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EXCITATION OF RECEPTORS IN THE PAD OF THE CAT BY SINGLE AND DOUBLE MECHANICAL PULSES

BY CHRISTINE J. ARMETT* AND R. W. HUNSPERGER†
From the Department of Physiology, University College London

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Information about the strength and position of one or more points of mechanical contact with the skin may be transmitted in a number of nerve fibres acting as an organized group. The coding of such information in a group of receptor fibres from the cat's pad has been investigated by C. J. Armett, J. A. B. Gray, R. W. Hunsperger and S. Lal (unpublished), who have also investigated the way in which this code is modified at the first synaptic junction. A single stimulus, having a particular position and strength, sets up in the primary fibres a pattern of activity which is, within limits, uniquely related to that stimulus. The mechanism which determines this pattern is naturally of interest, because an understanding of it would enable the patterns of activity set up by more complicated combinations of stimuli to be predicted. Basic points in this problem are the size of the receptive fields and the amount of overlap between them. Such receptive fields might be determined by a branching of the receptor nerve fibre to cover the area; on the other hand a single receptor in the centre of the field would be all that would be required if the stimulus set up a mechanical wave that travelled across the pad. The experiments described in this paper are concerned with this problem, and the results indicate that a mechanical wave does travel across the pad as a result of each stimulus and that this wave is important in determining the pattern of activity that results in the primary fibres.

The first section of the results deals with experiments in which single stimuli were used to excite single receptor units. The second section deals with the effects of a mechanical pulse on the excitability of the units to a second pulse.

METHODS

The experiments were performed on cats anaesthetized with chloralose, 0·05 g/kg, and urethane, 0·5 g/kg. The lumbar cord was exposed to give access to the dorsal roots, and the animal was then mounted rigidly in a frame (cf. Fernandez de Molina & Gray, 1957); steel

* Present address: Department of Pharmacology, Albert Einstein College of Medicine, Morris Park Avenue and Eastchester Road, Bronx, 61, N.Y., U.S.A.
† Present address: Physiological Institute, University of Zurich, Zurich, Rämistr. 69, Switzerland.

needles were passed ventral to the bodies of lumbar vertebrae, but dorsal to the transverse processes, and were then fastened to the frame. A hind foot was mounted, pad upwards, on a brass plate attached to the frame; the foot was held by a stitch, and the whole, including the pad, stabilized by embedding it up to the level of the pad surface in paraffin wax. The medial plantar nerve was exposed, laid over a pair of electrodes and then embedded in low-melting-point paraffin wax. The lateral plantar nerve was cut.

Mechanical stimulation. Mechanical pulses were derived from Rochelle salt crystals (Gray & Malcolm, 1950); in these experiments larger crystals 2·5 cm^2 were used and they were damped with silicone grease instead of oil. Two such crystals were needed and each was mounted on a manipulator, which was graduated in steps of 10 μ in the three planes at right angles to each other. The glass styli, by which the displacements of these crystals were transmitted to the pad, had tip diameters of *ca.* 0·5 mm. When a stylus was lowered to the surface of the pad, the point of contact could be seen by the electrical output from the crystal. The position of contact could be established in this way, correct to a few tens of micra, and the resting position was usually adjusted to be 0·3–0·75 mm deep to this position of contact.

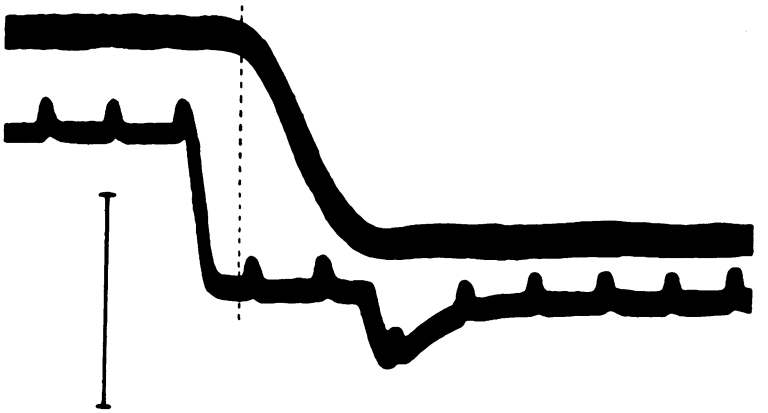

Fig. 1. Displacement of the moving corner of the crystal (top) after the application of a rectangular voltage pulse followed by a voltage pulse having an exponential decay (bottom). Calibration 50 V, time marker, 100 μsec. Note: the displacement of the crystal starts with a delay of about 80 μsec.

The crystals had a sensitivity of approximately 0·4 μ/V and the largest voltage used was 56 V. When a pulse of less than 20 V was applied to a crystal, the resulting displacement, if critically damped, was 90% complete in about 200 μsec. Imperfections in the voltage source introduced greater lags when pulses greater than 20 V were used. In a few experiments adequately damped pulses having shorter rise times were required; these were obtained by driving the crystals from a source having a sufficiently low output impedance at all pulse amplitudes, and allowing oscillation to occur; these oscillations were then counteracted by adding a brief pulse of suitable size, wave form and timing (Fig. 1).

Recording. Nerve impulses were recorded from fine filaments of dorsal-root or occasionally of medial-plantar nerve, with platinum electrodes under liquid paraffin and an amplifier system having a high input impedance and a frequency response which was adjusted to give the optimum conditions for determining the presence or absence of an impulse. The activity of a single receptor fibre excited by mechanical stimulation of the pad could be detected amongst considerable activities from other sources by using a superimposing technique; the stimulus sequence was repeated continuously at 10/sec, but the time base was switched on

and off by electrical means so that groups of 5 or 10 sweeps were superimposed on each photograph. The general activity could be reduced by cutting unwanted nerves in the leg.

Recording mechanical events. Displacements were recorded by a modification of the optical system described by Gray & Malcolm (1951). The optical part of this apparatus was used to record the displacements of a nylon bristle running in a guide (Fig. 2). The upper end of the nylon bristle held a flag, which interrupted the light beam of the optical system. The

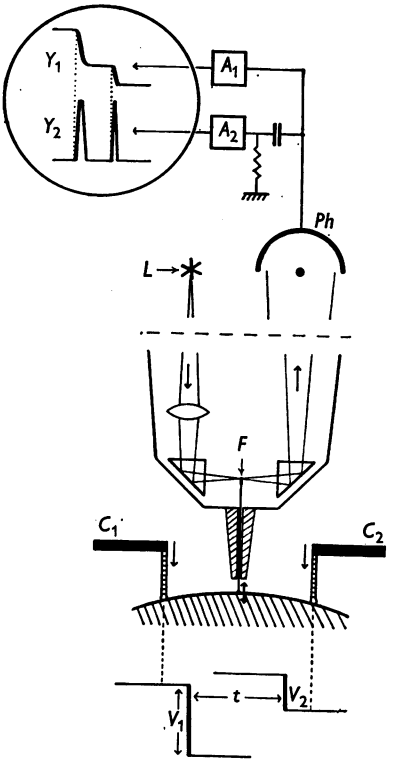

Fig. 2. Diagram of the method used for recording the displacement and the velocity of the surface movements of the pad. *L* light source, *F* flag on the recording stylus interrupting a focused light beam, *Ph* multiplier photocell. In this example a voltage pulse, V_1, is applied to crystal C_1; it causes a displacement of which the amplitude is recorded via A_1 and Y_1 and of which the velocity is recorded via A_2 and Y_2. After an interval t a voltage pulse V_2 is applied to crystal C_2 and the displacements due to this appear as the second deflexions on Y_1 and Y_2.

mechanical impedance of the system was kept as small as possible, the mass was 5 mg, the viscous resistance was small but was not satisfactorily measured and there was no elastic component. The restoring force provided by the weight of the system was small, and it was necessary, if movements were to be followed, to stick the bristle to the pad or crystal by means of collodion. When this recording device was attached to the moving corner of a crystal it was found that the photocell output was linearly related to the voltage input to the crystal. It may therefore be concluded that under these conditions, and over this working range, the output of the instrument was linearly related to the displacement of the nylon bristle. However, it was not possible to eliminate a tendency for the bristle to stick when

the forces were small, as was the case when small displacements of the pad surface were recorded; the method could not therefore be used for certain quantitative measurements. Displacements as small as 1 μ could be recorded. The velocity of the displacement was recorded by differentiating the output of the displacement recorder (Fig. 2). This was done by means of a circuit having a time constant of 20 μsec.

RESULTS

Responses of receptor units to single mechanical pulses

On-and-off responses. The receptors of the pad which could be excited by the means employed were, like other phasic receptors, excited both by the movement into the pad at the beginning and by the restoration movement at the end of a mechanical pulse having a duration of at least several milliseconds (for refs. see Gray, 1959); normally one impulse only was initiated by each movement when the displacement amplitude was 20 μ or less. Movements in both directions are thus able to excite. It is known that in the Pacinian corpuscle movements in both directions set up negative running receptor potentials and that these receptor potentials are able to sum in the usual way (Gray & Sato, 1953). The experiments described in this paper indicate that mechanical waves may occur in the pad and that the phases of such waves may add and subtract. It might be expected, then, that the effects of the two movements could sum under certain conditions. That they do so is indicated by the experiment illustrated in Fig. 3. In this experiment the threshold to a restoration movement was lower than that to the inward movement at the beginning of the pulse. It was possible to distinguish the responses to the two movements from each other by altering the duration of the pulse; the off-response moved in time with the end of the stimulus, while the on-response remained fixed in time. The line with the full circles (Fig. 3) is the strength–duration curve of the response occurring at the end of the pulse; the points for pulses of 3 and 5 msec duration indicate the threshold to the restoration movement alone; the amplitudes of pulses with durations between 0·7 and 2 msec did not need to be so large to produce a response, though it is certain that the impulse was initiated by the end of the pulse; the thresholds with the two shortest pulses were higher, and with these it was not possible to distinguish the effects of the two movements. It was possible to obtain a response to the inward movement of the pulse by increasing the amplitude of any of the pulses which had a duration longer than 0·7 msec; the threshold value for a response to this movement is shown by the open circles in Fig. 3, and it can be seen that it was unaffected by the duration of the stimulus. An increase in the excitability was thus observed when both movements were in a position to contribute, but not when the beginning of the pulse was in itself sufficient to excite.

This is not the preparation in which to study the meaning of the large amplitudes required for excitation by short pulses. It can, however, be said that the displacement of the pad normal to its surface at a distance of 1·5 mm from the stimulator was only slightly reduced when the pulse was as short as 0·3 msec; the record of displacement against time had a definite plateau when the pulse had a duration of 0·5 msec.

The relation between the parameters of the pulse and excitation. For excitation to occur in these receptors, as in other phasic receptors which are mechanically excitable, a minimum displacement and a minimum velocity (or critical slope) had to be exceeded. This is well illustrated by plotting,

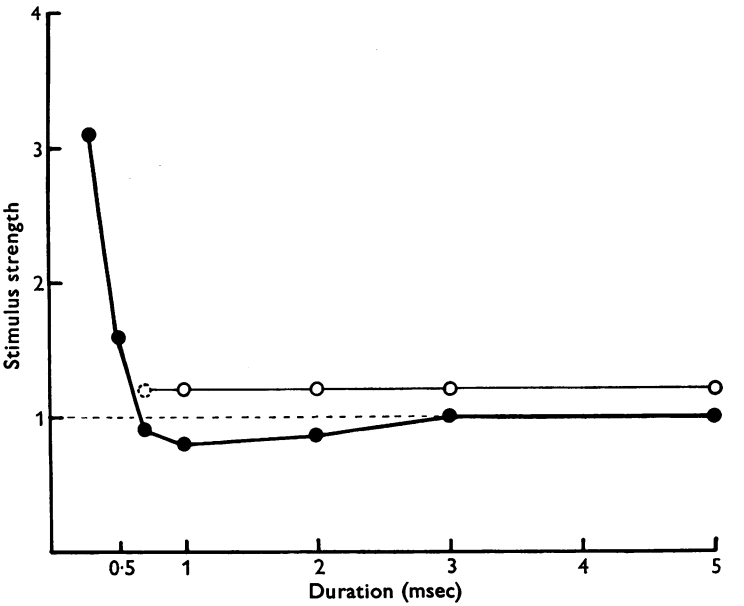

Fig. 3. Plot of the amplitude of displacement for threshold against pulse duration. Ordinate, stimulus strength in multiples of the threshold of a restoration movement. Abscissa, pulse duration. ●, lowest threshold; ○, threshold of the response locked to the beginning of the pulse. With pulses of 2 msec duration or less no stimulus excited more than one impulse; with longer pulses responses to both displacement and restoration could occur on the same occasion.

for threshold, the amplitude of displacement of a long pulse against the velocity of the initial movement. The results of two such experiments are illustrated in Fig. 4. The full curve was obtained when using pulses shaped by the method illustrated in Fig. 1; the displacement of the stimulating crystal was recorded throughout and four of the pulses are illustrated. The interrupted curve is taken from another experiment, in which the special technique for shaping the pulse was not used. Both curves are similar to those found with other receptors which can be excited mechanically (Gray

& Matthews, 1951; Gray & Malcolm, 1951) and show that when the velocity was above the critical value, threshold was determined by a critical level of the amplitude of the displacement, but was virtually unaffected by changes of velocity. In contrast, when the amplitude was above a certain value, threshold was determined by the velocity and was little affected by changes of amplitude. The critical slopes in three experiments were 1·3, 1·6 and 1·8 minimum thresholds/msec; the mean value for critical velocity in absolute units was 6·5 μ/sec.

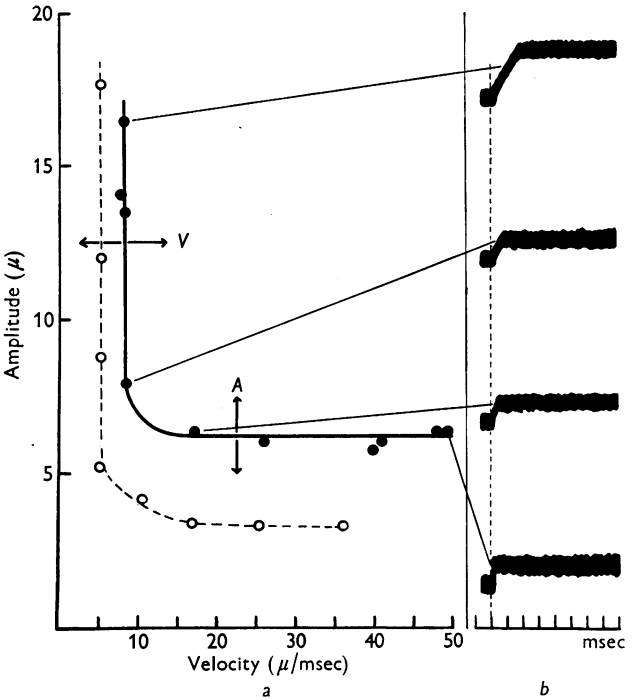

Fig. 4. Relation between amplitude and velocity of displacement for the excitation of receptor units. (*a*) ●—● curve found with pulses obtained by the method illustrated in Fig. 1. ○---○ curve obtained in another experiment with a single rectangular voltage pulse applied to crystal. Arrows: *A*, region in which amplitude determines excitation; *V*, region in which velocity determines excitation. (*b*) Records of the displacements used at threshold for the four different points indicated. Time marker, msec.

Receptive fields. It was possible to excite a single receptor unit over quite large areas. For example, with 14 units tested with brief (*ca.* 0·6 msec) mechanical pulses, having amplitudes up to about 20 μ, the areas from which responses could be obtained varied from 25 to 120 mm^2. Of these, the larger extended over the whole of the large pad; in one instance it was possible to excite the unit from one of the small pads as well as from the

whole of the large one. It must be emphasized that these areas are for one particular size of stimulus. A receptive field could be an area over which branches of the receptor neurone spread, but defined by this test method it could also be the area over which there is sufficient mechanical spread to excite a single receptor; or, of course, it could be a mixture of both. It will emerge later in this paper that mechanical spread is probably the major factor, and if that is so the area from which responses can be obtained will be determined by the size of the test pulse.

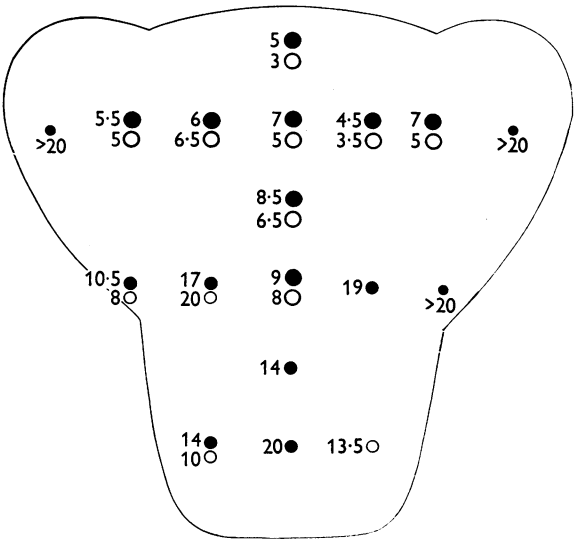

Fig. 5. Receptive field of a single receptor unit on the large pad. Separate threshold measurements for the displacement (●) and the restoration (○) of a mechanical pulse of 10 msec duration. The numbers indicate the amplitudes of the movements in μ; both thresholds were tested at all points. When a point is indicated by one symbol only, it means that a response could only be obtained to that type of stimulus. When neither direction excited, a small filled circle marked > 20 is used. The medium-sized circles indicate thresholds > 10 μ and the largest circles values < 10 μ.

In order to understand the signalling of information by primary and higher receptor neurones, it is important to consider certain factors about a receptive field defined in this way: these are the amplitude of displacement at threshold, the velocity of displacement at threshold, and the latency of initiation of an impulse at different points in the field. In all preparations there was an area of maximum sensitivity, and as the distance from this area increased the minimum displacement required to excite increased. Figure 5 illustrates a field which was tested with a long pulse in order that both on- and off-thresholds might be recorded. The numbers beside the filled circles indicate the amplitudes of the initial movements at

threshold, and those beside the open circles indicate the thresholds for the restoration movements. The pattern is not a simple one, but this like other experiments indicates that the excitability was much reduced at the periphery of the field. A corollary to this was found in examining the size of eleven such receptive fields mapped out with short (*ca.* 0·6 msec) pulses; the thresholds in the most sensitive area varied from 1·5 to 16·5 μ and those whose thresholds at the centre were lowest had the largest fields when explored with a 20 μ deformation (correlation coefficient = $-0{\cdot}69$). Since

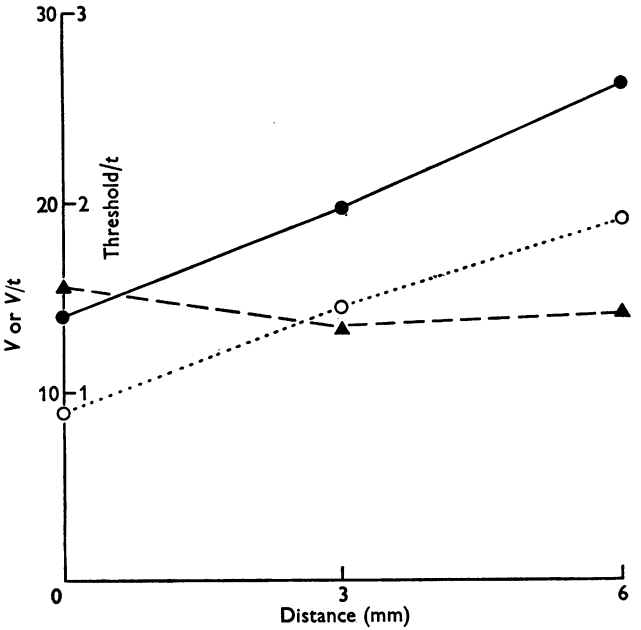

Fig. 6. Relation between threshold and distance. Ordinate, velocity or amplitude; abscissa, distance on the pad from the position of lowest threshold. ● Velocity at threshold expressed as (volts to crystal)/msec; ○ amplitude at threshold expressed as volts to crystal; ▲ velocity at threshold expressed as thresholds/msec., i.e. critical slope.

stimuli of the same size could excite from greater distances when the receptor was more excitable, it looks as though excitation at a distance was determined by mechanical spread.

The critical velocity required for excitation also increased with distance from the most excitable region. Figure 6 illustrates the change, with distance from the most sensitive region, in the size of the critical velocity (filled circles) and the critical amplitude (open circles) for excitation. The third line presents the same results in another way: the slope is plotted as multiples of threshold amplitude per unit time (i.e. critical slope). This line

is almost horizontal, and indicates that the time in which the minimum amplitude must be reached is constant over the receptive field.

The latency of the initiation of an impulse tended to increase with distance from the most sensitive region; the results were not, however, very consistent. There are two factors which account for this increase. One factor derives from the stimulus-strength–latency relationship (Fig. 7), which was similar to those found for other receptors (e.g. Gray & Malcolm, 1950, 1951); in this figure the ordinate is the increase in the latency above the minimum value. When the latencies were measured at threshold in different parts of the receptive field, fluctuations occurred and this accounts for much of the inconsistency referred to above. If, however, latencies were measured with a large pulse of constant amplitude (e.g. the largest available), then, in terms of the threshold, the stimulus was smaller at the periphery of the field, where threshold was high, than at the centre, where threshold was low. As was to be expected from Fig. 7, the relatively smaller stimulus given in the periphery was followed by a longer latency than the relatively larger pulse in the centre. In one experiment series of stimuli of different amplitude were used at a number of points throughout a receptive field. Each stimulus could then be recorded in multiples of the threshold at that particular position; the differences in latency to a constant stimulus in different parts of the receptive field could in large part, but not entirely, be accounted for by the differences in sensitivity of each point. The other factor responsible for the increase in latency with distance is the time taken for the spread of the mechanical events. An increase in latency due to this factor is illustrated in Fig. 11 (open circles); the reasons for attributing this delay to mechanical causes are given in a later section where this experiment is described.

Observations of the displacement of the pad surface in a direction normal to that surface were made in a number of preparations, using the optical method already described. All records of displacement at all distances from the stimulator were in the same direction, and the amplitude of this displacement decreased with distance from the stimulator; no oscillations were seen. On the average the amplitude of the displacement was reduced to a half at a distance of 2 mm; the rate of rise of the displacement was also reduced by the same factor, the time of rise or fall of the pulse being little altered at any distance. The displacement spread across the pad from the stimulator with a definite velocity, and this was found in three experiments to range from 11 to 13 m/sec, and in one to be 32 m/sec. The velocity inferred from the experiment illustrated in Fig. 11 was approximately 11 m/sec. These observations are consistent with the hypothesis that the changes in the amplitude at threshold, in the velocity at threshold, and in the latency observed in different parts of a receptive field, can be explained

by the spread of a mechanical wave. The distances required for attenuation to a half obtained from these mechanical observations, however, appear to be too small to fit the excitability results. On the other hand, displacement normal to the surface is unlikely to be the mechanical factor directly responsible for the excitation of the receptors.

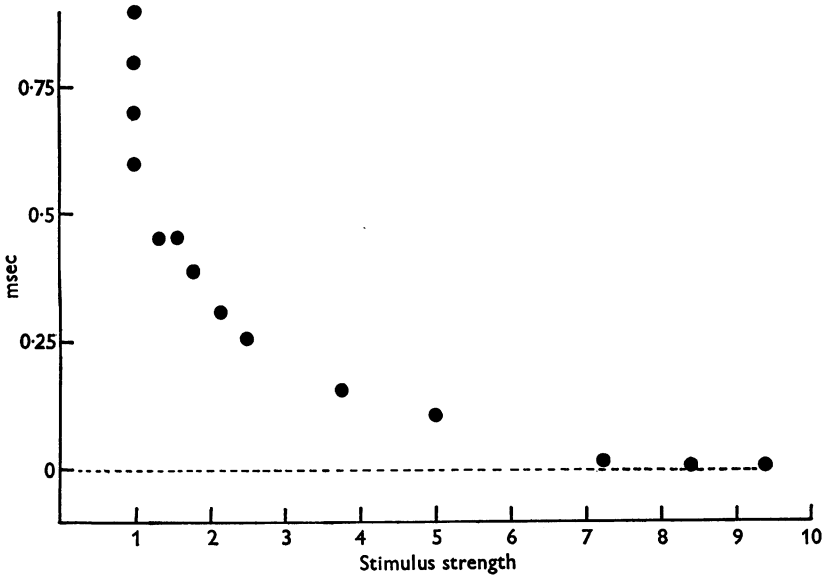

Fig. 7. Relation between stimulus strength and latency of the response. Ordinate, latency difference; abscissa, stimulus strength in multiples of threshold. Duration of the pulse 0·6 msec.

Recovery of excitability and conduction velocity of the nerve impulse. In these units a brief mechanical pulse (*ca.* 0·6 msec duration), just large enough to excite on every occasion, could excite again 1·8–2·8 msec (5 units) after the beginning of the first pulse. The largest available stimuli could not excite earlier than about 1 msec after the first pulse.

The conduction velocities of the nerve fibres of those units which could be excited by mechanical stimulation of the pad were measured in a number of experiments. A unit was identified as being excited by mechanical stimulation of the pad and its nerve fibre was excited electrically by means of a 20 μsec pulse applied to the medial plantar nerve, and the impulse was recorded in the dorsal root. At the end of the experiment the nerve between the two pairs of electrodes was completely excised and measured. In 9 units the mean velocity was 66 m/sec and the range 46–85 m/sec; 6 of the units had velocities between 61 and 67 m/sec.

Responses of receptor units to pairs of mechanical pulses

The remainder of the results described in this paper were obtained with two pulses applied to the pad, usually by means of two separate stimulators, which enabled the pulses to be separated both in position and in time. The simple application of the second stimulator to the pad frequently changed the threshold to a pulse from the first stimulator. This occurred even after any necessary correction had been made to the vertical position of the first stimulator. Decreases in excitability were usually seen when the second stimulator was applied within a few millimetres of the first and there was often an increase in excitability when the distance was greater.

Interaction following two brief threshold pulses. In a number of experiments a threshold pulse was found to alter the response to a second threshold pulse. With the two stimulators 3–5 mm apart on the large pad each was adjusted to deliver a pulse of 0·6 msec duration, of such an amplitude that it was just able to excite every time when it was applied alone. When both pulses were applied at an interval greater than 2 msec two responses were seen; when the interval was around 1·5 msec only the first pulse excited, because the excitability of the unit had not recovered in time for the second pulse to excite. When the two pulses were delivered simultaneously a single response was also obtained. The surprising result occurred when the interval was around 0·6 msec: at this interval no response of any kind was obtained, even though both pulses were above threshold when given alone. It appeared that a second stimulus was able to prevent the response to one that had already occurred.

Interactions following the association of a short test pulse with a short subthreshold conditioning pulse. The qualitative phenomenon just described was investigated by using a conditioning–test technique with short pulses (*ca.* 0·6 msec duration). One pulse, the conditioning pulse, was adjusted to about 80 % of its threshold value and delivered at zero time. The test pulse was derived from the other stimulator 4–9 mm away, and at times within 10 msec before (−) or after (+) the conditioning pulse; at each setting its amplitude was adjusted until the threshold for an impulse in the primary receptor fibre was reached. The result of such an experiment, which is typical of seven others, is shown in Fig. 8. The abscissa of this graph is time before or after the conditioning pulse and the ordinate is given as $(S_\infty - S_t)/S_\infty$, where S_∞ is the stimulus strength at threshold of the test stimulus alone and S_t is the stimulus strength at threshold at time t. In words, this function may be described as the fractional lowering of the test threshold resulting from the conditioning stimulus given t msec before. Figure 8 shows two major deflexions, a large decrease in excitability when the test occurred about 0·5 msec before the conditioning and a big increase

in excitability when the pulses were synchronous. There are also smaller deflexions before and after these. Other experiments showed similar patterns, though the relative sizes of the different peaks varied considerably. A common feature, which is small in Fig. 8, was a negative peak at about +0·5–+1·0 msec. The two main peaks of this experiment may be analysed in more detail by considering records of the amplitude and velocity of the displacement of the pad surface, normal to that surface, and at a point midway between the two stimulators (Fig. 2 shows the method). In Fig. 9 there are three sets of records. On top are the voltages applied to the two crystals (these are mixed on one beam in the oscilloscope) and 0·1 msec time marks; the lower rows indicate the velocity (into the pad = upward deflexions) and displacement (into the pad = downward deflexions) recorded from the mid point: in *a* and *b* the velocity is on top, in *c* it is below. These records are typical of a number obtained in this way. Record *a* shows the two pulses separated and giving two distinct displacements and two phases of positive velocity and two of negative; this picture corresponds to an interval when only minor changes in excitability occurred. Record *b* was taken at an interval which was practically identical with the duration of the pulses; under these conditions there is only one, though longer, displacement and the middle two phases of velocity are obliterated. This interval corresponds in all experiments to that at which there was a large decrease in excitability and at which two threshold pulses failed to excite any impulse. This result, like that illustrated in Fig. 3, suggests that each movement, regardless of direction, contributes to the excitation of the receptor unit. If, as in the Pacinian corpuscle, each movement sets up a negative running receptor potential (Gray & Sato, 1953) or if there is addition and subtraction of mechanical waves, a result such as that just described might be expected.

In three of these seven experiments a single brief pulse of 0·6 msec duration set up two impulses; the interval was about 2 msec. In these preparations a double-pulse experiment, such as that illustrated in Fig. 8, gave high positive values of $(S_\infty - S_t)/S_\infty$, not only when the pulses were applied simultaneously, but also when the interval between the pulses was the same as that found between the impulses of the double response. Double responses were exceptional amongst the whole series of experiments considered in this paper.

A conditioning pulse to a small pad has been seen to affect the threshold to a test pulse on the large pad.

Interactions following the association of a long test displacement with a long subthreshold conditioning displacement. The experiments with short pulses which have just been described illustrate in a dramatic way the interactions that can follow two mechanical pulses, and they also suggest

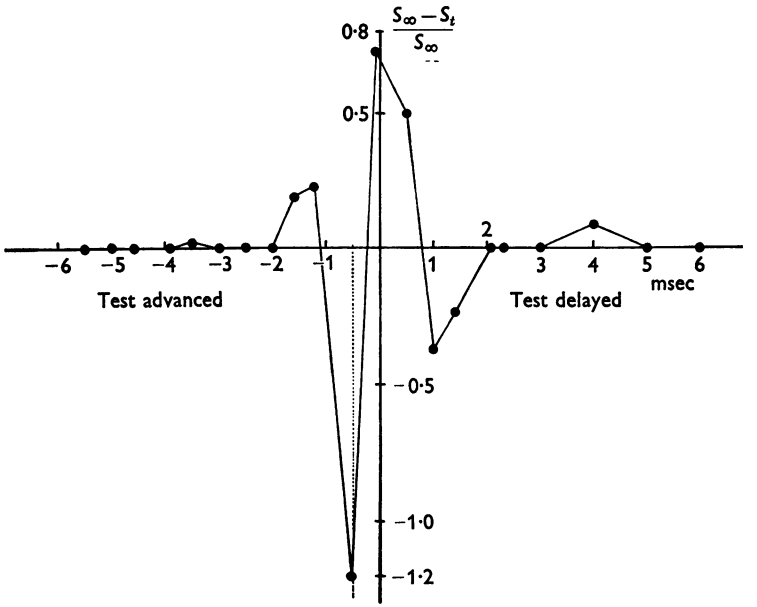

Fig. 8. Contribution of a subthreshold conditioning pulse to excitation by a test pulse. Ordinate, $(S_\infty - S_t)/S_\infty$; abscissa, time of test pulse in relation to conditioning pulse. Distance between the stimulating points 4 mm, pulse duration 0·6 msec. Conditioning threshold 2·9 times test threshold; conditioning used 2·2 times test threshold.

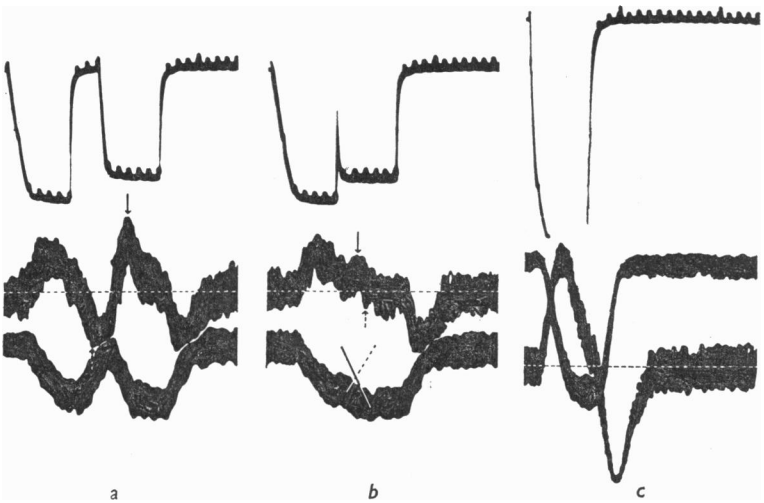

Fig. 9. Mechanical patterns on the surface of the pad following two mechanical pulses of 0·6 msec duration applied at different positions 4·5 mm apart and at different times. Upper row: voltages to both transducers mixed to one beam. Lower rows: displacements and velocities recorded on the pad midway between the stimulating points. Interval between the pulses *a*, 0·9, *b*, 0·6 and *c*, 0 msec. Records with dotted base lines are velocity records (note last pair reversed). The arrows in *a* and *b* indicate corresponding points at the end of the first pulse and at the beginning of the second. For further explanation see text.

that one important factor in this interaction lies in the mechanics of the pad. Short pulses provide a very useful experimental tool, but are not typical of natural stimuli; long displacements probably have more relevance to problems of discrimination and have been used in a further analysis of this phenomenon. Long displacements have another particular advantage; the results in the first section have indicated that the movement into the pad and the movement associated with restoration are separate stimuli, each of which can excite a single impulse if a critical amplitude is reached in a certain minimum time. The beginnings of long displacements of opposite polarity are thus approximately equivalent as stimuli, but they are mechanical opposites. In this section one experiment will be described in detail, as it illustrates all the relevant points. It is typical of two other relatively complete experiments and a number of others in which specific points were confirmed.

In this experiment the test displacement was always a movement into the pad and it was always applied at the same point, which was in the region of the greatest sensitivity; the test displacement, as in the experiment described in the last section, was altered in time relative to the conditioning pulse, and was adjusted in amplitude until an impulse was excited in response to half the number of stimuli. The conditioning displacement was applied in five positions; it was applied 2, 4, 6 and 8 mm from the test stimulator and also, by mixing the voltage into the same crystal as was used for testing, applied at the same point. At all positions conditioning displacements of both polarities were used and their amplitudes were adjusted to be approximately 80 % of the threshold amplitude at that particular point. There were thus ten conditioning situations, and a plot of $(S_\infty - S_t)/S_\infty$ against time was made for each. Six of these are illustrated in Fig. 10. In making these runs the intervals between the displacements were adjusted so that the points on the main peaks of the graph do represent the maxima and minima.

With two displacements of the same polarity, applied through one crystal (Fig. 10, top left), there was a large positive peak at zero time; this simply represents a single larger movement of the crystal. The next graph in the top row was obtained with the stimulators 6 mm apart and a similar positive peak was found, but it will be noticed that the peak is delayed by 0·45 msec. In the third graph, obtained with an 8 mm interval, the peak is delayed 0·75 msec. These delays are displayed in a plot against distance as the full circles in Fig. 11. This lag might be due to the time required for a travelling wave to pass from the conditioning stimulator to the test point, which was presumed to be near the receptors. If this were true, then an impulse excited by the conditioning stimulator should be delayed in respect of one excited by the test stimulator. This delay should

also be the time required for the mechanical wave to travel the distance between the two. These increases in the latency of the response at different distances from the most sensitive area were measured, and are indicated by the dotted lines in the graphs of Fig. 10; the values are also plotted against distance as open circles in Fig. 11. It will be seen that the lag in the positive peak of the graphs, and the increase in latency of impulse initiation, are very closely related and it seems reasonable to attribute them to the same cause. That this cause is the travelling of a mechanical wave is supported by the following evidence.

The three graphs in the lower part of Fig. 10 were obtained with conditioning pulses moving in the direction of restoration. It is immediately

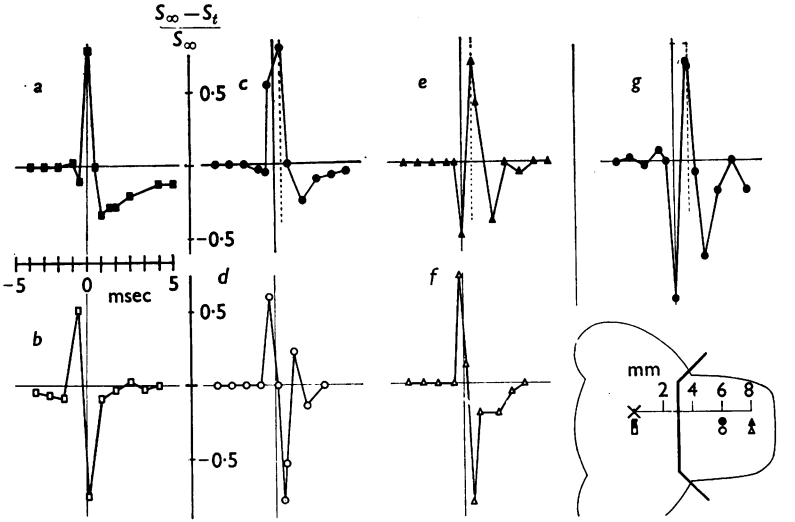

Fig. 10. Contribution of a subthreshold conditioning displacement to the excitation of a receptor unit by a test displacement into pad at different distances. Upper row, conditioning displacement into pad. Lower row, conditioning displacement out of pad. Ordinates, $(S_\infty - S_t)/S_\infty$; abscissae, time interval between the displacements (msec); test advanced negative. The inset in the right-hand bottom corner indicates the distances in mm of the conditioning displacement from the test displacement (×). The square bracket drawn on the pad marks the line of removal of the distal part of the pad. For further explanation see text. Conditioning displacements were as follows:

	Distance from test (mm)	Polarity	(%) of threshold at point used	Size relative to threshold at test point
a	0	In	85	0·85
b	0	Out	79	1·35
c	6	In	82	2·1
d	6	Out	82	4·7
e	8	In	86	3·4
f	8	Out	85	4·1
g	6	In (after cutting)	82	2·3

obvious that a negative peak in these records corresponds to the positive peaks in the upper graphs and that this negative peak shows the same lag with increasing distance. This reversal is exactly what would be expected if the interactions were mechanical, but not what one would expect if they were concerned with receptor potential summation and depression. In each instance the negative peak was preceded by a positive peak, and the time between these peaks was constant, within experimental error, at about 0·6 msec. Furthermore, in this experiment the latency from the

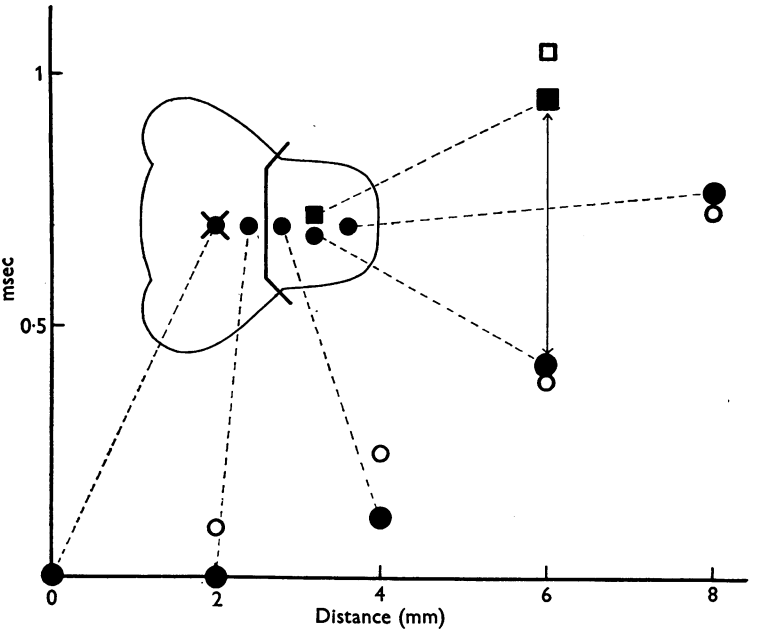

Fig. 11. Lag of peaks of increased excitability (Fig. 10, top row) (●) and increase in latency of a threshold response (○) with distance. Ordinates, lag and increase in latency; abscissa, distance of the conditioning displacement from the test pulse. The inset shows the positions of the points: X test, ● conditioning. The latency measurements were mostly repeatable within 0·1 msec, even though measured at threshold: □, ■, after cutting.

beginning of a stimulating displacement to the initiation of the impulse was 0·6 msec shorter when the displacement was *out* of the pad than when the movement was *into* the pad (the threshold for movements into the pad was, however, lower). These results are all explicable in mechanical terms, if it is assumed that a movement in either direction causes a brief mechanical change with two phases 0·6 msec apart, somewhere in the tissues, and that reversal of the applied movement reverses the order of its phases. It is further postulated that one phase only can excite; in this instance, that occurring first after a restoration movement. This would account for

the extra 0·6 msec latency after an inward displacement and also for the fact that an inward displacement needed to be applied 0·6 msec before an outward moving displacement if their excitatory effects were to sum. On this hypothesis one would expect that if a test displacement into the pad were applied 0·6 msec before a conditioning displacement in the same direction the excitatory phase of the mechanical change following the test stimulus would coincide with and be cancelled by an opposing phase following immediately on the application of second displacement. There is a small negative peak at the correct time when the two displacements were applied through the same stimulator; a corresponding negative peak is, however, much more obvious in results obtained with the two stimulators well apart (Fig. 10, row at the top). In the latter figure the whole graph is shifted to the right on the time scale, and on this hypothesis this shift is due to the spread of a wave at a finite velocity, which is indicated by the slope of the curve in Fig. 11.

Final proof that the major peaks of the interaction curves of Fig. 10 are mechanical in origin is afforded by the right-hand graph in this figure. After the sets of observations which have just been described had been completed, the pad was cut across as indicated by the line in the diagram. The part of the pad peripheral to this cut was then completely removed and stuck back again with paraffin wax. The test stimulator remained in the same place and the conditioning stimulator was placed at the 6 mm position; the latter could still excite at about the same amplitude and was again adjusted to 80% of its threshold. The result of this experiment is shown in the top right-hand graph. It is clear that the peaks are as large or even larger than before; the lag of the positive peak from zero was appreciably longer than before, and the dotted line in Fig. 10 and the point in Fig. 11 show that the latency of the response increased by the same amount. The close correspondence of these points after this large change confirms that the two measurements have the same origin. The increase in these times might well be due to a slowing of the mechanical wave in passing the discontinuity provided by the wax.

Records were made of displacement and velocity of the pad in a direction normal to the surface. These records showed that neither the amplitude nor the rise time of a displacement was affected by the application of a second displacement from another stimulator, either simultaneously or within milliseconds of it; displacements of either polarity from the two stimulators recorded separately at any point were combined algebraically when they were applied together. These recordings did not reveal any oscillations due to mass movements of the stimulator, the pad or foot; the direction and sensitivity of the recording instrument should have revealed any significant mass movements of this kind if they had existed. Further-

more, mass movements could not explain the time delays introduced by distance or by the discontinuity in the cut pad. The displacement records referred to in an earlier section showed that some mechanical change travelled across the pad with a velocity comparable to that found in this experiment, about 11 m/sec. However, the displacements recorded normal to the surface have shown no sign of the postulated brief mechanical change with two phases.

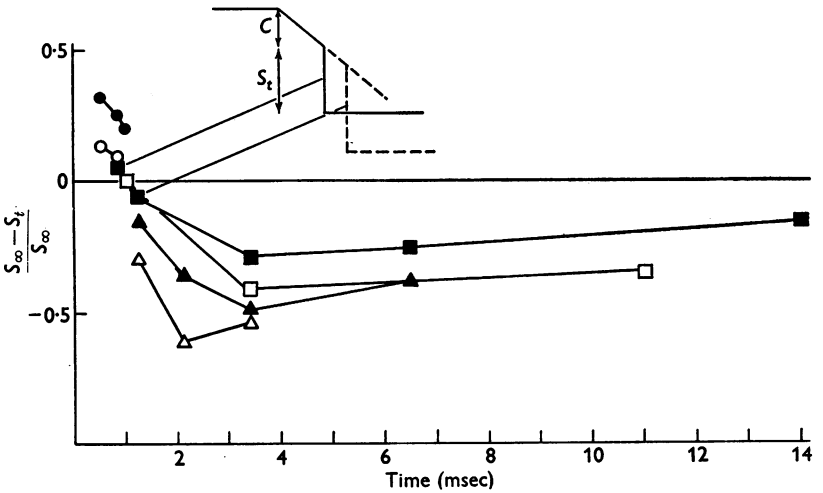

Fig. 12. Excitability changes during velocities below the critical value tested by a rectangular step (see inset); movements into the pad. Ordinate, $(S_\infty - S_t)/S_\infty$; Abscissa, time from start of velocity to test pulse. The slopes (thresholds/msec) were ○ = 0·65; ● = 1·1, △ = 1·4, ▲ = 0·8, □ = 0·55, ■ = 0·4. Critical slope = 1·75 thresholds/msec. S_t = test stimulus. C = conditioning amplitude.

These observations of displacements normal to the surface do not, therefore, provide a full explanation of the results. A few observations were, however, made with a Rochelle-salt crystal which was rigidly attached to a glass stylus. This stylus was applied to the pad. The system could respond to forces normal to the surface and also to forces tangential to the surface. Results obtained with it cannot therefore be analysed. None the less, some records obtained with this system showed deflexions which changed polarity within a millisecond of the beginning of the mechanical change. These records indicate that there are mechanical events which are not revealed by the measurement of displacements normal to the surface, and which may be more closely related to the excitation of the receptors.

It will be noted that the size of the positive peaks in Fig. 10 is approximately the same at all distances. This is to be expected since the size of the conditioning displacement relative to threshold was always the same. The

absolute size of the displacements was, however, greater at the larger distances: values are given in the legend to this figure.

Low-velocity pulses. All the experiments described so far, whether with short pulses or long displacements, were done with movements whose velocity was above the critical value. Slower changes may be of importance when considering the discriminative functions of skin. An experiment was therefore done in which the conditioning movement had a velocity which was varied, but always below the critical value (Fig. 12). The test displacement was a high-velocity movement of the same stimulator introduced at some point during the period of the conditioning movement. In this experiment all velocities caused a decrease in the excitability at times greater than 1 msec, and both positive and negative values of $(S_\infty - S_t)/S_\infty$ were greatest with the highest velocities. The rather prolonged, but not very profound, negative change was found in a proportion of results obtained with rectangular displacements, both short and long, and when this preparation was conditioned with a rectangular instead of a sloping displacement.

DISCUSSION

The purpose of this paper has been to consider how various stimulus patterns affect the excitability of certain receptor units which can be excited by mechanical stimulation of the cat's pad. It is clear that mechanical factors play a major part in determining the response of a unit.

In the experiment illustrated in Figs. 10 and 11 the amplitude of a displacement required to excite was approximately the same even after the part of the pad to which it was applied had been cut out and stuck back. A displacement on this inactive region was also able to modify, as effectively as it could before the area was cut out, the excitability of a unit tested by another stimulus. These facts show that mechanical events can spread across the pad and have effects on receptors at a distance. There is evidence that there is a mechanical wave which spreads across the pad at a definite velocity. This has been indicated in several ways: the latency of initiation of an impulse increased as the distance from the most sensitive area of the pad increased; the peaks of the interaction curves (Fig. 10) were delayed as the conditioning stimulus was removed further from the most sensitive area on which the test stimulus was applied. These two delays in impulse initiation and in all phases of interaction were, within the limits of error, identical at all distances, and even after the pad had been cut out and replaced. They can be accounted for by the time taken for a mechanical wave to travel the distance; the calculated velocity of this postulated wave was similar to the velocity with which a displacement of the pad surface, normal to that surface, was found to spread.

A mechanical wave spreading through the pad would be expected to become attenuated with distance. The amplitude required for threshold increased towards the periphery of receptive fields. The linear dimensions of receptive fields were negatively correlated with the absolute value of threshold in the most sensitive region. The velocity required for threshold also increased towards the periphery when recorded in absolute units, but was unchanged when allowance was made for the change in the amplitude required for threshold. These results all suggest attenuation of the amplitude of a mechanical wave, but little or no change in its time course. Displacements normal to the pad surface were found to decline with distance from the point of application, and the time course of these displacements remained unchanged.

A spreading mechanical wave will have a particular time course and a particular relationship to the applied pulse. Is there then a pattern that will fit the results presented in this paper? The units under discussion are phasic; like other phasic receptors, e.g. in frog's skin (Gray & Malcolm, 1951; Maruhashi, Mizuguchi & Tasaki, 1952) and the Pacinian corpuscle (Gray & Malcolm, 1950), these units respond with a single impulse or very few impulses to any movement regardless of direction. The velocity–amplitude curve for threshold found in the pad is very similar to those found for receptors in frog's skin (Gray & Malcolm, 1951) and for Pacinian corpuscles (Gray & Matthews, 1951). The adaptation of the receptors in frog's skin can be modified by mechanical means (Loewenstein, 1956) and the brief responses to movement and the shape of the velocity–amplitude curve of the Pacinian corpuscle have been explained in mechanical terms by Hubbard (1958) as a result of his investigations into the mechanics of the capsular structure. By analogy one might expect that movements both into and out of the pad might give rise to brief mechanical changes whose amplitude is dependent on both the amplitude and the velocity of the applied displacement.

A mechanical explanation is required for the interactions between two displacements. That these interactions are mechanical is shown by the cutting of the pad and by the fact that reversal of the conditioning displacement reversed the interaction curve; receptor potentials and other receptor processes would not be expected to reverse (for summary, see Gray 1959). The main peaks on the interaction curves, including their polarities, intervals and delays and the on-and-off responses, can be explained if it is postulated that movements into and out of the pad both give rise to a brief mechanical change having two phases of opposite polarity, whose order is reversed by reversing the polarity of the applied pulse; if it is assumed that only one of these phases is able to excite the receptors the results can be explained by the mechanical interference of

these phases. To avoid again describing results here explanations of the details in terms of this hypothesis have been given where the results are described.

There is no direct evidence of the mechanical process postulated. Displacements normal to the skin surface are certainly correlated with some of the properties required, but they are different in other respects. These differences do not, however, invalidate the hypothesis. For example, as the stimulus moves away from the point of lowest threshold the displacement is found to become attenuated more rapidly than does the threshold. This might be due to the receptor unit studied having receptors not only at the point of minimum threshold, but spread over some little area, so that certain receptors may remain close to the stimulus even when it is some distance from the centre of the receptive field. An alternative explanation of these differences in attenuation and of other discrepancies might be that the mechanical change that is important is not that recorded by the method used; observations made with a Rochelle-salt crystal suggest that there are other mechanical changes. A mechanical process which might possibly be more closely associated with the excitation of the receptors is a compression wave travelling in the plane of the skin. A variety of wave patterns is known to occur in skin (Békésy, 1955; Keidel & Schmitt, 1955).

Mechanical events can explain many of the observations described, entirely or in part. It must, however, be remembered that the properties of the receptors themselves are affecting the results. The most important of these are the summation (Alvarez-Buylla & Ramirez de Arellano, 1953; Gray & Sato, 1953) and depression (Gray & Sato, 1953; Diamond, Gray & Inman, 1958; Loewenstein & Altamirano-Orrego, 1958) of the receptor potential. Furthermore, there are the properties of the conducting part of the receptor unit, refractoriness and the interaction of impulses at junctions (Katz, 1950; Hughes & Wiersma, 1960). There are two observations which require comment here. The summation between the excitatory effects of the on-and-off movements of a single pulse (Fig. 3) could be mechanical, but the effect is longer than the likely half-period of the mechanical change postulated above (*ca.* 0·6 msec), and it seems probable that this effect is due to summation of the receptor potentials (see Gray & Sato, 1953, Fig. 14). The later parts of the interaction curves can also be explained by an extension of the mechanical hypothesis, but it is not improbable that depression and refractoriness play their part.

A single unit can signal that a certain amplitude of displacement has been exceeded, provided the velocity is high enough. Alternatively, if the amplitude of a series of displacements is considerably greater than the critical amplitude, then the unit can distinguish those with a velocity above

threshold from those with lower velocities. A single pulse applied to an area of less than half a square millimetre can excite or influence receptor units across the pad or even on another pad; the amplitude and velocity required for excitation and the latency increase with distance. These facts must be taken into account in determining the system of coding. Stimulus strength (either amplitude or velocity of displacement, or both) cannot be signalled by frequency coding under these conditions; however, with bigger stimuli the number of units activated increases, because of the greater distance that a large stimulus can spread and remain above threshold; work on this system still to be published (C. J. Armett, J. A. B. Gray, R. W. Hunsperger and S. Lal) indicates that stimulus strength can be coded by the number of primary receptor units activated. The position of a stimulus could only rarely be signalled by the firing of a single unit, but it could be signalled by the mean position of the population. Timing factors may also play a part.

The interactions which follow two pulses may also be of functional significance. Any pacing or exploratory movement of the pad is likely to encounter a complex pattern of stimuli, and these results show that complex interactions which are critically dependent on timing can take place. A dramatic example is the inability of two pulses, each above threshold when alone, to excite when applied at a suitable interval.

These experiments are also a necessary basis to any work in which double mechanical pulse techniques are used to investigate the way in which signals converge upon and are analysed by second or higher-order neurones. False conclusions about the role of a group of junctions may be drawn if these interactions are not taken fully into account.

SUMMARY

1. The activity produced in single receptor units, on mechanical stimulation of the cat's pad, has been recorded.

2. Both the displacement at the beginning and the restoration movement at the end of a mechanical pulse can excite or contribute to the excitation of the receptors. Excitation is determined by an amplitude required for threshold (range 1·5–16·5 μ) and a critical slope (mean, 1·6 × amplitude required for threshold per millisecond).

3. Receptive fields have dimensions which are negatively correlated to the minimum threshold. Both the amplitude required for threshold (μ) and the velocity required for threshold (μ/msec) increase with distance from the centre of the field; critical slope (amplitude required for threshold/msec) is constant. The initiation of impulses is delayed at the periphery of the field.

4. Major changes in the excitability of a receptor to a test pulse on the main pad often result when a subthreshold conditioning pulse is applied at a second point on the main pad, or even occasionally on a small pad. These changes in excitability can be greater than a factor of two and can be of either sign; the precise effect is critically dependent on timing, particularly when the pulses are applied at intervals shorter than 1 msec.

5. Comparable changes in excitability can occur even when the conditioning pulse is applied to an area of pad which has been cut out and stuck back.

6. This and other evidence which is presented indicate that the properties of the receptive fields and the interactions may be explained by a mechanical wave that travels across the pad with a velocity of the order of 12 m/sec. This hypothesis is supported by certain mechanical observations which were made.

7. The results need to be taken into account in considering the coding of information by this population of receptor units. Furthermore, the results indicate that facilitatory and inhibitory functions should not be attributed to central mechanisms until there is reason to exclude the possibility of more peripheral interactions.

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