na_2CO_3 was dissolved in 10 ml. of 1·15 N-HCl, and 100 ml. of distilled water was added.

^{24}Na *for soaking isolated corpuscles.* 1 g of irradiated Na_2CO_3 was dissolved in 12 ml. of N-HCl and made up to a total volume of 123 ml. A portion of this solution was then neutralized (pH 7·3–7·6) with a small quantity of N-HCl, and KCl and $CaCl_2$ were then added to make the final concentrations of these substances 0·042 and 0·024% respectively. In one experiment HCl was added to a portion of the bulk solution in a quantity sufficient for theoretical neutralization. This solution was then boiled; the volume was made up, the pH adjusted to 7·3–7·6 and the KCl and $CaCl_2$ added as before.

^{82}Br *for injection.* Irradiated NH_4Br was dissolved in water sufficient to make the solution isotonic.

^{42}K *for soaking isolated corpuscles.* 2 g of irradiated $KHCO_3$ were dissolved in 7·5 ml. of 1·15 N-HCl and 80 ml. of water. The following solution was then made up: NaCl 0·84 g, KCl and $KHCO_3$ (from bulk and calculated as KCl) 0·12 g, $CaCl_2$ 0·024 g, $NaHCO_3$ 0·015 g and H_2O to 100 ml.

Solutions used for soaking loaded corpuscles

Locke's solution: NaCl 0·92 g, KCl 0·042 g, $CaCl_2$ 0·024 g, $NaHCO_3$ 0·03 g, H_2O to 100 ml.

Na-free solution: choline chloride 2·6 g, KCl 0·042 g, $CaCl_2$ 0·024 g, $NaHCO_3$ 0·03 g, H_2O to 100 ml.

RESULTS

Loss of tracer ions from loaded corpuscles

^{24}Na *from groups of corpuscles* (*Method* 1). In the experiments, the results of which are illustrated in Fig. 1*a* and *b*, Pacinian corpuscles were taken from a cat which had been injected with a solution of ^{24}Na 14 hr previously, and groups of these corpuscles were then soaked for various times in the choline chloride

solution already described. The activity of each of these groups is plotted on a logarithmic scale, as a percentage of the initial activity, against the duration of soaking.

The general slopes of the two graphs in Fig. 1*a* and *b* are clearly different, and they represent the extremes of the range found in seven experiments with ^{24}Na. If the time taken for the relative activity to fall to 10% is used as an

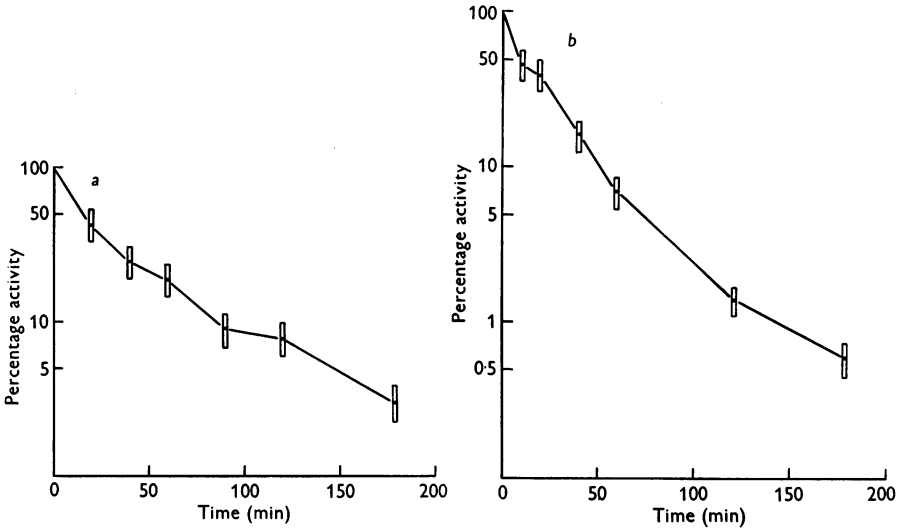

Fig. 1. Loss of ^{24}Na from groups of Pacinian corpuscles. Abscissa: time in min. Ordinate: activity, as a percentage of the initial activity (log. scale). The bars indicate ± twice the standard error of the estimate of relative activity and ±1 min (see section on errors). *a* and *b*, two different experiments.

index of the general rate of loss of the ion, the results can be summarized as in Table 1. The experiments illustrated (Fig. 1*a*, *b*) were obtained by soaking loaded corpuscles in choline solution, but there were others in which the corpuscles were soaked in Locke's solution. It can be seen from Table 1 that there was no significant difference between the results obtained with the two solutions. The mean value of the time to 10% activity in all the seven experiments obtained with this method was 68 min (S.D. 21 min).

^{82}Br *from groups of corpuscles.* One experiment was done in the same way as the experiments just described, but using ^{82}Br instead of ^{24}Na. The result was similar to those obtained with ^{24}Na. The time required to reduce the relative activity to 10% was 36 min, which was the shortest time observed in experiments with groups of corpuscles; however, there is no evidence that the rate of loss of ^{82} Br is different from that of ^{24}Na as the observed time only deviates from the mean ^{24}Na result by 1·5 × the standard deviation of the distribution of results with ^{24}Na.

^{24}Na *from single corpuscles* (*Method* 2). The results plotted in Fig. 2 were obtained by soaking single Pacinian corpuscles for 4–5 hr in a highly active ^{24}Na solution and then counting the activity of the corpuscle at various times while soaking in an inactive solution. Since in this method the changes of activity were followed in a single corpuscle, and it was possible to obtain more points than when using groups, the internal consistency of each run is better than that obtained by the group method.

TABLE 1. Rate of loss of radioactive ions from Pacinian corpuscles suspended in various solutions

Method	Tracer ion	Soaking solution	No. of expts.	Mean time to 10% (min)	S.D. (min)	S.E. of mean (min)
1	^{24}Na	Locke	4	64	24	12
1	^{24}Na	Choline soln.	3	73	20	12
1	^{24}Na	All results	7	68	21	8
1	^{82}Br	Locke	1	36	—	—
2	^{24}Na	Choline soln.	32‡	30	36	6
			28	22	17	3
2	^{24}Na	Choline soln.*	26‡	34	40	9
2	^{24}Na	Choline soln.†	6	15	3	1·3

* Excluding six results obtained on 1 day, when the corpuscles were loaded in an unneutralized solution.

† Results from these six corpuscles.

‡ Includes four extrapolations.

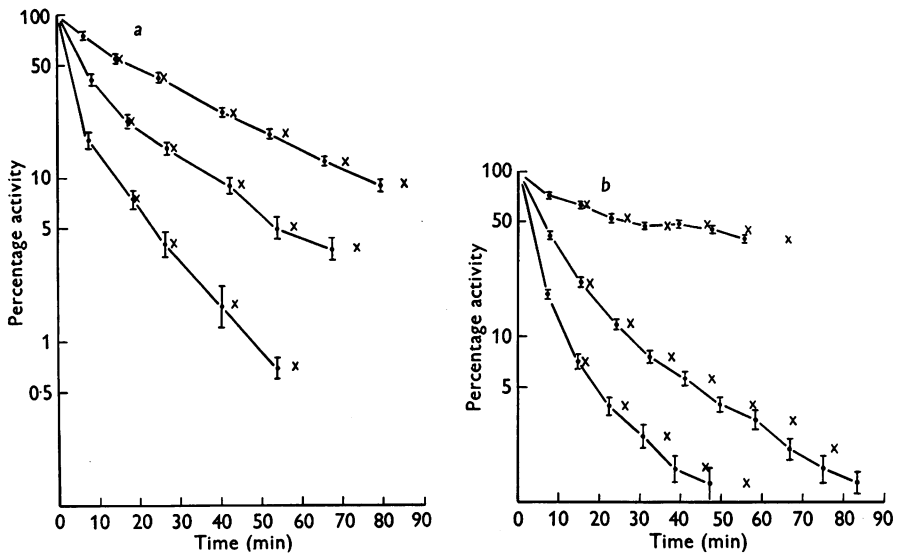

Fig. 2. Loss of ^{24}Na from single Pacinian corpuscles. Abscissa: time, min. Ordinate: activity as a percentage of the initial activity (log. scale). The bars indicate ± twice the standard error of the estimate of relative activity. The dots and crosses mark the limits of uncertainty in time (see section on errors). *a* and *b*, two experiments on different days.

The graphs relating the logarithm of relative activity to time show a curvature in the earlier stages of the process but tend towards a straight line as time proceeds. In all thirty-two experiments carried out with this method the later points can be fitted, within the limits of error, by a straight line.

The rate of loss of ^{24}Na was much more rapid in these experiments than in those done with groups of corpuscles. As can be seen in Table 1 the mean times required to reduce the activity to 10% of its initial value was only 30 min, S.D. 36 min. (These figures are means from thirty-two experiments of which the graphs of four had to be extrapolated, e.g. Fig. 2*a* top; means of the non-extrapolated observations are shown in Table 1, but these are clearly biased.) The variation between individual experiments was large, the times to 10% activity ranging from 5 min to something of the order of 3 hr, a result obtained by extrapolating from the top curve of Fig. 2*a*. This high rate of loss of ^{24}Na, as compared with the group experiments, may be due to the conditions under which the corpuscles were loaded; it is also possible that the tracer ion was not uniformly distributed throughout the corpuscle in the relatively short time that could be allowed, but in the light of the time taken to soak ^{24}Na out in the group experiments it does not seem likely that this factor could have had a very large effect on the results. The pH of the tracer solution was considered as a possible reason because in the six runs done on the first day the times to 10% activity were especially short (mean 15 min), and these corpuscles had been soaked in an alkaline tracer solution. On the other hand, all the other corpuscles were soaked in nearly neutral solutions; some of these were just on the alkaline side and one was on the acid side of neutrality, but no consistent differences in the results were observed.

Uptake of ^{42}K

Some experiments on the loss of ^{42}K from Pacinian corpuscles were attempted, but it was found impossible to give large enough doses of potassium to a whole animal. Experiments were also attempted in which it was hoped to follow the uptake of ^{42}K using the basket technique (Method 2); this method proved unsuccessful because of the difficulties of removing all the active solution during counts. One successful experiment was done, however, by allowing groups of corpuscles to take up ^{42}K from a solution for varying times and then macerating them in nitric acid and counting in a fluid counter (as described under Method 1). The result of this experiment is shown in Fig. 3, the number of counts being plotted against time; for purposes of comparison the experiment in Fig. 1*a* is plotted on the same co-ordinates. No definite conclusions can be drawn from this single experiment which did not last long enough to establish a steady state; the early stages, however, are similar in time course in both experiments.

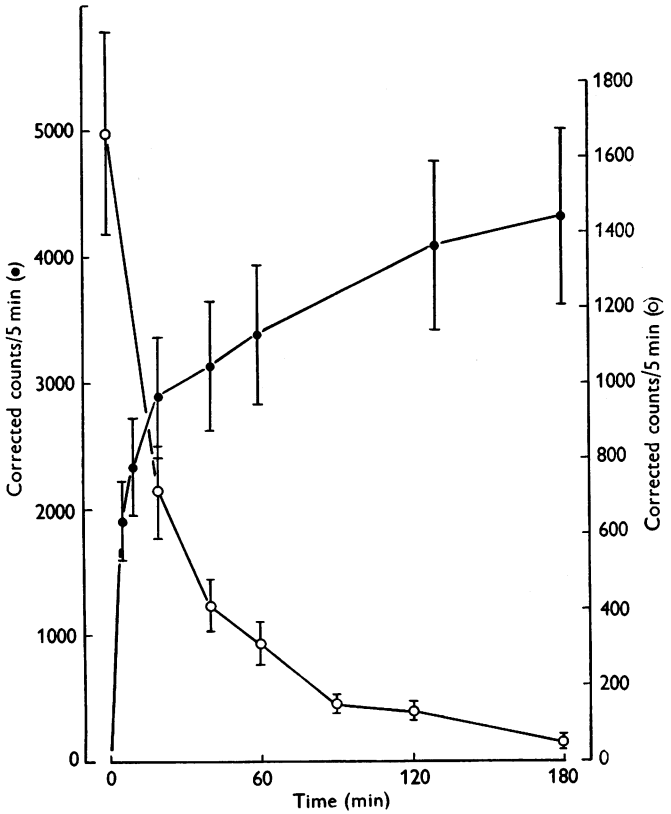

Fig. 3. Uptake of ^{42}K into groups of Pacinian corpuscles. Abscissa: time, min. Ordinate: corrected counts per 5 min. ●, uptake of ^{42}K; ○, loss of ^{24}Na (same results as Fig. 1*a*).

The distribution of ^{24}Na *in Pacinian corpuscles*

In most instances, when the rate of loss of ^{24}Na had been followed in a single Pacinian corpuscle, the corpuscle was divided and the activity of different layers determined. Usually four such parts were obtained and the activity of each was divided by its volume; these values were converted to percentages of that obtained for the whole corpuscle before soaking began. The final figures represent relative concentrations and are plotted in Fig. 4; the abscissa of this figure is radius (*r*) as a proportion of the outside radius (*a*) of the corpuscle. The value of radius plotted for each point was obtained by taking the cube root of the mean of the cubes of the internal and external radii of each sample. The different lines on the figure are from the results of different corpuscles, which were soaked for different times during the same experiment. Four such groups of graphs were obtained and the one illustrated is the one showing the most regular pattern. This pattern shows that there is a rapid loss of ^{24}Na from the

outer layers of the corpuscle, but that in the inner layers the concentration remains high for long periods.

The answer that was required from these experiments was the time course of the loss of ^{24}Na at different values of radius. This could only be obtained by combining results from different corpuscles as each one could represent only one time. However, the rate of loss of ^{24}Na from different corpuscles varied widely, and it was therefore necessary to adjust the time scales of each result in such a way that all results might be comparable. This was done by noting the times at which the ^{24}Na concentration in each corpuscle had fallen to 50, 20 and 10% of its initial value and taking the mean of these times; this value was then divided into the mean of the corresponding values of all the experiments done with groups of corpuscles. A constant was thus obtained by which the time scale relating to a particular corpuscle could be multiplied. The results from all the corpuscles, which were dissected, were treated in this way and it was then found that the curves relating percentage activity to this standardized time were superimposable, within their limits of error, except at long times when there were discrepancies. It was noted at what time, on the standardized scale, each corpuscle was dissected (i.e. in each curve of Fig. 4), and it was then possible to construct Fig. 5. This figure relates relative activity to standardized time for four different values of r/a. Since the standard to which all individual time scales were corrected was the mean time scale of the experiments using groups of corpuscles, the standardized time can be regarded as a mean value.

DISCUSSION

The Pacinian corpuscle is a laminated structure and the lamellae can be separated by dissection; the spaces between the lamellae are filled with fluid which can escape when the laminae are damaged (Pacini, 1840). The lamellae themselves consist, for the most part, of collagen with a small amount of elastic tissue and fibrocytes. From the histological evidence it therefore seems that there is little intracellular space in a Pacinian corpuscle; the only cells being the nerve fibre and the fibrocytes. The evidence provided in this paper neither supports nor contradicts this statement, and it seems reasonable to suppose that the observations with ^{24}Na, normally an extracellular ion, relate to Na in the extracellular fluid. The point of immediate practical importance is the rate at which the Na leaves the corpuscle, particularly the centre of the corpuscle. The rate of loss from the whole corpuscles was different with the two methods used. In the first method, in which the whole animal was equilibrated with the tracer ion, the corpuscles remained in what was presumably a healthy state until the time that they were removed from the animal. The corpuscles used in Method 2 were removed from the animal about 6 hr before soaking in the inactive solution; they were, for most of this time,

in a solution which was not identical with tissue fluids; and they were subjected to intense radiation for about 5 hr. There is every reason to suppose that the results obtained with the first method represent the more accurately the rate of loss of the ion in healthy Pacinian corpuscles at room temperature. The concentration at the centre of the body will fall more slowly than that of the whole. Fig. 5 is a compilation of results relating the logarithm of relative activity to a standardized time, based on the mean value obtained from the experiments with groups of corpuscles. Even in Fig. 5*d*, which represents the

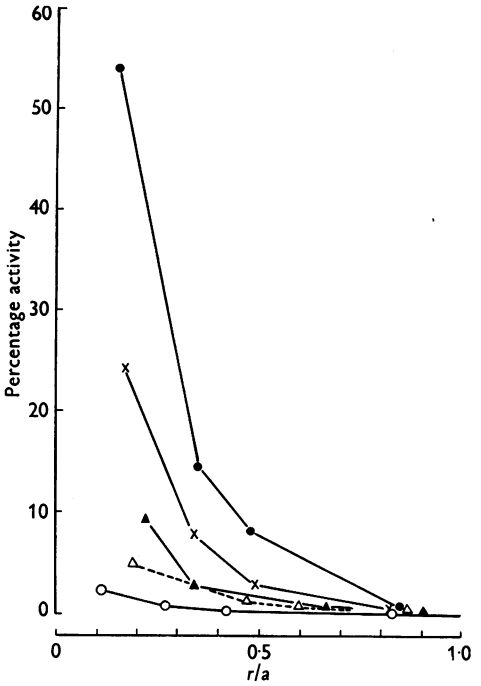

Fig. 4. Distribution of activity in five corpuscles soaked for different times. Abscissa: root mean cube radius of sample as proportion of radius of whole corpuscle. Ordinate: activity as a percentage of the activity of the unsoaked undivided corpuscle. The times of soaking were as follows: ●, 23 min 35 sec (142); ×, 41 min 25 sec (219); ▲, 74 min 15 sec (243); △, 56 min 35 sec (255); ○, 90 min 45 sec (420). The bracketed figure is that of the standardized time (min) referred to in the text.

time course of the concentration at a point where $r/a = 0{\cdot}2$, the relative concentration does not usually fall below 5% in under 5 hr. The central core of the corpuscle has an r/a value of *c.* 0·06 and here the concentration may be expected to be higher at any given time.

These experiments, therefore, show that at room temperature loss of Na^+ from a Pacinian corpuscle is very slow, too slow to be of use in the type of experiment mentioned in the introduction; furthermore, one experiment each

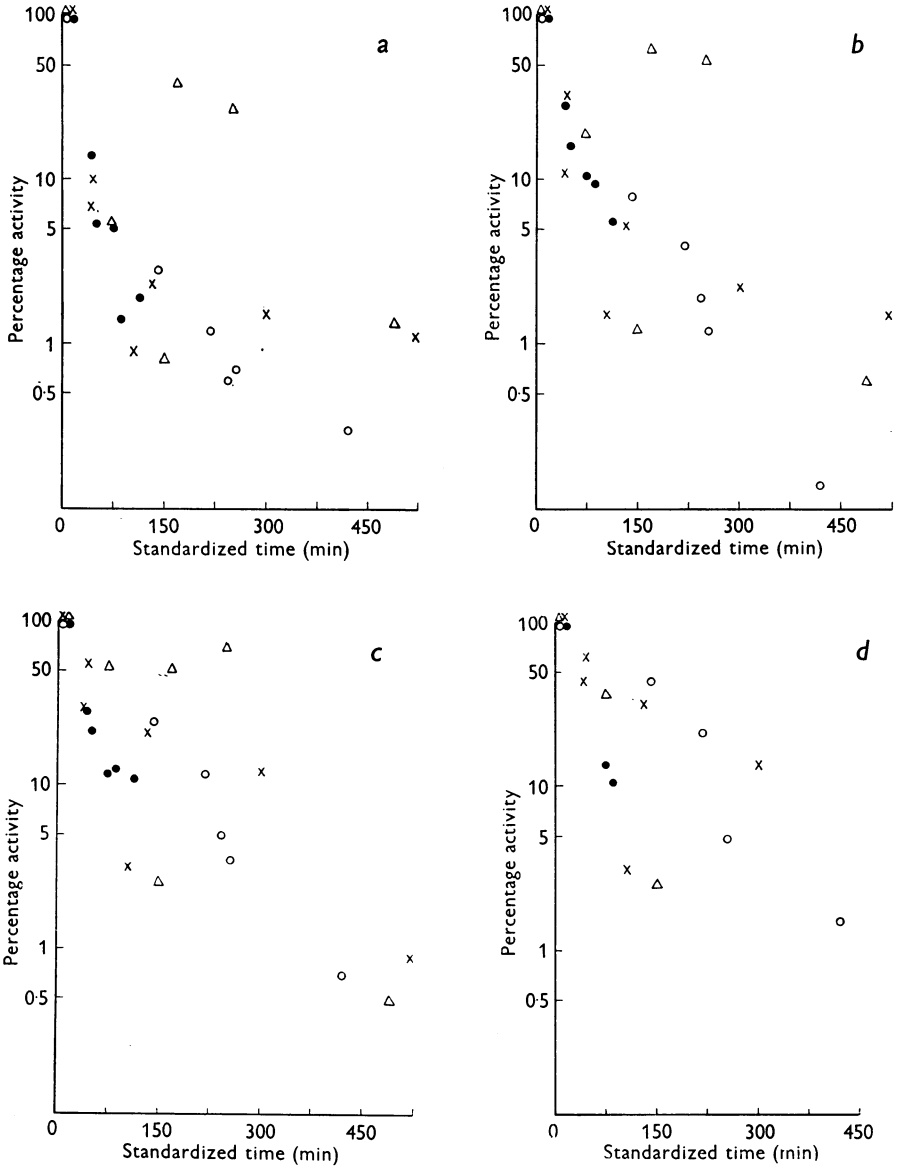

Fig. 5. Loss of ^{24}Na from Pacinian corpuscles at different distances from the centre. Abscissa: standardized time (see text) in min. Ordinate: activity as a percentag eof the activity of the unsoaked undivided corpuscle (log. scale). Each graph represents a different value of radius as a proportion of the outside radius: *a*, 0·75; *b*, 0·5; *c*, 0·3; *d*, 0·2. The different symbols indicate experiments on different days.

with Br^- and K^+ show that these ions move at a rate of the same order of magnitude as Na^+. It seems probable, from the structure of the Pacinian corpuscle, that movements of ions such as those described in this paper are due to diffusion. Such information in this paper as is relevant supports this view; the rate of loss of ^{24}Na is independent of whether the corpuscle is soaked in a solution of NaCl or choline chloride; in the one experiment, the rate of loss of ^{82}Br was of the same order of magnitude as the rate of loss of ^{24}Na and also as the rate of uptake of ^{42}K in the one successful experiment with this ion. If this is a process of diffusion through fibrous tissue lamellae the temperature coefficient is not likely to be high; but experiments have been done only at room temperature, the temperature so far used in experiments on receptor potentials.

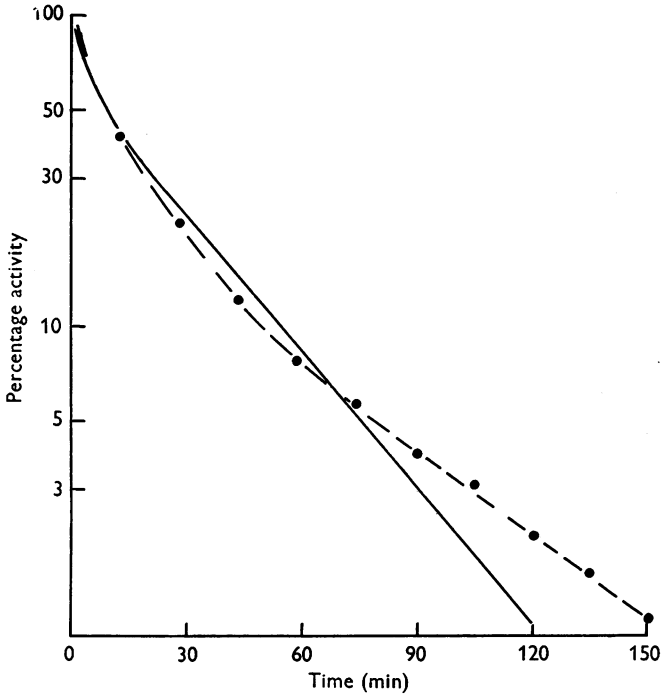

Fig. 6. Comparison of the rate of loss of ^{24}Na from a single Pacinian corpuscle ●—● with the rate of loss expected from a homogeneous sphere placed in a large volume of an inactive solution (full line). Abscissa: standardized time (see text), min. Ordinate: activity as a percentage of the initial activity (log. scale).

If the process is one of diffusion the experimental results might be expected to fit a suitably derived equation. The diffusion in an homogeneous sphere placed in a volume of solution of zero concentration of the ion in question is a case which has been solved. The Pacinian corpuscle is a spheroid and not a sphere, but it is composed of concentric lamellae and it is probable that the permeability of the lamellae is very low compared with the fluid between; an

ion at the centre would have to pass through the same number of lamellae whatever hemi-axis it moved along to reach the outside and it would therefore seem reasonable to consider the body as a sphere. The assumption of homogeneity implies that each barrier should have the same permeability, that the number of barriers should be large enough to justify regarding the system as continuous, and that the spacing between the barriers should be uniform. The first condition may be true but there is no evidence for it; the number of barriers, about 60 (Stöhr, 1928), should be sufficient for the system to behave continuously; the third condition is clearly not fulfilled as the lamellae are much farther apart in the periphery and more dense in the centre. The relation describing the behaviour of the homogeneous sphere has been given, with its solutions for heat transfer by Carslaw & Jaeger (1947, p. 206). The curve relating relative activity to time derived from their equation is shown in Fig. 6, together with a series of experimental points through which a smooth curve has been drawn. To scale the experimental points, one constant had to be calculated from the data and the abscissa altered by multiplying the time by this factor. It is clear that the two curves are different, though there are certain general similarities. Also the experimental results do not fit the family of curves which define the spatial distribution of concentration for different times in a homogeneous sphere, though these curves are similar in general shape to the experimental results illustrated in Fig. 4. All the discrepancies between the results and the relation for a homogeneous sphere are in the direction that would be expected when the outer lamellae are much farther apart than the inner. It is possible that a similar relation modified to include permeability as a function of radius might describe the situation; there is no evidence from these experiments to suggest that the system is not a symmetrical and effectively continuous one. The rate of diffusion in a longitudinal direction around the axon might be different from that in other parts of a corpuscle, but the experiments described are not accurate enough to detect the sort of discrepancies that would be expected in an experiment such as that shown in Fig. 4.

SUMMARY

1. Radioactive tracer ions have been used to follow the time course of loss and uptake of ions in Pacinian corpuscles of the cat. Also the relative concentrations of active material at different distances from the centre of corpuscles at different times have been measured. The experiments were done at room temperature.

2. Ionic exchange is slow. It is estimated that the concentration of ^{24}Na at 0·2 of a radius from the centre will not usually fall to 5% in under 5 hr. The concentration in the central core which has a radius of 0·06 of the outside radius is expected to be higher.

3. The results are discussed in terms of a physical model.

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REFERENCES

ALVAREZ-BUYLLA, R. & DE ARELLANO, J. R. (1953). Local responses in Pacinian corpuscles. *Amer. J. Physiol.* **172**, 237–244.

CARSLAW, H. S. & JAEGER, J. C. (1947). *Conduction of Heat in Solids.* Oxford: Clarendon Press.

GRAY, J. A. B. & SATO, M. (1953). Properties of the receptor potential in Pacinian corpuscles. *J. Physiol.* **122**, 610–636.

PACINI, F. (1840). *Micro Organi Scoperti nil Corpo Umano.* Pistoja: Tipografia Cino.

STÖHR, P. (1928). *Möllendorfs Hb. d. Mikr. Anat. IV. Nervensystem, I. Teil.* Berlin: J. Springer.