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THE RELATION BETWEEN MECHANICAL DISPLACEMENTS APPLIED TO A CAT'S PAD AND THE RESULTANT IMPULSE PATTERNS

BY D. R. G. FULLER AND J. A. B. GRAY
From the Department of Physiology, University College London

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SUMMARY

1. A way of determining an approximation to the distribution of impulses resulting from certain mechanical stimuli to a cat's pad is described. In essence this consists of calculating the results from a model of the way in which the impulses are set up.

2. The results of these calculations have been compared with results of experiments of a type different from those on which the calculations were based. Total numbers of impulses have been found by measuring mass action potential areas under appropriate conditions. The ranges of absolute numbers of impulses are similar for both calculated and direct results. The curves relating changes of number to changes of stimulus strength are similar in the two cases as are the effects of changing the position of the stimulus. Similar comparisons using two pulses at different times and distances apart have also been made. The over-all time distribution has been checked by reconstructing mass action potentials from the calculations and comparing these with those observed.

3. The calculations were carried out with values which were chosen in advance and which were based on previous experimental evidence; the results were in reasonable agreement with the experimental checks. It is therefore concluded that the results are a sufficiently good approximation to the neural responses of cats' pads to this type of stimulation to justify applying them in answering the questions posed in the Introduction.

INTRODUCTION

The problem of representation of information in a group of nerve fibres has been approached by posing three questions.

(*a*) How does the activity of each fibre in the group change when the stimulus is changed (for example in size or in position or in both together), and as a corollary how far is it possible to describe the stimulus from a knowledge of the response?

(*b*) How constant is the response to a given stimulus and as a corollary how precisely can a stimulus be described from a knowledge of the response?

(*c*) Which properties of this whole pattern of nerve impulses in the whole group of nerve fibres are important at any junctional region which follows?

The first question is basic and must be answered before the other two. It involves the quantitative relation between the response of the nerve fibres and the stimulus. The response cannot be measured in terms of impulse frequency alone; in any system impulse frequency in a unit may be changed by changing the stimulus in any one of a variety of ways; furthermore in some, perhaps many, systems which transmit information about rapid changes only a small part of the information is dependent on impulse frequency or other forms of pattern in time. It is therefore essential that the distribution of activity amongst the receptor units involved, i.e. the spatial pattern, should be determined. The group of receptor units involved in these experiments is that population which responds to small movements applied to a cat's pad. If a quantitative relation is to be obtained the stimuli must be precisely definable in a simple manner; the ones used in these experiments can be defined by three parameters—the amplitude of displacement and two numbers defining position. The first question may now be put in more specific terms: what are the quantitative changes which occur in the patterns of impulses in this population of units when the values of these parameters are changed either singly or in combination? The question can be extended to more complex stimulus situations and in this paper responses to pairs of stimuli are considered.

The use of these particular stimuli was determined primarily by practical considerations. It would, however, be wrong to think of them as unrelated to stimuli received by a cat's pad under natural conditions. The stimuli used were well within normal ranges, small in amplitude, and with a velocity at threshold only about twice the critical value. They differed from most common stimuli in being simple. However, in being simple and definable they offer further possibilities. Perhaps the most likely way in which it will be possible to predict the impulse patterns expected in response to complex stimuli will be by treating such stimuli as made up of large numbers of simple events appropriately arranged, just as a half-tone block or a picture on a television screen is built up from discrete dots each of which is defined by its brightness, position and time. Whether or not a point displacement could be used as an event for constructions of this kind can only be answered by further experiments, which would extend the work from pairs of stimuli to large numbers.

Having chosen the population of units and set of stimuli the next step is to determine the impulse pattern resulting from each stimulus. An approach to this problem has already been outlined (Armett, Gray, Hunsperger & Lal, 1962). Since each unit in this system fires only one or very few impulses in response to each stimulus, it is the spatial patterns which are important. The paper is concerned with the determination of these spatial patterns. This cannot be done directly, and the method used has been to measure the factors which determine the distribution of impulses, then to calculate the expected impulse patterns, and finally to check these answers against a different type of experiment.

METHODS

The observations described in the results section of this paper were obtained by monophasic recording from the nerve from the pad in the manner described by Armett *et al.* (1962). The values used for the calculations were all obtained by methods described either by Armett & Hunsperger (1961) or Armett *et al.* (1962).

Stimuli. All stimuli were step functions of mechanical displacement (not greater than 40 μ). These were delivered from Rochelle-salt crystals through glass styli with tips about 0·5 mm diameter. The crystals were mounted on manipulators graduated to 10 μ in all co-ordinates (for details see Armett & Hunsperger, 1961). The velocity of the displacement was sufficiently high (about twice critical at threshold) for the response of the receptor units to be determined solely by displacement amplitude and not at all by displacement velocity (see Armett & Hunsperger, 1961). Each stimulus could thus be defined by three parameters —the amplitude and two co-ordinates defining its position on the pad surface.

CALCULATIONS

The aim has been to calculate the time at which each impulse is initiated in each receptor unit of a model having properties based on the known properties of pads and their receptor units.

General basis of calculations. Armett & Hunsperger (1961) showed that a mechanical stimulus to the pad causes a mechanical process to spread and that this mechanical process is responsible for the excitation of the receptors. They further showed that this process has two phases of opposite polarity at a constant interval apart. On reaching a receptor one or other of the two phases may excite it after a latency dependent on the ratio of amplitude to threshold. As the distance of the stimulus from the centre of the receptive field is increased so is the amplitude of the displacement required to excite the receptor. The process can be described in terms of a damped mechanical wave, spreading at a finite velocity and attenuating with distance, but it is important to realize that this description is based on the behaviour of the receptor units and it remains a description of their behaviour even if the physical explanation should need modification.

The values used in the calculations have been obtained from the original results of Armett & Hunsperger (1961) and Armett *et al.* (1962), and from additional results (unpublished) of J. A. B. Gray & R. W. Hunsperger and of D. R. G. Fuller & A. Maillart using the same methods.

The data from which the calculations are made are (1) the number and distribution of units, (2) the properties of unit behaviour expressed in terms of a mechanical wave, (3) the distribution of excitability amongst the units and (4) certain processes in the initiation of impulses. From these, the times of impulses in all the units for any specified stimulus can be calculated.

Number and distribution of units. The number and distribution used by Armett *et al.* (1962) has been used again. The number was based on the observations of B. C. M. Williams (unpublished) that there are, in the nerve from the main part of the pad, 50–100 fibres having diameters consistent with the conduction velocities found by Armett & Hunsperger (1961). It was assumed that the receptive fields of the units are regularly spaced over the area of the central main part of the pad, about 120 mm^2. This assumption is consistent with Fig. 2*b* and leads to a spacing of 1·33 mm between the centres of the receptive fields of the units; a general arrangement is indicated by Figs. 3 and 4.

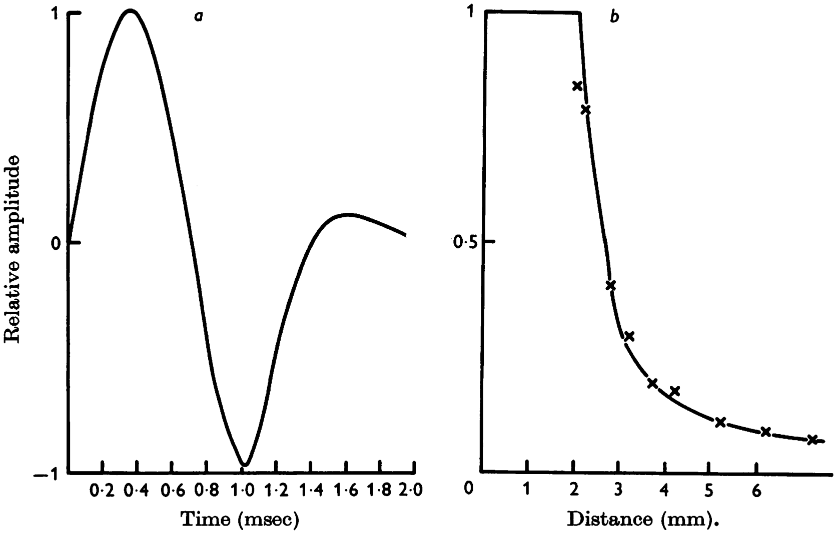

Fig. 1. Properties of the mechanical process in the pad. *a*, Time course of wave; plot of eqn. 1. Abscissa, time in msec; ordinate, relative amplitude. *b*, Attenuation of mechanical process with distance; line is plot of eqn. 2. The crosses are experimental points of displacement normal to the surface (J. A. B. Gray & R. W. Hunsperger, unpublished). Abscissa, distance in millimetres; ordinate, relative amplitude.

The properties of unit behaviour expressed in terms of the mechanical wave. Armett & Hunsperger (1961) have shown that the form of the excitability curves illustrated in their figs. 8 and 10 could be accounted for mechanically. The period of the wave, relative amplitude of the two main phases, and the time course of the subsequent decay were taken from the general pattern of such curves. The relation used in the calculations is shown in Fig. 1 *a*; it is a plot, against time, of

$$\left.\begin{array}{ll}\sin(2\pi t/1{\cdot}4) \text{ from } t = 0 \text{ to } t = 1{\cdot}05, \\ \exp[-(t-1{\cdot}05)/0{\cdot}3]\sin(2\pi t/1{\cdot}4) \text{ when } t > 1{\cdot}05,\end{array}\right\} \tag{1}$$

where t = time in msec. Armett & Hunsperger's observations indicate that most half periods lie in the range 0·5–1·0 msec.

The velocity of the mechanical wave was derived by them from observations on the displacement of the pad surface, and also by observations on the shifts in the time of excitation. Four measurements gave values between 11 and 13 m/sec, one gave 32 m/sec. A value of 13 m/sec has been used in these calculations.

Receptive fields have a central area of uniform threshold outside which threshold increases with increasing distance from the centre. Units with large receptive fields tend to have low thresholds. The method used to describe these properties was that suggested by Armett & Hunsperger (1961). The central area was given a constant threshold and outside this the rise in threshold was treated as the attenuation of a mechanical process. The latter was measured as displacement normal to the surface (Fig. 1*b*).

The resulting equation, in which a = attenuation factor and D = distance in millimetres, is

$$\left.\begin{array}{ll}a = 12{\cdot}5\exp\left(-\dfrac{D-2{\cdot}0}{0{\cdot}65}\right)+2{\cdot}7\exp\left(-\dfrac{D-2{\cdot}0}{6{\cdot}5}\right) & \text{when } D \geqslant 2{\cdot}0, \\ a = 1 \quad \text{when } D < 2{\cdot}0. & \end{array}\right\} \tag{2}$$

This is illustrated in Fig. 1 *b*.

Receptor unit threshold. The range of the thresholds of receptor units in any one cat was measured by D. R. G. Fuller & A. Maillart (unpublished). In each cat as many receptor units as possible were found and the threshold recorded at the most sensitive point in each receptive field. Each value was then scaled as a multiple of the most excitable unit found in that pad. The units from three pads were pooled and are shown in the histogram in Fig. 2*a*. The curve is that of the equation

$$\left.\begin{array}{ll}q = 1/11{\cdot}2\{29{\cdot}5\exp[-0{\cdot}446(T-1)]+25{\cdot}8\log_e T-29{\cdot}2\} & \text{from } T = 1 \text{ to } T = 3{\cdot}109 \\ q = 1/11{\cdot}2\{29{\cdot}5\exp[-0{\cdot}446(T-1)]\} & \text{for } T > 3{\cdot}109,\end{array}\right\} \tag{3}$$

where T is the threshold value relative to that of the most excitable unit and q is the ratio of the probability density to that of the most probable value. During the calculations each receptor unit of the model was assigned a threshold at random, but these were distributed according to the frequency distribution just described. That thresholds could be assigned at random is an assumption, but is not contrary to the evidence that has been obtained (see Fig. 2*b*).

The initiation of impulses. The simplest description, used in the earlier calculations, was to see that the quantity

$$aI/T+f \tag{4}$$

was greater than unity (where a = attenuation factor from equation 2, I = stimulus strength in multiples of the threshold of the most excitable unit, T = the threshold of the unit and f = a normally distributed fluctuation of threshold). If it was, then an impulse was taken to be initiated with a latency given by

$$0{\cdot}39\exp\left(-\frac{aI/T+f-1}{1{\cdot}05}\right) \tag{5}$$

after the time at which the mechanical wave reached the receptor.

In three curves analysed the proportionality constant ranged from 0·39 to 0·53 and the denominator of the exponent from 0·62 to 2·14.

In the fuller calculations a wave form (eqn. 1) was multiplied by the factor (4). A similar calculation was made for the second stimulus, if any, and, taking account of any delays in application or in the spread of the mechanical wave, the two were summed. The appropriate

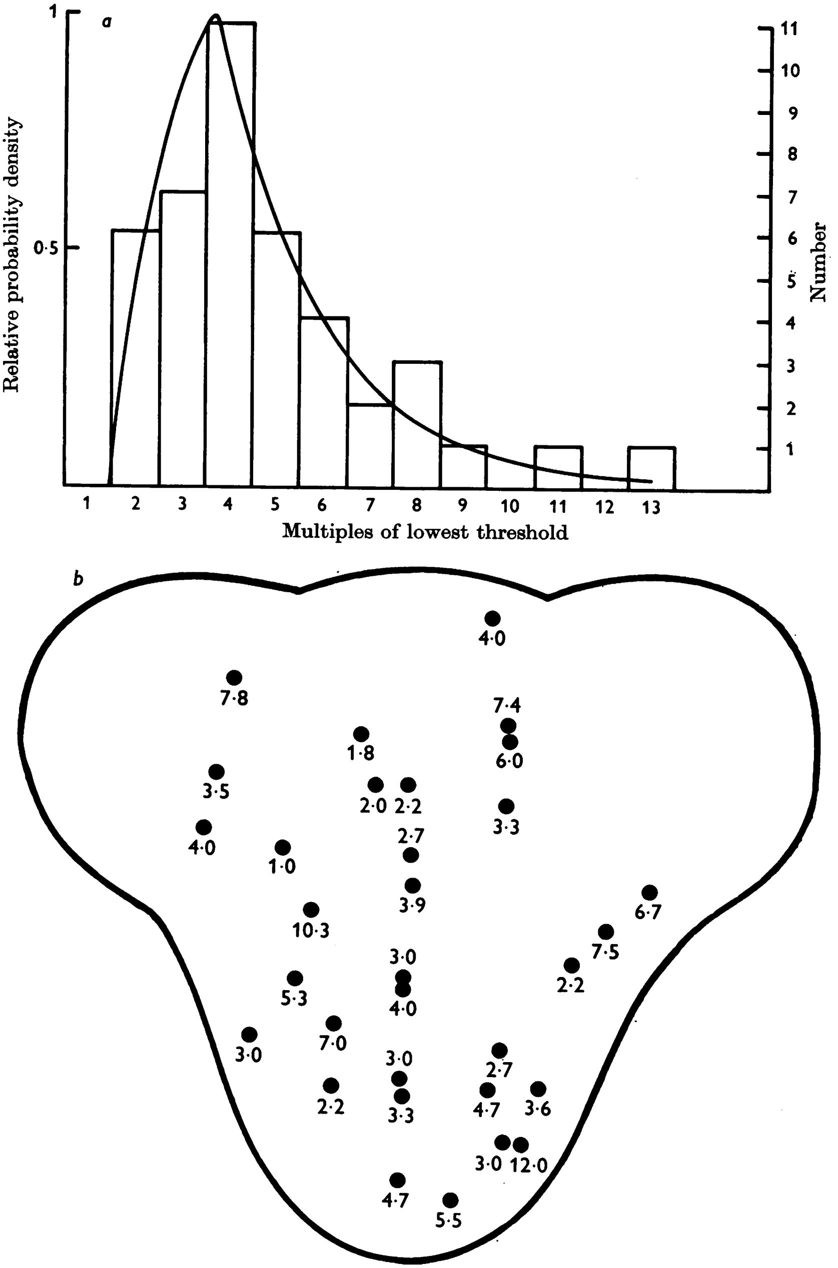

Fig. 2. *a*, Frequency distribution of thresholds of receptor units. Ordinate: left scale—relative probability density, right scale—number. Abscissa: threshold in multiples of lowest. Curve is a plot of eqn. 3. Histogram represents observations of D. R. G. Fuller & A. Maillart (unpublished). *b*, Plan of pad showing relative thresholds of a number of units and the approximate positions at which they were found.

receptor potential was then found by considering the wave in 0·1 msec steps and adding a quantity, related to the mechanical increment during the step, if both total amplitude and increment of the wave were of the same and correct polarity. About half the units respond to the positive phase of the wave and about half to the negative phase (Armett & Hunsperger, 1961); units were allocated at random to these classes. The excitation characteristics of these units are very similar to Pacinian corpuscles. The relation between stimulus displacement and receptor potential given by Diamond, Gray & Inman (1958; Fig. 4*d*) can be fitted closely by an exponential. The relation in the frog's muscle spindle (Katz, 1950) is similar. In these calculations the relation between the mechanical wave and the receptor potential was taken to be the same as in Pacinian corpuscles. Receptor potentials in Pacinian corpuscles decay exponentially with a time constant which is probably that of the nerve membrane (Gray & Sato, 1953; Inman & Peruzzi, 1961; Ishiko & Loewenstein, 1961; Sato, 1963). Account has been taken of this decay in the calculations, using a time constant of 1·7 msec. A suitable scaling factor was applied so that when the factor (4) was exactly unity, the peak of the receptor potential was also unity.

When the calculated receptor potential reached unity an impulse was recorded, unless the unit had fired previously in which case the threshold was taken, not as unity, but as

$$12{,}300\,(t_2' - t_1')^{-3\cdot 24} + 1, \tag{6}$$

where t_2' is the time of comparison and t_1' the time of the last impulse, both measured in units of 0·1 msec from the stimulus. The form of this relation is based on that used by Gray & Lal (1965) for second-order cells of this system and the constants are based on the points given by Armett & Hunsperger (1961) (see also Gray & Malcolm, 1950).

'Expected' number of active receptor units. The 'expected' number of receptor units activated in response to a single stimulus could be calculated more simply. The number of units at each distance from the stimulus was noted and the attenuation factor for each of these distances calculated. For any strength of applied stimulus the displacement at each distance could be found. A plot of the integral of eqn. 3 was prepared and the probability of a unit having a threshold less than a given value could be read off. These probabilities multiplied by the number in each class and summed over all classes gave the 'expected' number of active receptor units.

RESULTS

There are two sets of results to be described: those calculated from the properties of the pad and its units and those inferred from the areas of mass-action potentials. For convenience the former will be referred to as the calculated results and the latter as the experimental results. The experimental results are presented on the supposition that the area of the monophasically recorded potential is approximately proportional to the total number of impulses. The areas have been scaled in multiples of the area of the all-or-nothing deflexion due to a single impulse resulting from a just threshold stimulus obtained in the same run. Some of the results presented by Armett *et al.* (1962) were treated in this way and the justification of doing so was considered in that paper.

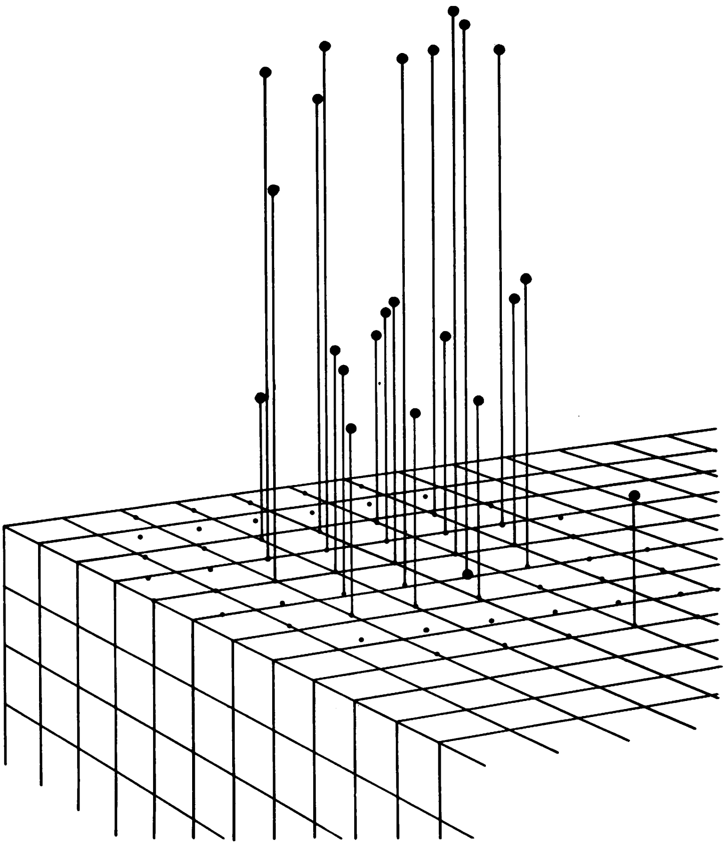

Fig. 3. Plot of a three-dimensional display on perspective paper to show a typical distribution of impulses obtained by calculation. Horizontal axes represent distances on pad—unit spacing 1·33 mm. Vertical axis represents time after stimulus; stimulus at top, largest latency at bottom. Filled circles indicate impulses. Single stimulus, strength 5·3, position central. The unit which fired twice fired at 0·1 and 1·5 msec.

The type of response obtained by calculation

The results are most effectively displayed on a three-dimensional model. Figure 3 is a plot on perspective paper of a display of this kind. The main features are that as distance increases from the point of stimulation density of activity decreases and latency increases, and there are two groups of impulses distinct in time. A more practical display is given in Fig. 4 for four different strengths of stimulus. The values of stimulus strength are comparable for the calculated and the experimental results.

The working reference point of the calculations has been the threshold of the most excitable unit in the population. In the experiments the reference point has been the smallest stimulus, at a random point, giving a response. To equate these two the stimulus scale of all calculated results has been corrected so that unity represents that stimulus strength at which there is a 0·5 probability that one of the seven units under or around the stimulus will fire; all calculations have been made with the stimulus exactly on a unit.

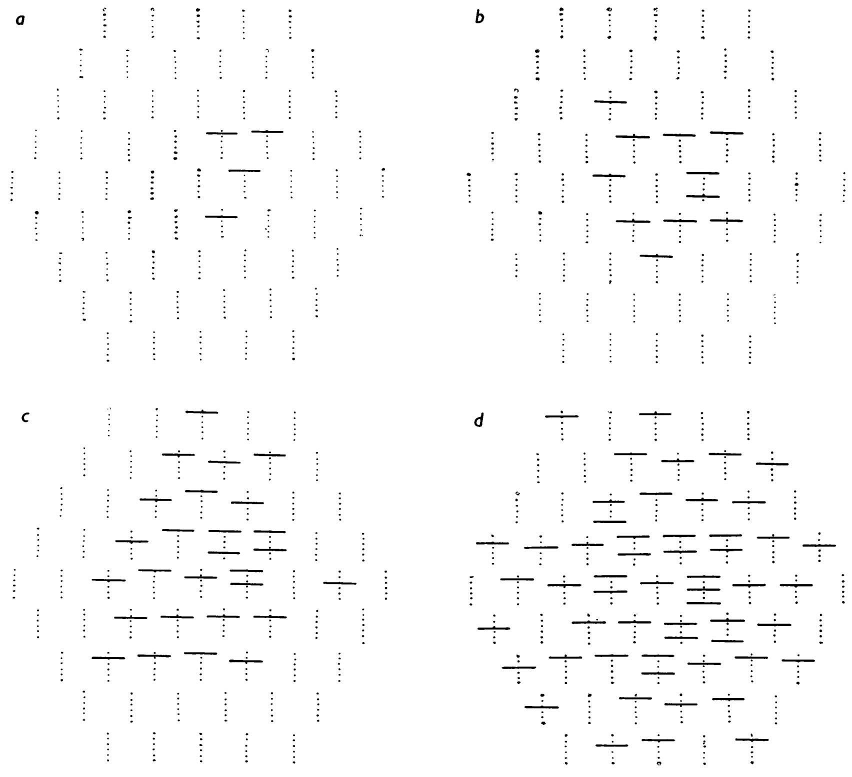

Fig. 4. Two-dimensional displays to represent dimensions shown in Fig. 3. Columns of small dots represent time scales with 0·5 msec intervals at receptor unit positions. Stimulus at top, maximum latency at bottom. Bars indicate impulses. All responses to single stimuli at centre; each part indicates a different stimulus strength, all other factors in the calculation being constant. *a*, 1·9; *b*, 3·7; *c*, 7·4; *d*, 14·8. (See text for scaling.)

Dependence of the calculated response on the constants used. The earliest calculations differed in two main respects from the later ones; first, threshold and latency were determined without calculating a mechanical wave form and receptor potential (see above); secondly, the frequency distribution of threshold was taken as rectangular from 1 to 5 instead of that given in Fig. 2*a*. Graphs plotting stimulus strength against number of impulses for five different random allocations of excitability are shown in Fig. 5*a*. These may be compared with Fig. 5*b* which was calculated with the final programme.

Using the earliest programme a number of calculations, in which certain constants were varied, were made. It will be sufficient here simply to quote the total number of impulses corresponding to the largest stimulus in each series. The mean value of the points at the largest stimulus strengths in Fig. 5*a* is 36. When the 'plateau' dimension in eqn. 2 (Fig. 1*b*) was reduced from 2·0 to 1·0 mm the number fell to 19. When the width of the rectangular distribution of thresholds was changed from that of 1–5 to other values the results were: 1–2, 60; 1–3, 48; 1–4, 45; 1–9, 22. When the mechanical attenuation function, eqn. 2, was replaced by a single exponential term, the range of exponential constants which approximately fitted the experimental results was from 1·2 to 1·9. The results obtained on calculation were: 1·2, 37; 1·5, 42; 1·9, 53.

Throughout the rest of this paper the calculations quoted were made using the values given in the sections headed calculations; these were chosen on external evidence before the calculations were done.

Comparison of calculated and experimental results

Single stimuli

Comparison of numbers of impulses. There are four comparisons to be made: (1) of the absolute numbers, (2) of the relation between number and stimulus strength, (3) of the relation between number and position of the stimulus, and (4) of the occurrence of repetition.

Figure 6 shows a number of experimental curves plotted together. There are considerable differences in the positions of the curves; impulse numbers at the stimulus strength corresponding to the numbers quoted in the last section range from about 14 to 50. It is not surprising that there are considerable variations. These curves are all scaled in terms of the area of a single all-or-nothing impulse. Since the nerve must be undamaged if the total number of impulses is to be measured, a single impulse is bound to be near noise level and measurements of its area are bound to be subjected to considerable errors, which are then reflected in the whole position of the curve. It is clear however that the model using the values obtained on external evidence gives absolute values in the same range as those found experimentally.

The relation between number of impulses or active units and the amplitude of the stimulus is shown for direct observation in Figs. 6 and 7 and for calculations in Figs. 5 and 9.

Change in position of the stimulus has little effect on the number of impulses fired according to the calculations, though there is some decrease in number as the stimulus is moved from the centre owing to the effect of the pad edges. Direct observation has shown that curves of number against stimulus strength do not change as the position of the stimulus is moved more than would be expected from the various errors involved.

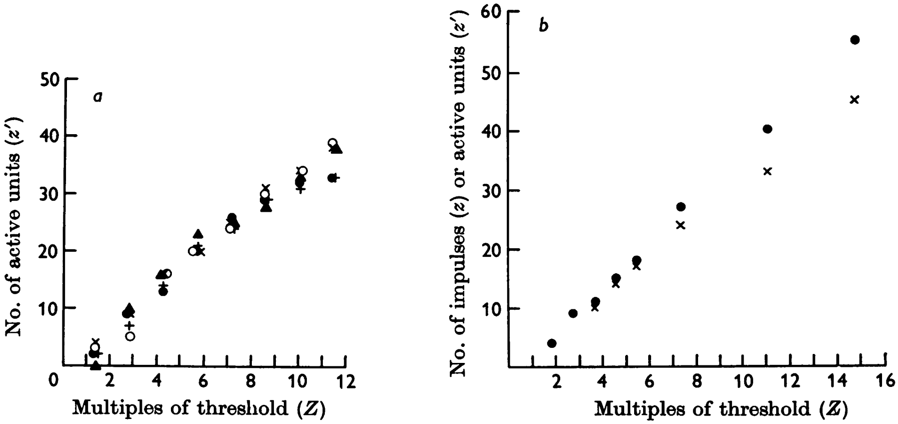

Fig. 5. Plot of calculated number of impulses or active units, ordinate, against stimulus strength, abscissa. *a*, Five sets of calculations with the first programme showing the effect of different random allocation of excitabilities. *b*, An example calculated with the final programme. Filled circles, total number of impulses; crosses, number of active units.

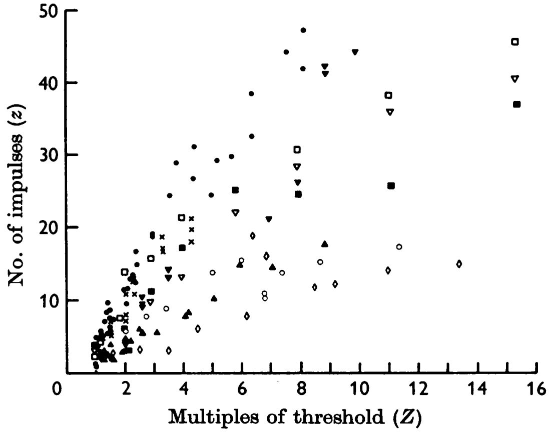

Fig. 6

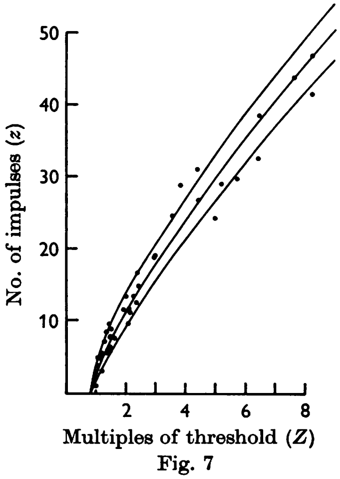

Fig. 7

Fig. 6. Plot of number of impulses, ordinate, against stimulus strength, abscissa, for direct experiments. Each symbol represents a separate set of results.

Fig. 7. Plot of number of impulses (z) against stimulus strength (Z) for one experimental result. Line of fit is $\bar{z} = 9{\cdot}86\,(Z-0{\cdot}8)^{0{\cdot}774}$. The error lines are ± one standard deviation, the standard deviation being proportional to the square root of the number.

Multiple firing in a unit may occur with the larger stimuli (Fig. 4). The largest stimuli used experimentally by Armett & Hunsperger (1961) were about 8 times threshold. They reported double firing in three out of seven units used for a particular experiment, but state that double firing was 'exceptional' in their whole series. In the calculation illustrated in Figs. 4 and 5*b*, three units out of twenty-four fired twice at a stimulus strength 7·4 times threshold. In Fig. 5*b* the crosses indicate the number of active units and the points the total number of impulses discharged.

Time course. The time course of the total activity determines the shape of the monophasically recorded action potential. If the time course of the calculated patterns is similar to the real patterns then the monophasic action potentials constructed in the computer should be similar to those recorded from the animal. Figure 8 shows a series of comparisons. In Fig. 8*a* the responses were calculated with identical values except that the distribution of excitabilities to the individual units was different in each case (see Fig. 5*a*). The experimental responses have been obtained with the same stimulus strength as the calculated ones in five different experiments. They have been chosen to match the calculated ones and each record has had to be independently adjusted in amplitude. Figure 8*b* is a comparison of a single set of calculations with a single experiment, in both of which only the stimulus strength was altered. In this comparison the amplitude scale of the experimental responses was adjusted at one point only. Figures 8*c* and *d* are referred to below. The experimental records chosen for these comparisons can be regarded as typical of records obtained, with the qualification that there are amongst the experimental results a number of examples showing smoother shapes (e.g. record in Fig. 8*d*) than have been found in the calculated series. The calculations assume constant characteristics over the whole system; variations in these from one part of the pad to another would, in general, be expected to smooth out the overall response.

Scatter. Figure 7 shows the scatter of values, partly experimental and partly inherent, found in a good experiment. The points have been published previously by Armett *et al.* 1962) (fig. 1). In the present figure, curves have been added. The central line was fitted by least squares on a log-log transformation. A power function fitted a number of experimental and calculated curves reasonably well, but this form could not be regarded as applying to all results (cf. Werner & Mountcastle, 1965). The outer lines represent plus and minus one standard deviation, which has been calculated by making the variance proportional to the number of impulses fired. Proportionality between variance and number has been found to be a better fit than proportionality between standard deviation and number or a constant standard deviation for both experimental and calculated

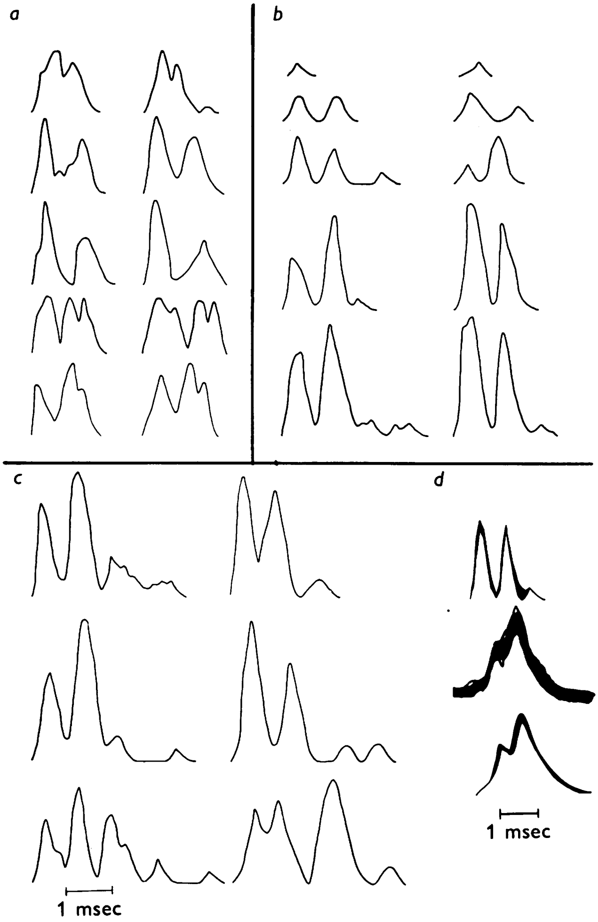

Fig. 8. Comparisons of calculated (left) and observed (right) monophasic action potentials from the whole nerve from the pad. *a*, Calculations with different random distributions of excitability, stimulus strength 4; observed from different experiments stimulus strength about 4. *b*, One set of calculations, stimulus strengths 1, 2, 3, 5, 8; one set of observations, stimulus strengths 1, 2, 2·8, 5·4, 8. *c*, One set of calculations with two pulses compared with one experiment; amplitude adjusted in 2nd pair; conditions as follows:

Calculated				Experiment			
Stim. 1	Stim. 2.	Int.	Dist.	Stim. 1	Stim. 2	Int.	Dist.
5	5	0	1·33	5·4	5·4	0	1·33
5	5	0·2	4·0	5·4	5·4	0·3	4·0
5	5	0·7	4·0	5·4	5·4	0·7	4·0

a, *b*, *c*, on same time scale; *d*, error fluctuations. For further details see text.

results. Theoretical consideration of the model leads to an expectation that the results might approximate to this relation. This arises since the variance of a sum of random variables is the weighted sum of the individual variances, and the number of units which, in this case, need to be considered as random variables is approximately proportional to the number of units fired.

In the calculations it was assumed that the thresholds of receptor units fluctuate in a normal manner independently of each other. This must be generally true of local factors, but would be untrue of those involving whole sectors of the mechanical wave. Calculations of responses to a constant stimulus were repeated and the standard deviation of the number of impulses calculated. These were done at three strengths of stimulus and taking a coefficient of variation of threshold at each unit of 10 %. This was considered to be an upper limit in view of the results of Diamond *et al.* (1958) and Loewenstein & Ishiko (1959) on the receptor potentials of Pacinian corpuscles and of the values given by Armett *et al.* (1962) for threshold measurements on one group of cells, second order to the system discussed here. The standard deviation of the number of active receptor units was also found in the course of calculating the 'expected' number of active receptor units by the method described in an earlier section. The standard deviations obtained by the two methods agree within 10 % and in Fig. 9 lines indicating plus and minus one standard deviation (proportional to square root of number) are drawn; in this curve the points are the 'expected' number of active receptor units. Figure 9 may be compared with Fig. 7, the scatter in the latter, which includes random measuring

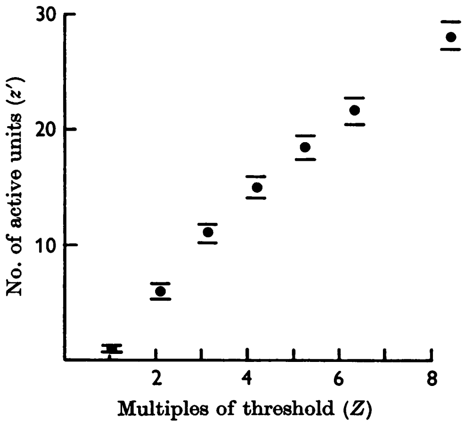

Fig. 9. Plot of 'expected' number of active receptor units against stimulus strength. Bars are ± one standard deviation, the standard deviation being proportional to the square root of the number.

errors, being about 2·5 times that in the former. Figure 8*d* illustrates the effect on a constructed mass response of introducing in the calculation a 10 % coefficient of variation of threshold at each receptor. The calculated response shows the range within which ten calculations fell; the photograph is a record of some ten to twenty superimposed traces; the final picture is derived from the photograph by subtracting the range of fluctuation occurring before the response from the ranges measured at different times during the response.

Pairs of stimuli

Series of experimental observations and series of calculations have been made of two stimuli at varying distances apart from 1·33 mm to 5·33 mm at various intervals up to 1·4 msec, and at various stimulus strengths. Results have been analysed for each stimulus strength, by taking means of all times at each distance and of all distances at each time. Plots have been made of number of impulses against time and against distance. Results experimental and calculated are shown in Fig. 10. Some comparisons of the shape of monophasic action potentials recorded and reconstructed are shown in Fig. 8*c*. This is a comparison of a single set of calculations with a single experiment; as in Fig. 8*b* the amplitude of the experimental results has been adjusted at one point only.

DISCUSSION

Any discussion of the results described in the last section depends on the acceptance of these results as a first approximation to the patterns of impulses set up in the animal under the restricted conditions imposed in these experiments; that is, dealing solely with one or two rapid displacements applied to small points when there is no pressure on the rest of the foot. The extension of the analysis to more complex, and more biological, situations depends on satisfactory results in the simplest situations. The calculations are based on a series of experimental observations which have been described earlier in this paper. The main results depend on (1) the number and distribution of receptor units, (2) the properties of the units as expressed in terms of a mechanical process, and (3) the distribution of thresholds of the receptor units. Figure 9, for example, was calculated on these three factors alone. All the values used in the calculations were chosen in advance on the basis of experimental evidence. The effects of varying some of these values on the absolute number of impulses fired have been considered in the second section of results.

Are the patterns of impulses calculated in this way a first approximation to those occurring in the animal? The absolute values of total numbers of impulses found in the experiments range around the calculated value;

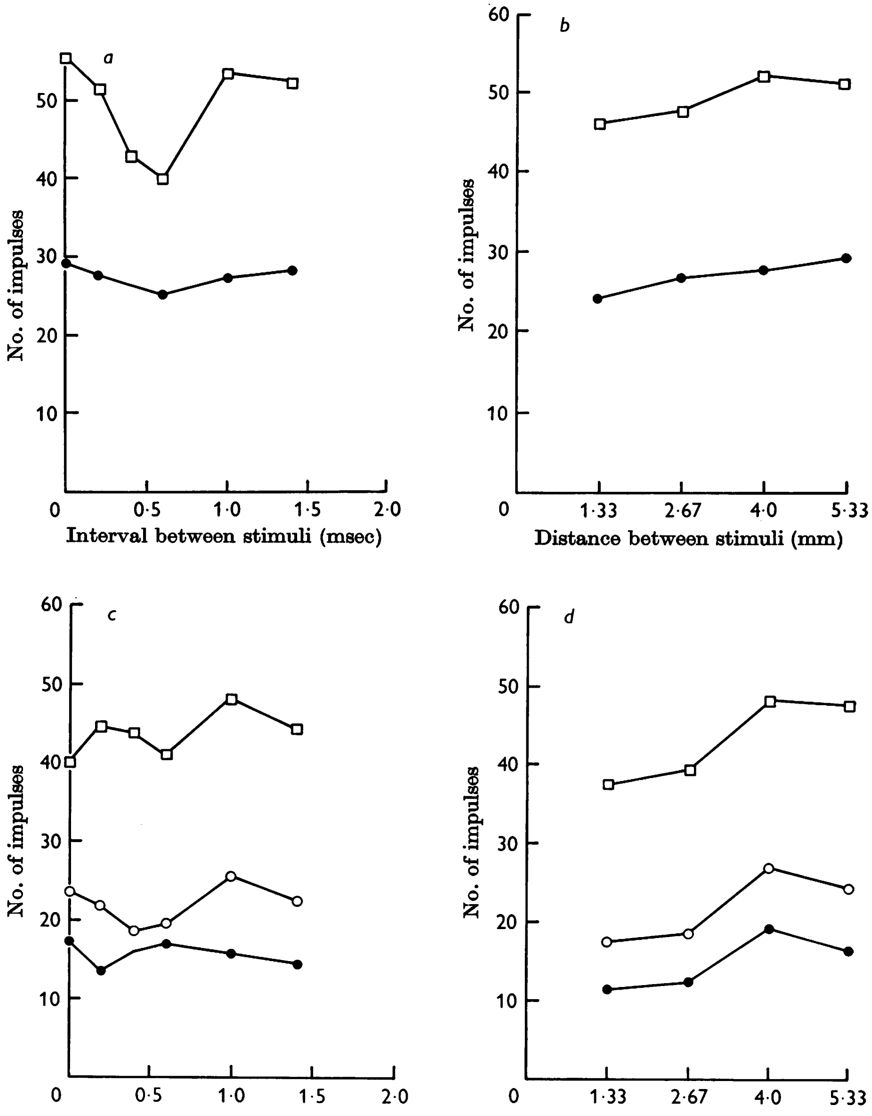

Fig. 10. Results of experiments and calculations with two stimuli. *a* and *b*, calculated; *c* and *d*, experimental. *a* and *c*, plots of number of impulses against time interval between stimuli averaged over all distances. *b* and *d*, plots of number of impulses against distance between stimuli averaged over all time intervals. Stimuli had same strength for both stimuli in each pair; values were experimental 8, 5·4 and 4 times threshold and calculated 7·4 and 3·7 times threshold.

since the frequency with which units fired more than once was approximately the same for both types of result, it can be said that the number of units active is similar in the two cases. The total number of units of this type in the main section of the pad cannot, therefore, be much less than the number used, and the fibre counts mentioned in the section on calculations set a clear upper limit. The numbers of impulses for any given stimulus strength do not change significantly when the position of the stimulus is changed. Either the system is uniform or all stimuli in all positions are equally available to all units. The second alternative is incompatible with the nature of the receptive fields, and hence the distribution of units and their excitabilities must be reasonably uniform. The general form of the impulse distributions must therefore be similar to that predicted by the calculations. This leaves the question of the area covered by any particular pattern. The rate of change of impulse number with stimulus strength is nearly the same for both calculated and experimental results; this is determined both by the increasing spread of excitation with increasing stimulus strength, i.e. the characteristics of the receptive field, and by the distribution of excitabilities. The balance of these two factors also determines the area over which the fixed number of impulses corresponding to a particular stimulus will be distributed. This means that if the areas found are wrong, there must be errors in both the observations of receptive fields and of the excitability distribution in such a way that they compensate each other in respect of the stimulus/number relation. The shapes of the curves relating to pairs of stimuli and the time distributions of the activity also show reasonable agreement between the calculated and experimental results.

It is therefore concluded that the results of the calculations are a sufficiently good approximation to the general behaviour of cats' pads to this type of stimulation to justify applying them in answering the questions posed in the Introduction.

These questions require, for their answer, some analysis of the results. Such analyses simply involve relating the set of stimuli, each member of which can be defined by three parameters, to the corresponding responses as worked out above; the responses to single point stimuli can also be described by three parameters. There is a choice in deciding which measurements are to be used, but in any case the analysis is simply a restatement of the results already described and involves no further results or assumptions. The interest of relations between stimulus and impulse pattern and the consistency of such relations is in general twofold. First, how much can be learnt about a stimulus from a knowledge of an impulse pattern in the population of primary receptor units; that is, looking at the problem of the primary mechanism as a problem in its own right without any regard to what information is subsequently used. Secondly, what factors in the primary patterns are of significance to the first junctional zone and how do the primary patterns relate to those in the second-order cells. For the present our concern is solely with the first view point. It is not possible to describe the analyses in detail, but the following is a brief summary of the behaviour of the population of units from the pad as indicated by the results given above. The total number of impulses and the number of active units are related to the amplitude of displacement and are nearly independent of position. The spatial distributions of impulses set up by single point stimuli tend towards being radially symmetrical as numbers increase. The positions of the centres of these distributions can be estimated and they relate closely to the positions of the stimuli, the accuracy of the estimates being a function of stimulus amplitude. If an impulse pattern is known, it is possible, from the stimulus–response relation and the known errors of this relation, to make a statement about the stimulus associated with the pattern. Such a statement can indicate the expected amplitude of displacement and position of the stimulus and can also indicate confidence limits within which the characteristics of the stimulus would be expected to lie. The potential accuracy and precision of the system are of interest in that they are important consequences of the mechanisms investigated. Any particular means of extracting information from the impulse patterns may not reveal all the available information, but will indicate a lower limit to what is available; the means employed by the first junctional zone are not necessarily the most efficient. The best precision which has been obtained from the results given in this paper is that there would be a 0·68 probability that the stimulus had an amplitude within 10 % of the expected value and that the position was within 0·3 mm. of the expected position (see Gray 1966).

The results with two stimuli described in this paper give a basis for work on more complex stimuli. It may be that any stimulus may be defined in terms of a sufficient number of points having suitable temporal and spatial relations. It is now possible to make predictions on this basis and it should be possible to design experiments to check such predictions.

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