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THE EXCITATION OF TOUCH RECEPTORS IN FROG'S SKIN

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An account has already been published (Gray & Malcolm, 1950) of some experiments on the initiation of impulses in mesenteric Pacinian corpuscles. It was found that both the 'on' and 'off' of a mechanical pulse could excite, and that after a short (approx. 200 μsec.) pulse there was a latency before the initiation of the impulse which had a maximum at threshold of about 1·5 msec. and a minimum with large stimulus strengths of about 0·5 msec. It was felt that it would be of interest to see if other mechanical receptors behaved in a similar manner, and some of the observations described in this paper were made with this purpose in view.

It has often been thought that the adaptation of sensory receptors is related to the accommodation of nerve and some observations have, therefore, been made to see whether the behaviour of a mechanical receptor to linearly increasing stimuli was similar to that of nerve.

The experiments described here on the mechanical receptors of the frog's skin are similar to many that have been carried out on nerve using electrical stimuli, and the behaviour of a mechanical receptor can thus be compared in general terms with that of nerve. Such a comparison can only be general with results obtained on frog's skin, since, in this preparation, the receptor is not isolated, and it is not easy to obtain comparable results from the receptor's own axon. Direct comparisons have, on the other hand, been made on Pacinian corpuscles (Gray & Matthews, 1951). Because the receptors are not isolated the results obtained on this preparation are much less consistent than those that can be obtained with single separated Pacinian corpuscles. The experiments have been done, none the less, because it is important that more than one type of receptor should be investigated by these methods.

A preliminary report of some of these results has been published (Gray, Malcolm & Matthews, 1950).

METHODS

The skin over the dorsal lymph sac of the frog (*Rana temporaria*) was removed and the dorsal cutaneous nerve divided as near as possible to the muscles of the back. It was pinned out flat, the inside being placed upwards over a platinum covered earthed plate. A nerve was placed on a pair

of platinum wire electrodes which led through a pair of cathode followers and an amplifier to one beam of a double beam cathode-ray oscillograph. This beam recorded the action potentials initiated by mechanical stimulation of the skin. The second beam was used (e.g. Fig. 3) to record the form of the potential applied to the crystal stimulator referred to below. The experiments were done at room temperature, which ranged from 20·6 to 29·6° C.

For stimulating the skin a specially devised crystal stimulator was used; this has been described in detail (Gray & Malcolm, 1950). It consists essentially of a Rochelle salt (piezo-electric) crystal, which is mounted so that the application of a potential across the crystal causes one corner to bend. This movement is transmitted to the preparation by a short stylus. The maximum movement obtainable with this crystal is about 20 μ. The form of the movement follows that of the applied voltage, so that it is possible to use rectangular pulses or linearly increasing movements of varying durations and slopes. After a linearly increasing movement the displacement can be maintained or cut off sharply. The crystal used in these experiments, when critically damped, had a rising time of about 0·3 msec., so that the term 'rectangular pulse' is not strictly accurate, but will be used for convenience. The stylus of the stimulator was placed on a selected area on the inside of the skin and, by careful placing, it was possible to stimulate the termination of a single axon. When the crystal was mounted, as described previously (Gray & Malcolm, 1950), it was not possible to obtain a record of its movement. In the course of the experiments, however, it became necessary to ascertain during each experiment the exact relationship between the movement of the stylus and the shape of the applied voltage. For this purpose, the stimulator was rebuilt so that the movement of that corner of the crystal which actuated the stylus interrupted a light beam whose intensity was recorded with an electron multiplier photo-cell. The arrangement is shown diagrammatically in Fig. 1. A light source (*a*) is focused by lens (*b*), through prism (*c*) on to the edge of the flag (*d*) on the moving corner of the crystal (*e*) (Rothermel, 4D41). Fine adjustment of the position of this image is obtained by adjustment of the lamp house. The light passing the 'flag' is reflected by the prism (*f*) and the area of light narrowed so as just to cover the cathode of the electron multiplier photo-cell (*g*) (Mazda 27M2) by lens (*h*). The form of the stimulator movement could then be recorded with the cathode-ray oscillograph (Fig. 2) at any time during an experiment, and this enabled the rising phase of the applied voltage to be so adjusted as to produce a movement either critically damped or of some other from. The need for a damping oil film as previously used was thus avoided.

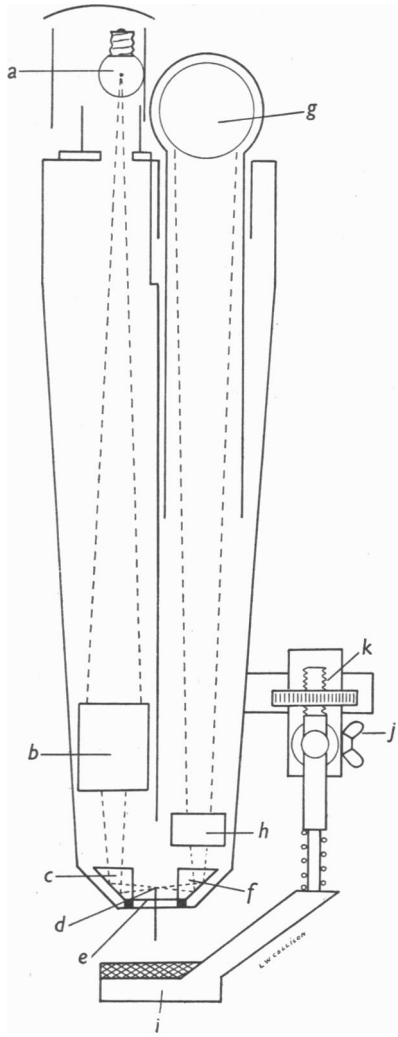

Fig. 1. Section of mechanical stimulator and optical recording system. (*a*) 6 V. bulb; (*b*) lens; (*c*) prism; (*d*) 'Flag' on moving corner of crystal; (*e*) crystal; (*f*) prism; (*g*) multiplier photo-cell; (*h*) lens; (*i*) cork-covered stage; (*j*) universal clamp; (*k*) screw adjustment of stage height.

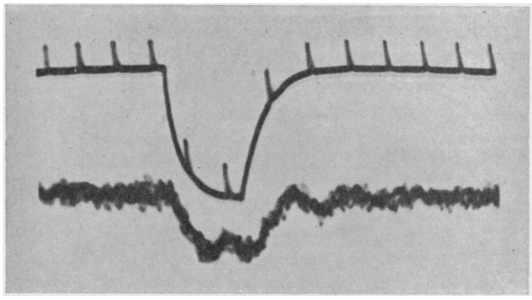

Fig. 2. Record of pulse shape from the optical recording system of the stimulator. Top trace, exponentially changing voltage pulse as applied to crystal—maximum 9·3 V. Bottom trace, mechanical movement as recorded—maximum movement about 4 μ. Time marks, 3 kcyc./sec.

RESULTS

Threshold

A rectangular mechanical pulse of longer duration than the refractory period of the preparation, when applied to the skin, can set up one or more impulses at both the 'on' and 'off' of the pulse (Fig. 3*a*, *b*). The threshold at the 'on' was always appreciably lower than that at the 'off' and about ten times greater than that observed by us with the Pacinian corpuscle preparation. This result was to be expected, since the nerve endings in the frog's skin preparation were not isolated. Thresholds also tended to be irregular, probably because of small movements between the skin and stimulator. As a result of the high threshold, and the limitations of the stimulator, the maximum stimuli obtainable were between 2 and 6 times threshold. Threshold stimulation at 'on' or 'off' always resulted in a single impulse; repetitive discharge has sometimes been obtained, however, with larger stimuli. In the following observations we have confined ourselves to an analysis of the 'on' response.

The threshold for a second action potential was measured in seven preparations, two of which were from the same animal. In most of these the maximum available stimulus failed to elicit a second response, the result is indicated in Table 1, col. 6, as greater than the maximum available stimulus. This is expressed as a multiple of the threshold observed for a single impulse, when stimulated by a rectangular pulse of infinite duration. In the other three, the threshold for a second impulse ranged from 1·4 to 5·7 times that of the first.

When a comparison of the thresholds with mechanical pulses of short (approx. 0·4 msec.) and infinite duration was made, considerable variations were found between individual experiments and between different observations during one experiment (see Table 1). Col. 4 gives the thresholds to short stimuli as multiples of those to long ones. As the photoelectric arrangements

for recording exact mechanical pulse shapes were not introduced until late in the series of experiments, we had inadequate information about the pulse shape at short durations and, hence, strength-duration curves are not given.

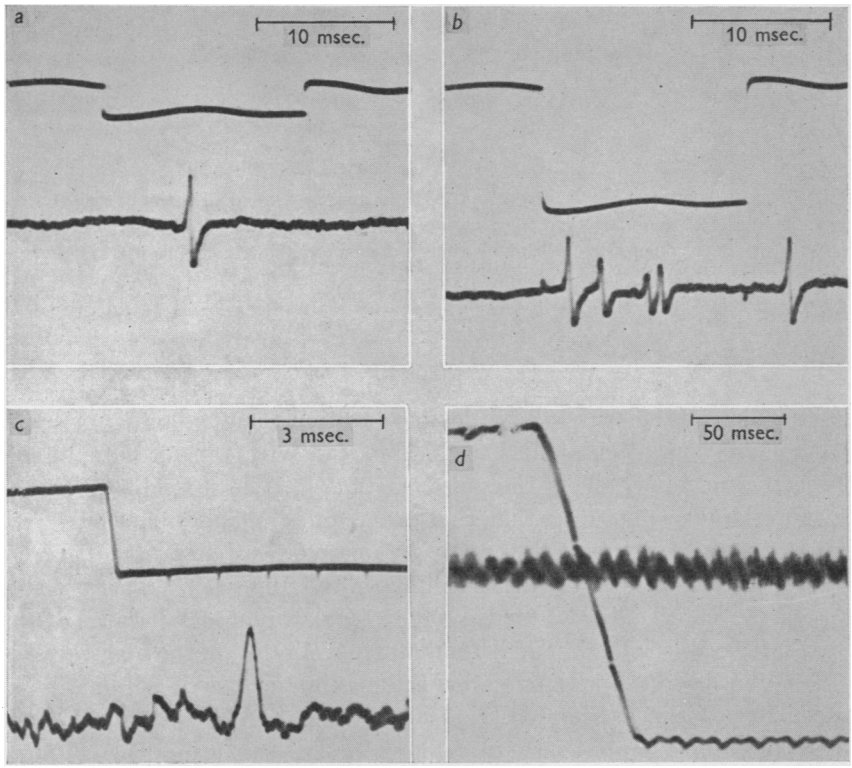

Fig. 3. (*a*) Top beam marks stimulus strength and duration; bottom beam, record from cutaneous nerve. On threshold. Latency from beginning of stimulus to on response = 5·9 msec. Time bar = 10 msec. (*b*) Ditto, same amplification and time. Off threshold. Stimulus = 3·7 × threshold. On latency = 1·5 msec. The small action potentials come from other endings. (*c*) top beam, stimulus; bottom beam, recording from cutaneous nerve. Threshold to stimulus with rising time of 0·3 msec. Time bar = 3 msec. (*d*) Ditto, same amplification, but time bar = 50 msec. No excitation with a stimulus rising in 52 msec. to a strength 3·7 × rheobase. (*a* and *b*, same preparation as Fig. 4; *c* and *d*, same experiment as Fig 5.)

In the range from 0·35 to 0·45 msec., we were sure that the damping was not reducing the maximum stimulus amplitude, and therefore the means of those observations whose duration fell within this range are given in Table 1, col. 5. The mean of these values is 1·3 with a standard deviation about the mean of 0·2.

Latency

The interval between the beginning of a rectangular mechanical pulse and the appearance of an impulse at the recording electrodes was recorded for different stimulus strengths (Fig. 3*a*, *b*). A typical curve for a stimulus of

TABLE 1. Thresholds for short pulses and for repetition with long pulses (thresholds as multiples of that for a pulse of infinite duration)

Preparation (1)	No. of observation (2)	Duration of short pulse (3)	Threshold to short pulse (4)	Daily mean (pulse duration 0·35–0·45 msec.) (5)	2nd action potential with infinite duration pulse (6)
19. v. 49	1	0·30	2·2	—	>4·8*
	2	0·29	1·5	—	>3·8*
7. vi. 49	1	0·43	1·2	1·2	—
8. vi. 49	1	0·45	1·4	—	—
	2	0·54	1·2	—	—
	3	0·45	1·1	1·3	—
13. vi. 49(*a*)	1	—	—	—	1·4
13. vi. 49(*b*)	1	—	—	—	1·7
	2	—	—	—	1·7
16. vii. 49	1	0·39	0·9	—	—
	2	0·39	0·9	—	—
	3	0·43	1·1	1·0	—
28. vi. 49	1	0·4	1·4	—	—
	2	0·42	1·4	—	—
	3	0·42	1·1	—	—
	4	0·4	1·3	1·3	—
27. vii. 49	1	0·43	1·5	—	—
	2	—	—	—	>3·9*
	3	0·41	1·5	—	—
	4	0·41	1·6	1·5	—
24. viii. 49	1	—	—	—	>3·3*
	2	0·36	1·5	1·5	—
	3	—	—	—	>4·0*
22. ix. 49	1	—	—	—	>5·8*
	2	0·28	0·8	—	—
27. ix. 49	1	0·43	1·0	1·0	—
28. ix. 49	1	0·39	1·2	—	—
	2	0·39	1·1	1·2	—
30. ix. 49	1	0·31	0·8	—	—
	2	0·31	0·8	—	—
8. xi. 49	1	0·46	1·7	—	—
	2	0·44	1·4	—	—
	3	—	—	—	5·7
	4	0·42	1·6	1·5	—
				Mean 1·3	
				S.D. 0·2	

* Maximum available stimulus.

duration 0·43 msec. is given in Fig. 4. The observed time includes the conduction time between the sense ending and the recording electrodes, and the true latency between the beginning of the stimulus and the initiation of the nerve impulse. Since the ending was not isolated, it was neither possible to measure the true latency directly nor the conduction time alone, and to deduct

it from the obtained value. Essentially the shapes of the curves obtained with long and short duration stimuli were the same. With increasing stimulus strengths the two curves always approached each other until they reached the same level. There was, however, this difference, that the maximum latency was longer with long than with short duration stimuli. The possibility that the bigger stimuli excited more central points on the nerve cannot be excluded. However, the sharp localization of each sensitive point makes such an explanation improbable.

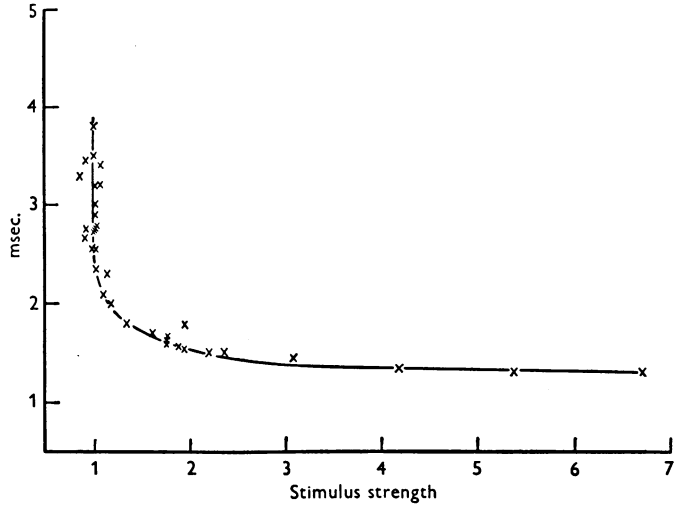

Fig. 4. Latency curve. Ordinate, latency and conduction time, msec. Abscissa, stimulus strength as multiple of threshold. Pulse duration, 0·43 msec.

In Table 2 the results of all experiments have been tabulated in such a way that the relevant points can easily be seen. Cols. 3 and 5 give the largest and the smallest observed intervals between the beginning of stimulus and appearance of action potential for long and short duration stimuli. Another measure of maximum value was obtained by taking the mean of all the intervals recorded with stimuli within 10% of threshold strength. These values are given in col. 4, the number of observations being given for each value in brackets. The figures in col. 6 were obtained by subtracting the smallest from the largest intervals. Since it is improbable that the conduction time, even after threshold stimuli, is longer than the recorded minimum interval, this difference represents something smaller than the true threshold latency.

The results show: (*a*) that the mean latency for short duration stimuli must be greater than 3·1 msec. with a standard deviation of 1·4 msec.—this time is long compared with the latencies found in experiments on electrically stimulated frog's nerve (Blair & Erlanger, 1936); (*b*) that there are definite differences in the latencies after short and long duration stimuli. As is seen from the figures

of col. 7, the observed intervals for short duration stimuli are in the mean 0·71 times (S.D. 0·21) those for long duration stimuli. Since in these calculations the conduction time could not be excluded, the true difference would be even greater. In this respect the results differ from corresponding results so far obtained on Pacinian corpuscles.

TABLE 2. Latencies in initiation of impulses after long and short duration stimuli

Preparation (1)	Duration (msec.) (2)	Max. latency (msec.) (3)	Mean threshold latency (msec.) (4)	Min. latency (msec.) (5)	Col. 3 – col. 5 (6)	Ratios short to long stimulus: col. 3 (7)	Ratios short to long stimulus: col. 4 (8)
19. v. 49	0·30	5·1	3·4 (8)	*c.* 0·7	—	0·77	0·64
	∞	6·6	5·3 (6)	*c.* 0·7	—	—	—
	0·29	3·7	3·0 (7)	*c.* 1·2	—	0·69	0·57
	∞	5·4	5·3 (3)	*c.* 1·2	—	—	—
7. vi. 49	∞	6·3	4·7 (11)	—	—	0·70	0·87
	0·43	4·4	3·7 (10)	—	—	—	—
8. vi. 49	∞	2·5	2·3 (5)	—	—	0·80	0·83
	0·45	2·0	1·9 (7)	—	—	—	—
13. vi. 49	∞	13·0	8·5 (11)	1·3	11·7	—	—
	∞	14·6	12·6 (8)	1·6	13·0	—	—
16. vi. 49	∞	5·7	4·2 (12)	1·2	4·5	1·10	1·02
	0·43	6·3	4·3 (15)	1·2	5·1	—	—
28. vi. 49	0·40	2·9	2·3 (18)	1·1	1·8	0·21	0·35
	∞	13·8	6·6 (25)	1·1	12·7	—	—
	0·39	4·6	3·0 (9)	1·1	3·5	0·92	0·91
	∞	5·0	3·3 (10)	1·1	3·9	—	—
27. vii. 49	∞	5·8	4·5 (12)	1·3	4·5	0·66	0·67
	0·43	3·8	3·0 (18)	1·3	2·5	—	—
28. viii. 49	∞	3·5	2·8 (17)	1·3	2·2	0·80	0·76
	0·36	3·2	2·5 (11)	1·3	1·9	—	—
	∞	4·4	3·8 (11)	1·3	3·1	—	—
8. xi. 49	∞	7·3	5·8 (6)	—	—	0·38	0·43
	0·46	2·8	2·5 (9)	—	—	—	—
	∞	6·0	4·9 (5)	—	—	0·42	0·47
	0·44	2·5	2·3 (5)	—	—	—	—
	0·42	3·1	2·6 (6)	—	—	0·27	0·31
	∞	11·5	8·3 (6)	—	—	—	—
Mean of daily means long pulse		6·8	5·1	—	6·5	—	—
S.D. of daily means		3·3	2·3	—	3·9	—	—
		—	—	—	—	0·71	0·72
		—	—	—	—	0·21	0·19
Mean of daily means short pulse		3·8	3·1	—	3·1	—	—
S.D. of daily means		1·3	0·9	—	1·4	—	—

Linearly increasing displacements

A series of experiments have been carried out to measure the changes of threshold associated with different rising times of stimulus. Linearly rising pulses have been used and, in the majority of experiments, the displacement remained at a steady level after the end of the rising phase. In one late experiment, we were able to cut off the pulse at the end of the rise, the falling time being just slow enough to prevent oscillation, and to compare it directly with

maintained pulses. There was no significant difference between the thresholds obtained with the two types of pulse except with short rising times, when the ordinary difference between the threshold to short and long pulses was observed. In all experiments the rising time was set to the required value for each observation, and the threshold found by adjusting the stimulus strength (Fig. 3*c*, *d*).

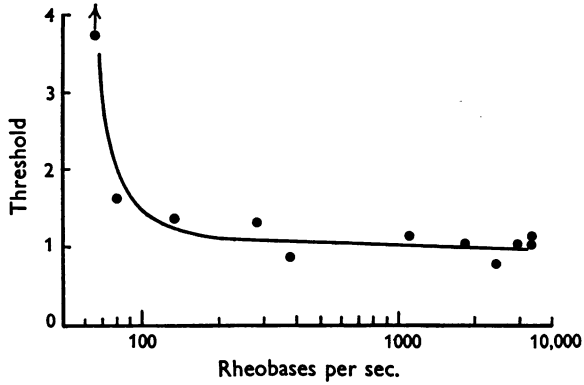

Fig. 5. Thresholds with linearly rising pulses—plateau maintained. Ordinate, threshold as multiples of rheobase. Abscissa, speed of rise of pulse in rheobases per sec. (log scale). Rheobase = threshold to a rectangular mechanical pulse of infinite duration.

TABLE 3. Values of critical slope

Preparation	Slope (rheobases/sec.)	Reciprocal of slope (msec.) (approximating to λ)
19. v. 49	26	38
8. vi. 49	260	3·8
28. vi. 49	60	17
27. vii. 49	32	31
24. viii. 49	73	14
22. ix. 49	24	42
28. ix. 49	33	30
	44	23
30. ix. 49	25	40
	43	23
8. xi. 49	<2	>500
Daily mean	61	—
Daily mean excluding 8. vi. 49 and 8. xi. 49	41	29

A typical example is shown in Fig. 5, in which rate of rise of the stimulus is plotted against stimulus strength. It will be seen that there is a critical slope, at which point the curve turns towards an infinitely high threshold. Table 3 gives the values of these critical slopes in terms of rheobases per sec., and its reciprocal, in msec., which approaches Hill's λ (Hill, 1936).

Except for two experiments, the results are moderately homogeneous. Of the two exceptions, the low value <2 *R*/sec. (18 Nov. 1949) was probably due to the fact that the frogs had hibernated by the time this experiment was done.

The interval between the end of the rising phase and the action potential did not shorten significantly until the critical slope was approached. For example, in the experiment of 8 June 1949, in which the critical slope was 260 rheobases per sec., i.e. 1 rheobase in 4 msec., the interval shortened when the rising time was increased to between 4·5 and 6 msec. (Fig. 6). In the experiment of 24 Aug. 1949, in which the critical slope was 73 rheobases per sec.,

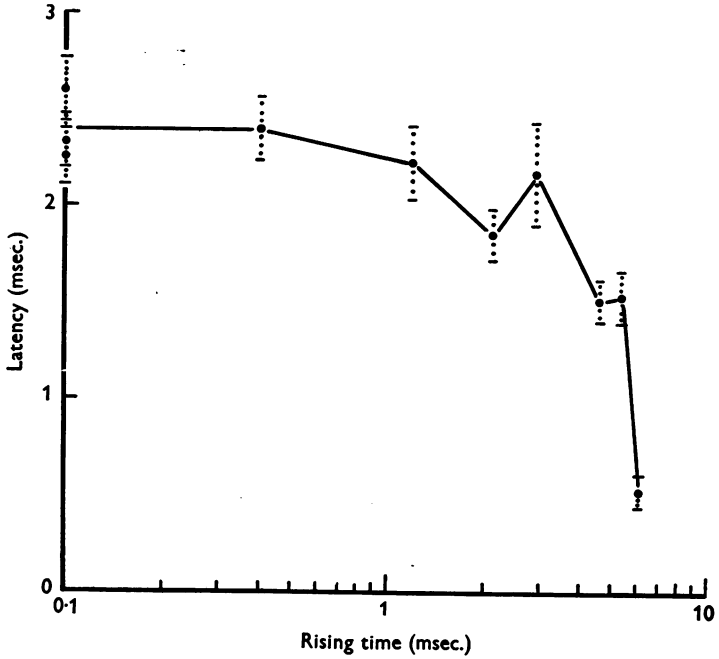

Fig. 6. Intervals between the end of the linearly rising phase of a long mechanical pulse and the action potential. Ordinate, interval msec. Abscissa, rising time of pulse, msec. The points are means of several observations and the limits represent 2 × standard error of the mean.

i.e. 1 rheobase in 14 msec., the interval shortened between 10 and 18 msec. rising time; while in the experiment of 8 Nov. 1949, with a critical slope less than 2 rheobases per sec., i.e. 1 rheobase in more than 500 msec., the interval shortened when the rising time was between 50 and 90 msec. From these experiments it is obvious that there is some relation between the rising time at which the interval shortens and the time required for the rise of 1 rheobase at the critical slope, and it is almost certain that a part at least of this decrease is because conditions adequate for excitation are established before the end of the stimulus rise. The fact that the latency from the end of the rise of the stimulus remained nearly constant except at the longest rising times, suggests that the latency is determined by a process that does not commence until threshold is nearly reached.

Summation

In four experiments the 'excitability' of the ending was tested at various intervals after the beginning of a subthreshold stimulus. The test stimulus was always a short mechanical pulse of a duration between 0·35 and 0·54 msec. The experiments were done with conditioning stimuli of duration both infinite and of the same order as the test stimulus. The results of the experiment shown in Fig. 7 are typical, except the last point with the long conditioning stimulus. In this experiment at the point at 49 msec. the contribution of the conditioning stimulus was zero. In all other experiments, however, including another four in which test stimuli were applied at intervals from 20 to 360 msec., it was found that, at intervals longer than 40 msec., the threshold remained constant and the conditioning stimulus still contributed up to 35% of the threshold to a test stimulus. The results obtained with short conditioning stimuli gave no definite evidence for or against alteration of 'excitability' after the end of the stimulus. The small negative deflexion in Fig. 7 was not consistently observed. Because of the irregularities in threshold (see 'Threshold'), it has not been practicable to describe the curves obtained in more exact quantitative terms.

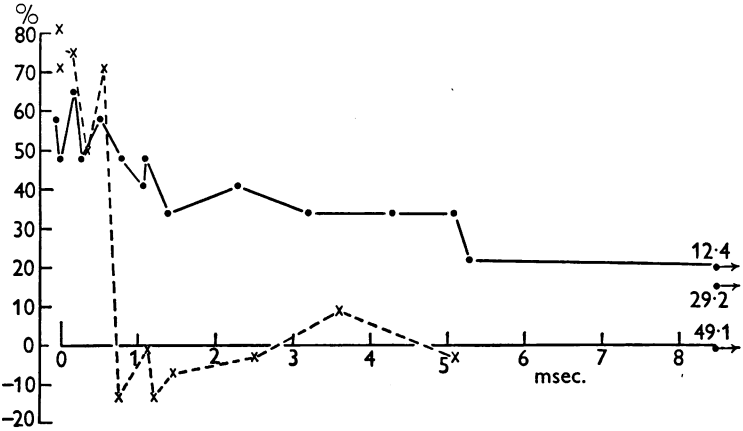

Fig. 7. Summation curves. Ordinate, contribution of conditioning stimulus as a percentage of the test pulse threshold, i.e. $100\,\frac{(S_0 - S_t)}{S_0}$, where S_0 = threshold of test shock alone, S_t = threshold of test shock at time t after beginning of conditioning pulse. Abscissa, time after beginning of conditioning stimulus, msec. ●—● conditioning stimulus of infinite duration at 66% of its own threshold. Test shocks 0·42 msec. duration. × — × conditioning stimulus of 0·6 msec. duration at 80% of its own threshold. Test shock 0·34 msec. duration.

DISCUSSION

Our results obtained on the touch receptors of the frog's dorsal skin with long, rectangular, mechanical pulses have shown the threshold for a repetitive discharge to be usually above the limit of our stimulator, i.e. 3·3 to 5·8 times

threshold for a single impulse. These figures are high compared with the majority of the figures given by Erlanger & Blair (1938), who used bundles of sensory fibres from the leg. These fibres must have included many from proprioceptors, which might be more slowly adapting than frog's touch receptors (Adrian, Cattell & Hoagland, 1931). By using bundles of fibres they were, of necessity, recording from those fibres with the lowest threshold for repetition and, in consequence, their experiments are not strictly comparable with ours.

No complete strength-duration curve has been obtained, but the ratio between the thresholds for long and short (0·4 msec.) stimuli gives one point on this curve (Table 1, col. 5), and this may be compared with the corresponding points on the curves given by Lucas (1907*a*) and Blair & Erlanger (1936) for nerve. Such comparison suggests that the curves may be similar in nerves and touch receptors.

The latency curves obtained here have the same general form as those found with the cat's mesenteric Pacinian corpuscle (Gray & Malcolm, 1950). In the present experiments on frog's skin it was impossible to find out the exact minimum latency between stimulus and initiation of action potential, but even if the observed minimum interval was entirely conduction time, the maximum latency observed after a short pulse was still approximately twice as long as that recorded from the Pacinian corpuscle. The minimum latency is obtained from the touch receptors in frog's skin with stimuli of three to four times threshold. In corresponding experiments on Pacinian corpuscle, the minimum latency was only obtained if the stimulus was greater than ten times threshold.

These long latencies after short (0·4 msec.) pulses are of quite a different order of magnitude from the latencies in nerve after electrical pulses of the same duration (Blair & Erlanger, 1936). The latencies in Pacinian corpuscles have been explained on the assumption that the part of the nerve depolarized by the mechanical stimulus is shorter than the length essential for propagation, but that if this depolarization is great enough it may spread until a sufficient length is depolarized for the initiation of a propagated response. The same explanation could apply to the even longer latencies observed in frog's touch receptors. The parameters of these latency curves must depend on a number of factors if our explanation is correct; the physical properties of the membrane, the time course of the active process and the structure of the ending may all play a part. Structurally, the Pacinian corpuscle and the touch receptor of frog's skin are very different. The Pacinian corpuscle has a highly specialized capsule, the axon terminating in only a few, probably only one or two, short branches, and it is rare for one axon to supply more than one corpuscle, though it may supply some small capsulated endings of much simpler structure (Sheehan, 1933). On the other hand, the frog's touch receptors are networks

of branching axons; there is no capsule or specialized histological structure and each axon branches into a considerable number of long, terminal filaments, which spread out over areas as large as 100 sq.mm. (Ecker & Wiedershein, 1896; Adrian, 1926; Adrian *et al.* 1931). Ecker & Wiedershein also describe a more specialized type of ending, and these may have been stimulated in some experiments, but it seems unlikely that these formed the majority. It is interesting that two such different types of ending should show the same type of behaviour as far as the latency after a short mechanical shock is concerned.

With maintained mechanical pulses, the maximum values are appreciably bigger than after short pulses. This difference suggests that an appreciable depolarization must be maintained during a steady pressure. In this respect the result differs from that so far obtained from the Pacinian corpuscle.

The curves relating threshold to the rate of rise of the stimulus are of some interest. The curves have the same general form as those obtained by Lucas in nerve with linearly increasing currents, and the numerical values found, though variable, are of the same order of magnitude (Lucas, 1907*b*; Fabre, 1927). The relation between a local potential and the rate of rise of stimulus must be considered in interpreting these results. Katz (1950) has shown that in the frog's muscle spindle there is a local potential change whose magnitude is dependent on the rate of increase of the tension. He considers whether a change of membrane capacity might be able to explain this effect. If this were true of frog's touch receptors one would expect a considerable increase of threshold if the rising time of the stimulus were as long as, or longer than, the membrane time constant. The longest membrane time constants for nerve so far reported are 6·8 msec. for crab axons (Hodgkin, 1947), and 2·3 msec. for lobster axons (Hodgkin & Rushton, 1946); but these are shorter than the rising times at which we found an increase of threshold in frog's touch receptors. It would seem, therefore, either that these endings do not show a velocity sensitive component of the local response, or the velocity sensitive component is not explicable in this way. The curves of rate of rise of stimulus against threshold could be explained entirely as nerve accommodation to a steady local depolarization, and the general quantitative agreement between our figures and those given for frog's nerve would fit with this view.

It has been suggested in connexion with the latencies between the end of the linearly rising stimulus and the action potential, that the process responsible for the latency does not begin till the stimulus approaches threshold. Thus our results are consistent with what is known of the development of the local response which, while detectable with smaller stimuli, is of appreciable size only when the stimulus approaches threshold (Hodgkin, 1938).

The summation curves using a mechanical test shock are complicated by the long latency that normally follows this short test shock. On this account one

would not expect to detect a gradual building up of potential at the ending, even if it occurs. It is, therefore, not surprising that the beginning of these summation curves is different from the first part of those presented by Erlanger & Blair (1931*b*) for the electrical excitation of frog nerve, and different from the curves we published previously of the excitability of Pacinian corpuscles after short, subthreshold, mechanical pulses tested with short electrical shocks. However, the falling part of our curves with long subthreshold conditioning stimuli are similar to those presented by Erlanger & Blair. In comparing the beginning of the curve with the facilitation curves of our previous paper, it must also be remembered that there is a spatial difference; in the previous experiments the electrical test shocks were applied perhaps as much as 1–2 mm. from the site of initiation of the non-propagated response. Furthermore, after the end of a short conditioning pulse we have not seen any summation, and in this our present results differ from those described previously, but the nature of the test shock would tend to obscure such an effect. Also if, as we have suggested, spatial spread is involved in setting up a propagated response, the test shock would be producing a non-propagated potential in a region whose excitability might be depressed by a first non-propagated potential (Erlanger & Blair, 1931*a*).

In this discussion some general comparisons between our results on the touch receptor and some of the classical results on the excitation of nerve have been made. Such comparisons must inevitably be vague, since the nerves used, the temperature, and other conditions, have differed. Also the classical work was largely done on bundles of fibres, a procedure which usually emphasizes the slowly accommodating fibres, whereas the response of only a single fibre has been observed in these experiments. The reliability of some of the work on accommodation has been questioned on two grounds. Parrack (1940) suggested that accommodation was found only in excised nerves, and that under normal conditions in the intact animal accommodation did not occur. Others, however, have found accommodation in man (Solandt, 1936; Granit & Skoglund, 1941; Kugelberg, 1944) and in non-excised mammalian nerve (Skoglund, 1942; Gray & Matthews, 1951). Polarization in the preparation, and in particular of the nerve sheath (Bishop, Erlanger & Gasser, 1928; Rashbass & Rushton, 1949) during a constant current may be partly responsible for some of the results obtained and such changes would, of course, have no bearing on the accommodation of sensory endings. All experiments on accommodation can be criticized on one or other of these grounds, and it is difficult at present to say how far polarization changes have distorted any particular result.

As the adaptation of the ending may be brought about by processes other than the accommodation of the axon, it is obvious that our results cannot give information about nerve accommodation.

SUMMARY

1. The behaviour of touch receptors in the frog's skin has been investigated by stimulating with mechanical pulses of controllable shape, duration and size.

2. Repetitive firing was seen in only two animals, when using maximum stimuli, which varied from 2 to 6 times threshold. The mean ratio between the threshold for pulses of approx. 0·4 msec. and infinite duration was 1·3, the standard deviation between preparations being 0·2.

3. The mean threshold latency for stimuli of infinite duration was 5·1 msec., with a standard deviation between preparations of 2·3 msec. With short stimuli the corresponding figures were mean 3·1 msec. and standard deviation 0·9.

4. Using linearly rising pulses, a critical slope was found, below which it was impossible to stimulate. The mean value of the critical slope was 61 rheobases per sec.

5. The excitability during and after both short and long subthreshold conditioning pulses has been tested with short mechanical pulses. After the beginning of the long pulse, the contribution to threshold provided by the conditioning stimulus fell until not later than 40 msec. it ceased to decrease, while still contributing up to 35% of the threshold level. After the end of the short conditioning pulses no residual excitability was seen.

6. These results are compared with the findings of other authors on frog nerve, and with our own results on Pacinian corpuscles. Their significance is discussed.

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