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THE MECHANORECEPTORS OF THE RABBIT MANDIBULAR INCISOR

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The study of the innervation of dental tissues has been dominated by the use of histological techniques and, in comparison, little work has been devoted to the physiological properties of dental nerves.

Pfaffmann (1939*a*, *b*) was the first to take electrical recordings of impulses in dental nerves. He studied the responses of mechanoreceptors of the maxillary teeth of the cat and also demonstrated responses apparently resulting from noxious stimulation of the dental pulp. Some recent papers show a renewed interest in the use of electrical techniques in the investigation of dental innervation (Brookhart, Livingston & Haugen, 1953; Scott, Schroff & Gabel, 1953).

The present study forms part of a general exploration of the properties of dental receptors, for which the rabbit mandibular incisor was chosen as the experimental object for three main reasons. First, the rabbit incisor is an example of the continuously erupting tooth, which is characteristic of rodents and also found in species of most mammalian orders. It was thought that comparison of its innervation with that of the cat, an animal more closely resembling man in tooth form, might be instructive. Secondly, the incisor nerve of the mandible is readily accessible for a sufficient length. Thirdly, specific information was required on the innervation of the rabbit's incisor teeth, since the continuous eruption process was to form the subject of a separate study.

This paper describes investigations into the distribution of the mental and incisor nerves, and into the types of response recorded from dental mechanoreceptors. Special interest was taken in the relationship between the response of slow-adapting receptors and the direction in which a stimulus was applied.

METHOD

The experiments were performed on rabbits, anaesthetized with urethane, and held in the supine position. A tracheal cannula was inserted to facilitate work on the mouth region. Through a midline incision, that portion of the mandible overlying the inferior dental nerve (Fig. 2*a*) was exposed, the facial vessels and accompanying tissue being ligated, cut and retracted. After reflexion of the periosteum, the inferior dental nerve was exposed in its canal, overlying bone being pared away with a dental chisel. The nerve was cut centrally and the incisor and mental branches separated by running a fine knife between them from the bifurcation. Although the bifurcation varies slightly in position, it can be revealed if sufficient bone is removed rostrally. Fine branches running to the cheek teeth were separated from the mental nerve. Cotton-wool plugged into the vacant canal prevented troublesome bleeding. The tissues were irrigated with Locke's solution (NaCl 0·9%, KCl 0·042%, $CaCl_2$ 0·024%, $NaHCO_3$ 0·015%, glucose 0·1%).

To record impulses, the nerve under experiment was laid over fine bright platinum wire electrodes. These led through a cathode follower and pre-amplifier to a cathode-ray oscilloscope and to a loudspeaker unit. The frequency response of the system in early experiments was constant between 15 and 1000 c/s; a new pre-amplifier was then introduced, altering the frequency response of the system to be constant between 25 and 5000 c/s.

If preliminary recording showed the dissected nerves to be in good condition, a jaw clamp was applied. Steel needles were so set into the faces of the clamp that their points gripped the cheek-teeth region of the right mandible when the jaws of the clamp were opposed.

Functional single-fibre or few-fibre preparations were dissected with needles, under a binocular microscope. A thin, black glass slip, on a rigid platform, was the background for dissection.

In plotting the distribution of mechanoreceptors, and in exploratory stimulation of incisor nerve preparations, manual touch and pressure were the stimuli, applied, when necessary, through a convenient instrument. The five basic directions in which the incisor crown was stimulated are shown in Fig. 2*b*.

For quantitative stimulation of the incisor crown, traction was applied. To test the responses to forces in the same direction but of different magnitudes, weight-and-pulley systems were employed. For testing the responses to forces of the same magnitude but in different directions, a system using elastic traction was developed: Fig. 1 shows a typical assembly for these experiments. By cutting with a dental fissure bur, the incisor was reduced to a round peg, about 1 mm from the incisal edge. A freely moving wire link was placed round the peg and attached to one end of a length of rubber elastic. A thread, attached to the other end of the elastic, was led out through one of the small metal loops placed at 10° intervals round the circumference of a protractor made of Perspex sheet. The protractor was rigidly held with its plane at right angles to the flat labial aspect of the incisor and at right angles to the incisor's long axis. A knot provided a stop, ensuring that, on pulling the thread, a force of constant magnitude was applied to the incisor: which force could be easily calibrated by extending the elastic to the stop by weights, acting over a pulley.

When series of recordings were to be taken, the edges of the skin incision were drawn up by threads to form a recording bath. The bath was filled with liquid paraffin; this was usually added at room temperature, but in a few experiments a continual flow of paraffin at 38° C was maintained.

Rectal temperature was kept about 38° C, fell at a mean rate of 1° C/hr when the table heaters were turned off, and was never allowed to vary beyond the limits 36–39° C. Temperature measurements showed that the incisor receptors could be regarded as being about 3° C below rectal temperature, their fibres running out through a temperature gradient to an inter-electrode temperature of about 28° C.

Oscillograph records were taken on paper: in the records shown the spikes have been intensified with pencil. The magnitudes of spikes were compared with a calibrating voltage. Since the camera speed was found to be not quite constant, frequency of impulses was never determined by measurement of the interval between impulses, but was estimated from the number of impulses counted in $\frac{1}{2}$ sec intervals taken from a 100 msec time mark on a second beam of the oscillograph.

In this paper, the word 'crown' defines that part of the incisor protruding from the gums, and 'root' denotes the rest of the tooth.

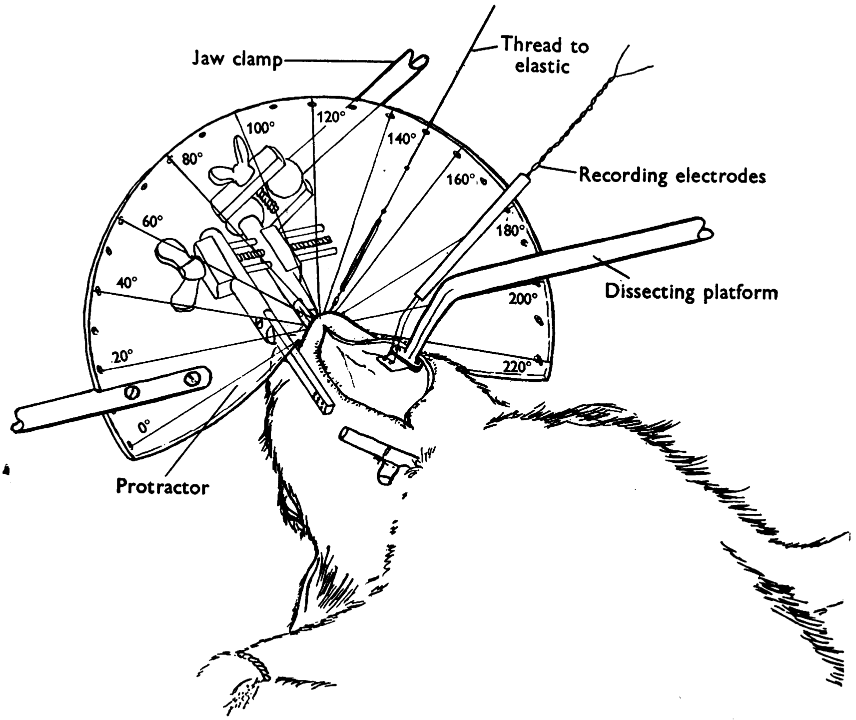

Fig. 1. Sketch of a typical assembly for experiments on directionality. In this view the elastic attached to the left incisor, and the main body of the jaw clamp, are seen through the Perspex protractor.

RESULTS

Distribution of mechanoreceptors

When pressure was applied to the incisor crown, the whole incisor nerve being on the electrodes, an asynchronous discharge was recorded (Fig. 3) during the duration of the stimulus. If the application of force was rapid the asynchronous response was preceded by a spike compounded of the synchronous discharge of many individual receptors (Ness, 1953). Similar responses were obtained from the mental nerve when the lower lip was stimulated mechanically, except that the compound spike produced by a rapidly applied stimulus was never completely synchronous. Such responses, to careful exploratory stimulation, were used to determine the distribution of the mechanoreceptors of the mental and incisor nerves.

Mental nerve. The distribution found in seven experiments is shown in Fig. 2*c*. No responses were produced in the mental nerve by gentle pressure on the incisor crowns, or on the lingual aspect of the inter-incisal papilla of gum. Lateral to the incisor, it was not found possible to define the extension of the distribution into the mouth, owing to the discharge present when the lip is lifted; however, this extension is not great. The caudal boundary of the distribution may have been artificially limited by the undercutting of the skin in dissection. But the main trunks of the mental nerve were not disturbed by the dissection, and the constancy of this boundary in all experiments argues against such a limitation.

Incisor nerve. Responses were recorded from the incisor nerve during the application of force to the ipsilateral incisor crown. There is good evidence that the receptors responding to forces applied to the tooth crown are located in the periodontal membrane: extirpation of the dental pulp does not appreciably diminish either the sensation of pressure from the teeth in man (Stewart, 1927) or the responses to pressure recorded from dental nerves in the cat (Pfaffmann, 1939*a*). As the rabbit incisor pulp is roughly conical with its broad base in continuity with the periodontal tissues of the base of the socket, extirpation of the pulp was not attempted, since it would be impossible to know how much such treatment would have damaged the main nerve bundles going to the periodontal tissues. The periodontal membrane may be taken to be the site of the rabbit incisor mechanoreceptors, however, since there is no reason to suppose that the rabbit differs from cat and man in this respect.

In man the inferior dental nerve sometimes crosses the mid-line, reaching as far as the second incisor (Starkie & Stewart, 1931). The existence of a similar condition in rabbit would seriously affect the conclusions to be drawn from experiments involving unilateral denervation. In testing for crossed innervation in the rabbit it seemed reasonable to suppose that any periodontal mechanoreceptors whose fibres crossed the mid-line would have a similar threshold to those of the incisor on the same side as the nerve under test. Care was taken to ensure absence of mechanical interconnexion between the incisors. A gap was cut between the incisor tips when necessary, and the gums were kept moist, since it was found that dried gum and mucus effectively transmit applied forces across the mid-line. In thirteen experiments, no evidence was found of crossed innervation.

Similar regard being had for threshold and absence of mechanical connexion, no evidence was found for innervation of gum or other tissue adjacent to the incisor crown, by the incisor nerve.

Mandibular symphysis. In the forty-one rabbits studied, the mandibular symphysis was found to be mobile, though not to the extent found in rats and mice. Histological examination has shown that the opposed halves of the mandible are joined by a small patch of cartilage rostrally, and by fibrous tissue elsewhere. When pressure was applied to the mandibular angle, the gap between the tips of the incisors could be seen to widen; concomitantly, a small asynchronous discharge was recorded from the incisor nerve (Fig. 3*a*). When the application or removal of force was rapid, a marked burst of impulses

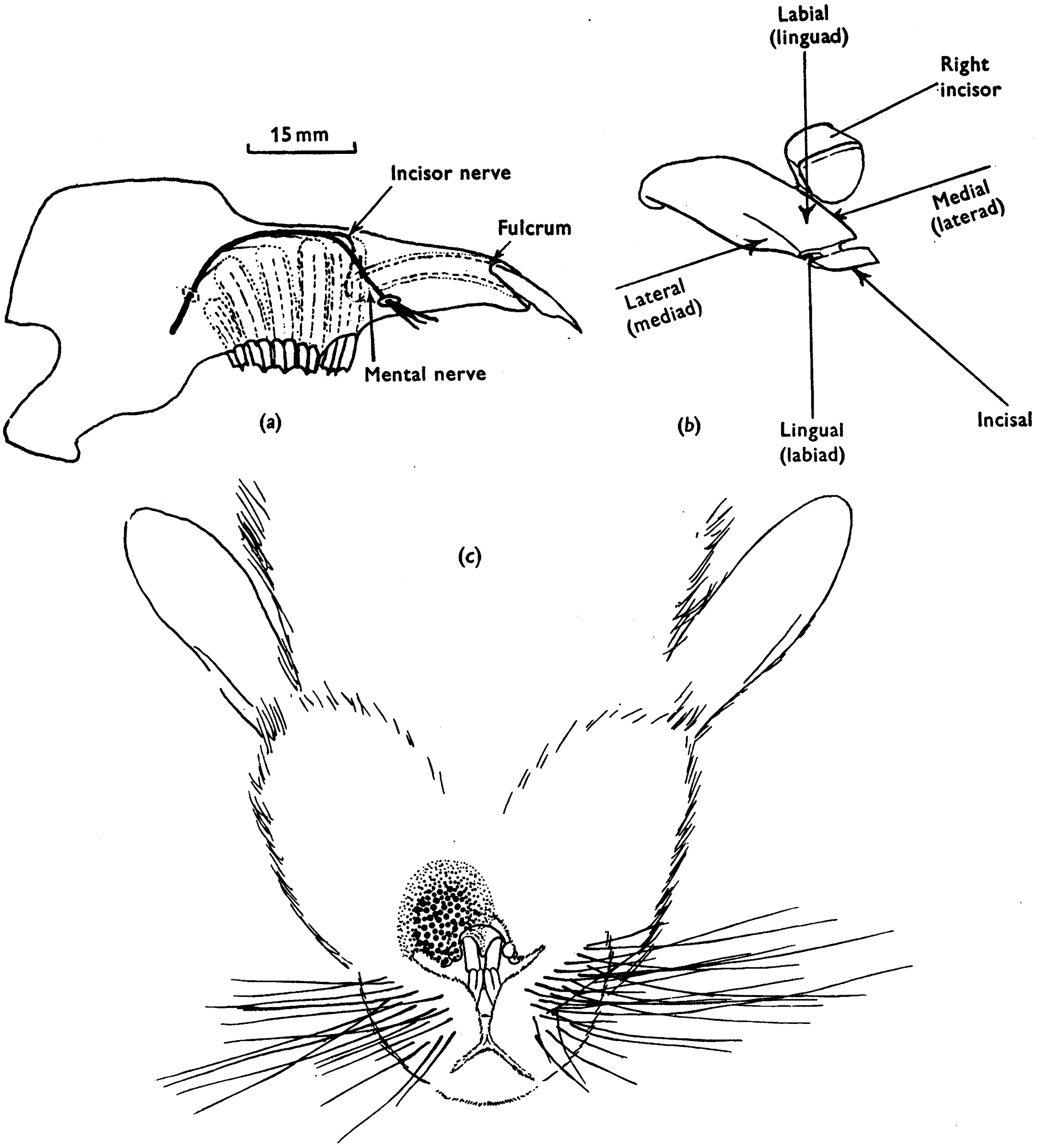

Fig. 2. (*a*) Diagram of the course of the inferior dental nerve in the rabbit mandible. The scale lies over the 12–15 mm lengths of nerve which are exposed for recording. The position of the fulcrum for laterad-mediad movement is shown by an arrow (see text). (*b*) Diagram of the mandibular incisors, prepared as for elastic traction on the left incisor, the labial aspect being seen, as in experiment. The tip of the left incisor has been cut to a peg and the right incisor cut back to allow full access to the left. The five basic directions in which forces were applied to the incisor are shown. (*c*) The ventral aspect of the rabbit head, with the distribution region of the mechanoreceptors of the mental nerve shown stippled. The weight of the stippling is proportional to the magnitude of responses found. The lower lip has been withdrawn to expose the distribution on the incisor gums.

occurred at the 'on' or the 'off' of the stimulus (Fig. 3*a*). However, it was found that the continuous discharge disappeared when the incisor gums were swilled with Locke's solution (Fig. 3*c*)—thus removing dried mucus connecting the incisors. But the short bursts of impulses at 'on' or 'off' persisted (Fig. 3*c*), even after the ipsilateral incisor had been ground down to below the level of the socket margin, that is, when all connexions between the two incisors over the inter-incisal septum had been severed. The persistence of these responses was taken to indicate that, either there are rapidly adapting mechanoreceptors in the symphysis supplied by the incisor nerve, or that movement at the symphysis produces a distortion of the periodontal mechanoreceptors sufficient to excite a few impulses—the socket wall facing the symphysis is fairly thin. Effects of symphyseal movement on the frequency of spontaneous discharge will be noted later.

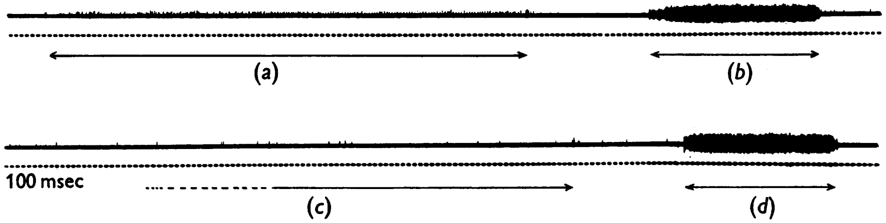

Fig. 3. Recordings from the whole left incisor nerve, parts of a continuous record. (*a*) Pressure, mediad, on the left mandibular angle. (*b*) Heavy incisal pressure on the left incisor. (*c*) Repeat of (*a*). (*d*) Repeat of (*b*). Between (*b*) and (*c*) water was swilled over the incisor gums: note the disappearance of the main body of the response to mandibular pressure. Note also the sporadic discharge of a single fibre developing after heavy pressure in (*b*) and continuing into (*c*). (Rabbit 91—retouched.) The durations of the stimuli are indicated by arrows beneath the records.

Types of incisor mechanoreceptor

According to the properties of their discharge, units have been classified as 'fast-adapting', 'slow-adapting' and 'spontaneously discharging'—reasons are given below for distinguishing between the last two. A train of impulses throughout mechanical stimulation of the incisor crown was the characteristic of slow-adapting discharge, in contrast to the one or two impulses, at the 'on' or at the 'off' of a stimulus, which comprised fast-adapting discharge. Spontaneously discharging units were found to emit, in the absence of overt stimulation, a continuous steady stream of impulses, whose frequency could be altered by appropriate manipulation of the incisor and of the mandibular symphysis.

The preponderance of the slow-adapting type was obvious in the experiments, from the magnitude of the discharge produced in the incisor nerve by steady pressure on the incisor, and from the proportions of the three types dissected, as unit preparations. Spontaneous discharge was observed in only eleven of the forty-one animals studied, and no more than three units were ever distinguished as active at one time in a nerve trunk. The occurrence of fast-adapting responses could only be distinguished in dissected preparations, since the impulses of slow-adapting discharge may be synchronized at the onset or fall of a stimulus. Thirty-seven slow-adapting, five fast-adapting and five spontaneously discharging units were dissected: there may have been subjective discrimination in favour of choosing those twigs, split from the nerve trunk, which contained one of the rarer types of discharge.

When different types of discharge have been present in the one preparation, the order of the amplitudes of their fibre spikes has always been: fast-adapting > slow-adapting and slow-adapting > spontaneously discharging. The largest spike size recorded from a fibre during the course of an experiment was measured: when such measurements were collected, the following distributions were found:

29 slow-adapting units	Mean 0·92 mV, S.D. 0·63
5 fast-adapting units	Mean 2·65 mV, S.D. 1·91
5 spontaneously discharging units	Mean 0·17 mV, S.D. 0·04.

If the variations in recording conditions were taken as random, the use of Student's '*t*' test showed the differences between these distributions to be significant at the 5% level of probability. No significant effect on the distributions could be traced to the use of different pre-amplifiers during the experiments.

No change in the discharge of either slow-adapting or spontaneously discharging fibres was observed when the level of urethane in the circulation was raised by 20%.

The division of rabbit incisor mechanoreceptor discharge into three patterns, and the association of a specific spike size with each pattern, has been taken as evidence of the existence of three types of receptor: the properties of each of these will now be described in more detail.

Slow-adapting receptors. Pfaffmann (1939*a*) investigated such receptors in the cat, and measured their responses to forces of varying magnitude applied in a chosen direction to the tooth crown. He also noted that one direction of stimulation was the most effective and that 'from the maximal position, there is a decrease in stimulating efficiency until a position of about 90° on either side is reached where the stimulus is no longer effective for that particular fibre'. In all preparations of the present study, this general relationship of response to the direction of the stimulus has been shown to hold good. Fig. 4 shows the responses of five slow-adapting units to pressure applied in the five basic directions to the incisor crown. It also illustrates the diversity of spike sizes which were recorded from units in the same dissection.

From Fig. 4 it can be seen that any estimation of the 'directionality' of a receptor should be made in three dimensions: in the present study elastic traction was applied varying in one dimension only. Fig. 5 shows action potentials from two sections of a record of slow-adapting receptors, the stimulus varying 20° in direction between the two. It will be seen that changes of

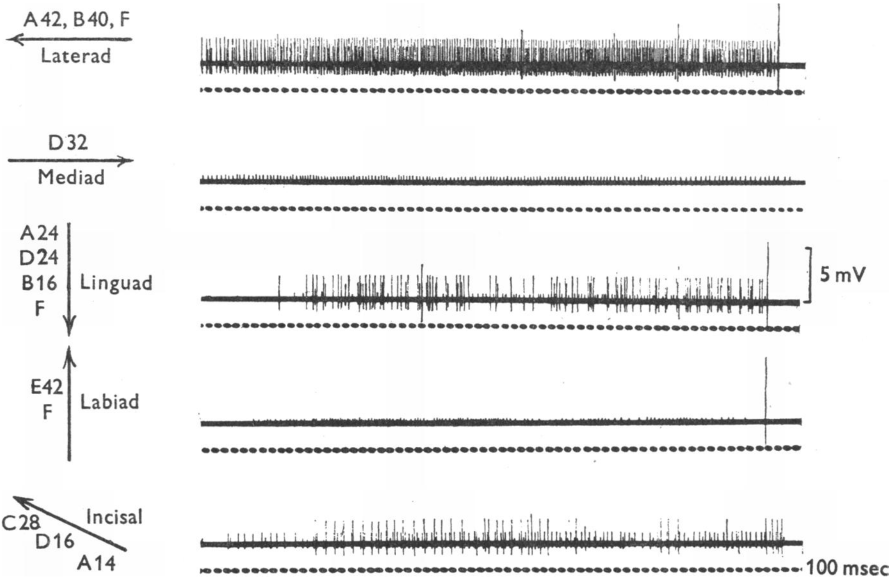

Fig. 4. Recordings of action potentials from a few-fibre preparation of the incisor nerve, showing the responses obtained on pressing the left incisor in the five basic directions. Five slow-adapting units (named A–E in order of their potential magnitudes) and one fast-adapting unit (F) are seen. To the left of each record the direction of stimulus during the taking of the record is shown, together with the fibres in action during that stimulus and the maximal frequency reached by a unit for that direction of stimulus. (Rabbit 83—retouched.) Records to be read from left to right; in the top two records, the beginning of the period of stimulation is not shown.

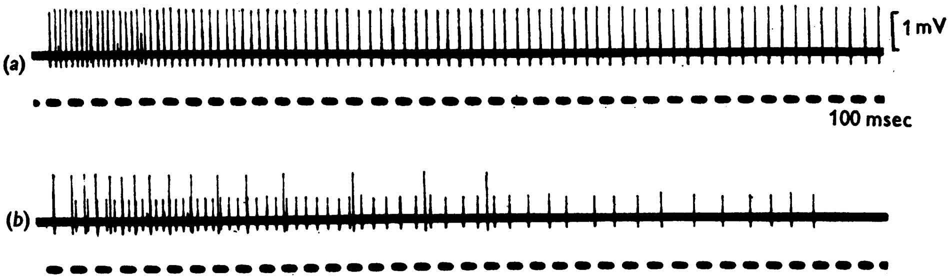

Fig. 5. Action potentials from three fibres of the left incisor nerve. The units are shown responding to elastic traction of magnitude 75 g, applied to the left incisor crown in (*a*) direction 180°, and (*b*) direction 200°. (Rabbit 89—retouched.)

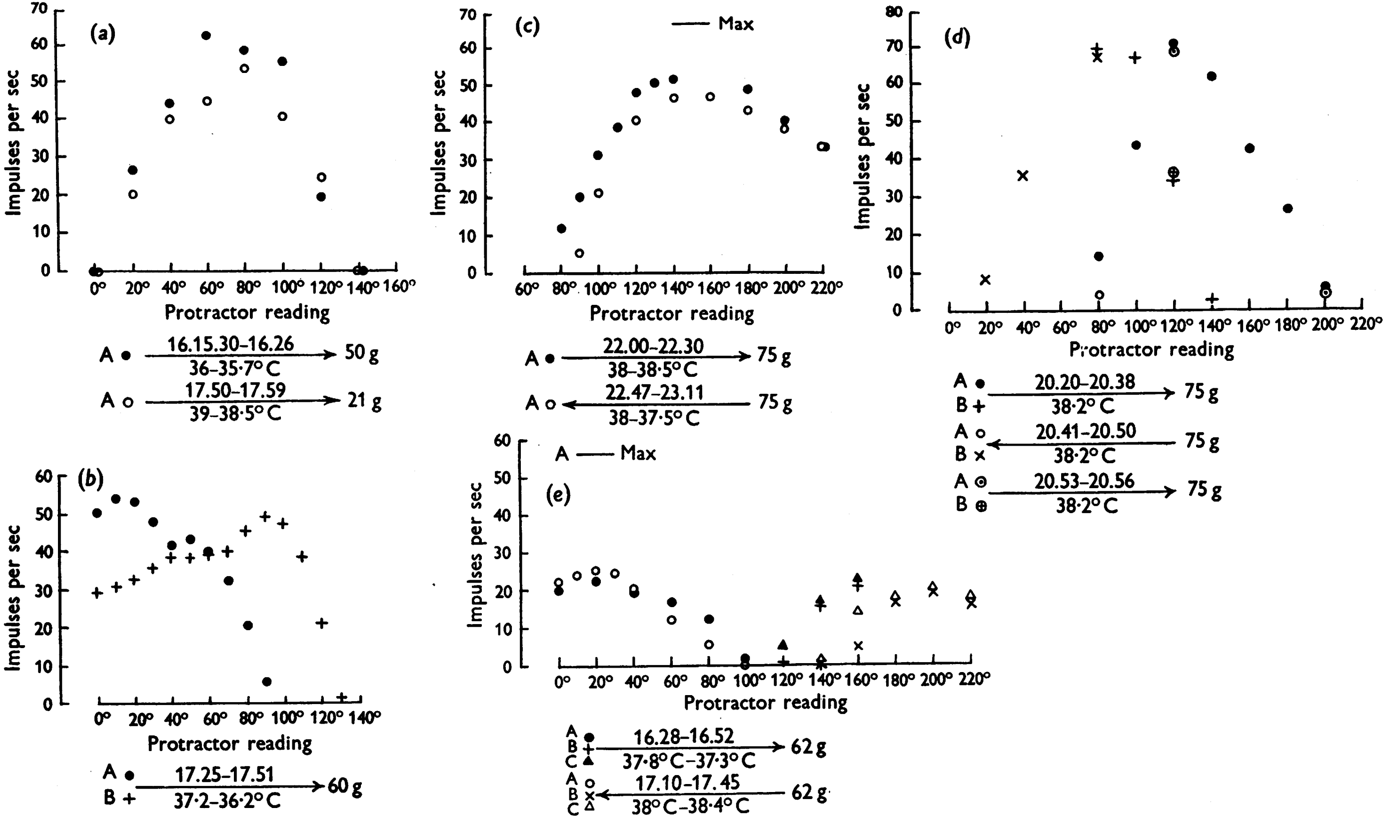

Fig. 6. Graphs of responses from single slow-adapting units to forces of the same magnitude applied in different directions, in the same plane, to the incisor crown. Arrows beneath the abscissae indicate the order round the protractor in which a series of readings was taken. Against each such arrow are the symbols representing units in action during the series, the time over which the series was taken, the rectal temperature during that period, and the magnitude of the force. Response was measured as the mean frequency, in impulses/sec, over the first 2·5 sec of a response. (*a*) Rabbit 84. Traction every 1½ min for ½ min. Fibre A: 1·54 mV. (*b*) Rabbit 86. Traction, every 2 min for 20 sec. Fibre A: 1·74 mV; fibre B: 0·82 mV. (*c*) Rabbit 88. Traction, every 3 min for 5 sec. Fibre A: 0·72 mV. Paraffin recording bath kept at 38° C. (*d*) Rabbit 89. Traction, every 3 min for 5 sec. Fibre A: 1·24 mV; fibre B: 0·84 mV. (*e*) Rabbit 90. Traction, every 3 min for 5 sec. Fibre A: 0·40 mV; fibre B: 0·30 mV; fibre C: 0·20 mV. In (*c*) and (*e*) lines marked 'Max' indicate the maximal frequency reached by the units over whose curves they are drawn, in response to heavy finger pressure in the sensitive direction.

frequency and of duration of discharge between (*a*) and (*b*) are in the opposite sense for the two large fibres: the stimulus was moved away from the sensitive direction of the largest fibre and towards the sensitive direction of the other. It may also be noted that the interval between the first impulses of the two fibres is less in (*b*) than in (*a*); in the experiments such intervals showed a variation of 0–250 msec. A few impulses of a third, small, unit can be seen: the plane of the protractor was not suitably aligned to test its responses.

The effects of the direction of a stimulus may be summarized in the statement that, the nearer a stimulus is to the most sensitive direction of a receptor, so response frequency will be greater, threshold will be less, discharge will last longer, and the first impulse will be initiated earlier.

The results of five quantitative experiments on directionality have been plotted in Fig. 6. The mean frequency of the first 2·5 sec of discharge has been taken as the index of response.

It can be seen from Fig. 6 that each slow-adapting receptor shows a 'most sensitive direction', responses falling away on either side. The curves of (*a*) and (*d*—fibre B) appear symmetrical about the most sensitive direction, that of (*d*—fibre A) is slightly skewed, those of (*b*—fibre B) and (*c*) are markedly skewed; the other curves are too incomplete for judgement. Fair agreement was found between determinations of the same point, except as shown in (*e*—fibres B and C); in these the initial frequencies were the same but adaptation differed. The notches in the curves of (*b*) might be accounted for by the wire links attaching the elastic to the incisor having locked incorrectly during traction, producing errors of direction and magnitude.

The responses to forces of different magnitude applied in one direction was not tested in those preparations used in the detailed experiments on directionality. When such responses were examined in other preparations results were obtained essentially similar to those of Pfaffmann (1939*a*) in the cat. In Fig. 7*a* responses in a single fibre have been plotted against time; a phenomenon common to the experiments is shown. That is, that when the applied force was large enough, a steady level of discharge was reached after initial adaptation; whereas with smaller forces the response became irregular and rapidly fell to silence, as soon as frequency had reached a level, characteristic for the preparation, of about 10–20 impulses/sec.

In Fig. 7*b* the responses of two units in another preparation have been plotted against the logarithm of the magnitude of the stimulus. A linear relationship in such a graph was typical of the experiments, but was often only well shown when the means of several readings of each point were plotted, as in the figure. For traction in the sensitive direction the linear relation held only for stimuli less than about 100 g.

The rates of rise of stimuli used in the experiments were estimated by substituting, in place of the incisor, a differential transformer, wired in a circuit so that minute changes in position of the transformer core could be recorded as changes in voltage. By this means the rising time of stimuli was estimated to vary between 120 and 170 msec when using weight-and-pulley systems and between 90 and 250 msec when using elastic traction. These times provide an explanation for the length of intervals found between first impulses of units in the same preparation in the directionality experiments; they may be borne in mind when considering threshold estimations given below.

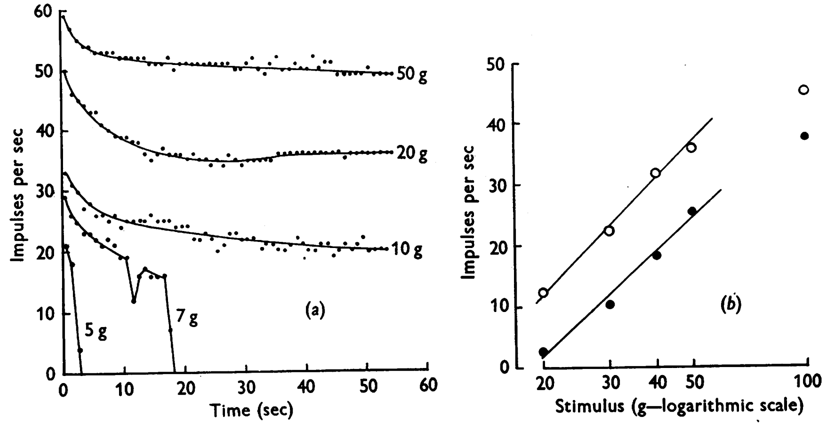

Fig. 7. Graphs of the responses from single slow-adapting fibres of the incisor nerve, to stimuli of different magnitudes, applied in the same direction to the incisor crown. (*a*) Graph of the responses of a single unit, in which the numbers of impulses in each second of a response have been plotted and smooth lines drawn through the points, making use of mean values. Deviation of more than 2½ imp./sec is shown only in the response to 7 g. (Rabbit 38.) (*b*) Graph of the responses of two units, the mean frequencies over the first 2½ sec of responses being plotted against the logarithm of the magnitude of the stimulus. (Rabbit 83.)

When records were taken from the whole incisor nerve, it was found that a force of 1 g applied in the labiad, mediad or laterad directions to the incisor crown produced a faint whisper from the loudspeaker, while 2 g evoked a burst of impulses lasting about a second and 5 g a response lasting minutes. Values between 3·5 g and 10 g were found for the thresholds of unit preparations when the force was applied in the most sensitive direction for the unit under test. The differences between the unit thresholds, and their difference from the threshold of 1–2 g found for the whole tooth, may be taken to indicate real variation of threshold between individual receptors, or differences of distance from the tooth fulcrum, or both.

The highest frequency at which units could be made to discharge, under steady pressure on the incisor, was measured. In eleven preparations hard finger pressure in the sensitive direction was the stimulus; this pressure was subsequently measured with a spring balance as varying between 1000 and 4000 g. The mean of the highest frequencies produced was 67·5 imp./sec, S.D. 19·9. In twelve other preparations, the maximal frequencies in response to forces of 50–200 g, applied over pulleys, were available: these showed a distribution of 56 imp./sec, S.D. 19·2. Student's '*t*' test showed these distributions to be different only at the 20 % level of probability. The similarity between the two distributions supports the finding that response is linearly related to the logarithm of the magnitude of stimuli only for forces below 100 g. The highest frequency recorded, using either means of stimulation, was 109 imp./sec; it is perhaps interesting that 'supra-maximal' stimulation of the same preparation, given by twisting a flat instrument held between the incisors, produced a frequency of 120 imp./sec. It would seem that the upper limits of frequency of preparations were imposed more by the extensibility of the periodontal membrane than by any inherent characteristic of the receptors.

It was characteristic of slow-adapting receptors that all those examined discharged for more than 5 sec, if the stimulus was sufficient. The longest time for which a unit was followed was 10 min, at which time the response to 20 g applied in a sensitive direction had ceased after becoming sporadic; increased loading then produced a renewal of the discharge. In records from the whole nerve, the discharge of some fibres was still vigorous after 4 hr, with a stimulus of 50 g.

Normally, the response of slow-adapting receptors ceased with the stimulus. However; after heavy or prolonged pressure on the incisor crown, a discharge from a few fibres was sometimes recorded from the whole nerve. Such 'after-discharge' was always sporadic (Fig. 3) in contrast to the steady frequency of spontaneous discharge.

In seven experiments, an attempt was made to locate the approximate position in the periodontal membrane of a receptor whose responses had been studied. A watch-spring, its leading edge sharpened, was pushed down the socket, in the hope of destroying the receptor. In practice, the only aspect of the socket whose curvature and bone thickness allowed such an operation was the labial. In no case was the response of a mechanoreceptor silenced, even though subsequent dissection showed the spring to have been pushed down to the base of the incisor.

Spontaneous discharge. In the eleven animals from which spontaneous discharge was recorded no evidence could be found that constant stress was being applied to the ipsilateral incisor, or to the mandibular symphysis, by any part of the experimental arrangement. The frequency of discharge was steady, but might vary over long periods, during the course of an experiment. For example one unit, when set up after dissection, was firing at a mean frequency of 31·2 imp./sec, S.D. 0·91: 2 hr later the mean frequency had fallen to 21·4 imp./sec, S.D. 0·82. It was possible to measure the frequencies of eight spontaneously discharging units: their distribution had a mean value of 24·5 imp./sec, S.D. 6·5.

The frequency of discharge could be controlled by pressure on the ipsilateral incisor and on the mandibular angle. It is thus certain that the continuous discharge came from specific receptors and was not an injury discharge. Further, if pressure in one direction increased the frequency, pressure in the opposite direction decreased the frequency (Fig. 8). These spontaneously discharging receptors may thus be considered to exhibit directionality; however, there were two exceptions: in both of these pressure in any direction on the incisor crown produced an increase in frequency followed by a period of silence on removal of the stimulus.

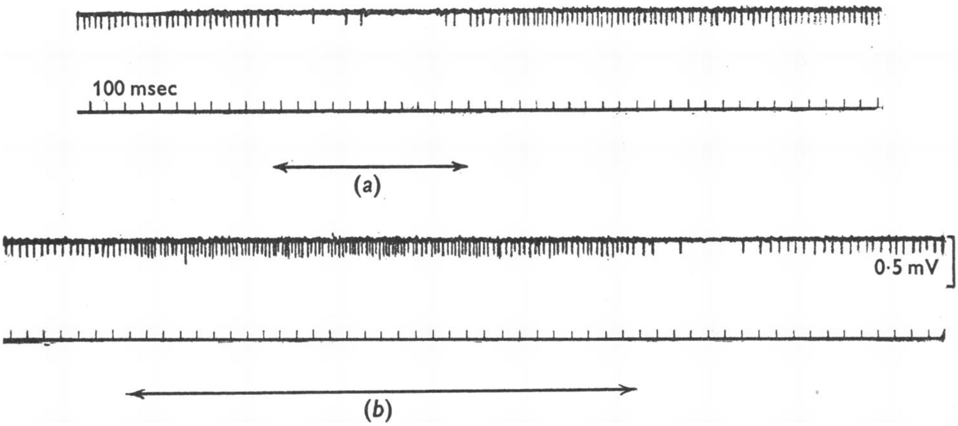

Fig. 8. Action potentials from a spontaneously discharging fibre in a dissected preparation of the incisor nerve. The opposite effects of pressure on the incisor crown (*a*) mediad, and (*b*) laterad, are seen. (Rabbit 18—retouched.) The durations of the stimuli are indicated by arrows beneath the records. The two sections were cut from a continuous record, a piece representing 3 sec of undisturbed spontaneous firing intervening between (*a*) and (*b*) in the original.

The effects of pressure on the mandibular angle were, in some experiments, transitory, the discharge returning to its initial frequency even while the stimulus was maintained. In one experiment, the discharge could be temporarily silenced by light pressure on the inter-incisal papilla from a blunt needle.

The maximal frequencies attained by three units, in response to heavy finger pressure on the incisor in an appropriate direction, were 56, 34 and 34 imp./sec. These maximal frequencies are not significantly different (as analysed by Student's '*t*' test) from those recorded from slow-adapting receptors.

Fast-adapting receptors. In five dissected preparations, a response was obtained to mechanical stimulation of the incisor crown, consisting of 1 or 2 large spikes at the 'on' or at the 'off' of the stimulus (Fig. 4). Such fast-adapting responses remained constant over long periods. This distinguished them from the 'rapidly adapting' responses of moribund slow-adapting units

—in some dissections in this work, preparations were obtained whose response consisted of a short train of impulses whatever the magnitude of the stimulus: such preparations rapidly failed.

In three experiments fast-adapting responses were recorded from dissections including slow-adapting units, as shown in Fig. 4. In such experiments it was important that the spike size of the fast-adapting response could not be equated to the sum of the spikes of the slow-adapting receptors, because the spikes of slow-adapting units can be summed to form a smooth single spike, if the application or removal of force is rapid. In the records shown in Fig. 4 the arithmetical sum of the spikes of the slow-adapting units does exactly equal the spike size of the fast-adapting unit: but the different directionalities of the slow-adapting units make it impossible for their potentials to have summed arithmetically.

The fast-adapting receptors showed directionality in the same sense as the slow-adapting receptors: this is demonstrated in the records shown in Fig. 4.

Incisor movement

When a force was applied to the incisor crown, the tip of the incisor could be seen to move in the direction of the stimulus. It was possible on removing small amounts of bone from the labial aspect of the socket, and observing the shape of the fluid meniscus in the periodontal membrane space thus revealed, to determine the fulcrum of the tooth in relation to forces applied in the laterad and mediad directions to the crown. The fulcrum was found to lie two-fifths of the distance along the labial arc of the tooth, measured from the incisal tip. The position of this fulcrum has been marked in Fig. 2*a*: it will be seen that it lies at the top of the socket. Therefore, when the crown moves in one direction, the root moves in the opposite direction. This is in contrast to the movement of conically rooted human teeth, which are said to tip about a point approximately on the apical third of the root (Smith & Storey, 1952).

DISCUSSION

Types of discharge in the incisor nerve

Three types of discharge in incisor nerve fibres have been described, and evidence has been presented that these responses emanate from three groups of sense organs, distinguished by the spike size of their fibres. In addition, responses have been observed consisting of a short burst of impulses at the beginning and the end of movement of the mandibular symphysis. It is not clear if these latter responses, and the modification by symphyseal movement of the frequency of spontaneous discharge, indicate a specific innervation of the symphyseal joint.

Pfaffmann (1939*a*) found slow-adapting and occasional spontaneously discharging fibres in the nerves of the maxillary teeth of the cat. He specifically denied finding fast-adapting receptors such as he found in the cat's tongue; but he noted that some 'slow-adapting' receptors gave only 5–6 impulses in response to a stimulus of 100 g. The differences in technique make difficult comparison with Pfaffmann's quantitative observations. He reported initial frequencies of up to 1200 imp./sec from slow-adapting units, taking frequency as the reciprocal of the measured interval between impulses. However, his figure for the threshold of the canine tooth of the adult cat is of the same order as that here reported for the rabbit incisor, and the frequencies shown in his Fig. 4 are also comparable. Boyd & Roberts (1953) have reported a similar frequency range for the slowly adapting receptors of the cat's knee-joint. In making comparison it must be remembered that the present measurements were made on receptors 3° C below rectal temperature, that rectal temperature was not rigidly fixed, and that it is possible that the use of an anaesthetic modified the responses, although no effects on discharge were noted when the concentration of circulating urethane was increased. Sand (1937) found a depressant action of urethane on the spontaneous discharge of sense organs of the lateral line of fish.

Boyd & Roberts (1953) found 'rapidly adapting' receptors scarce compared with 'slowly adapting' ones in the cat's knee-joint, the ratio being 1/17, in comparison with the 1/5 ratio found in the present study. They also found the spikes of their 'rapidly adapting' discharges to be about 2½ times as large as those of the 'slowly adapting' type: a similar ratio has been here reported. It is of great interest that Boyd (1954) has been able to identify the 'rapidly adapting' receptor of Boyd & Roberts as an elongated lamellated corpuscle and the 'slowly adapting' receptor as a spray (or Ruffini) ending, since Lewinsky & Stewart (1936) illustrate apparently similar endings found in preparations from the periodontal membranes of cat and rabbit.

Directionality

A relationship between the direction of a mechanical stimulus and the response of a stimulated sensory receptor has been observed in mechanoreceptors of the lateral line organ of fish (Sand, 1937), and of the teeth (Pfaffmann, 1939*a*), vibrissae (Fitzgerald, 1940), and knee-joint (Boyd & Roberts, 1953) of the cat. The incisor tooth of the rabbit has provided a suitable preparation for examining this relationship in some detail. The following discussion deals with the slow-adapting discharge; as well, the fast-adapting and spontaneously discharging responses have been found to be directional.

Several mathematical treatments were considered, in attempts to relate the direction of the stimulus to the response obtained. In the simplest of these the stimulus is considered as acting at one end of a straight lever with a universal joint as fulcrum. Then the component given in any direction at a point in the periodontal membrane, by a force F acting on the tooth crown at an angle θ to that direction, can be described by the equation

$$P = kF \cos \theta, \tag{1}$$

where P is the magnitude of the component and k a constant derived from the lever-arm ratio between the point and the point of application of the force.

From the present results, the response of a receptor to stimuli, of magnitudes less than 100 g, applied in the same direction, may be described by the equation

$$R = K \log S + c, \tag{2}$$

where R is the response, S the magnitude of the stimulus, and K and c constants characteristic of the receptor under consideration.

Then, if the component given in the most sensitive direction may be considered the effective stimulus, and if the stimulus is applied at an angle θ to the most sensitive direction, (1) and (2) above may be combined giving

$$R = K \log \cos \theta + K \log (kF) + c,$$

and, if the magnitudes of the stimuli are identical,

$$R = K \log \cos \theta + C. \tag{3}$$

It will be seen that, in equation (1), k could be determined if the location of the receptor in the periodontal membrane were known, and that, in equation (2) K and c could be determined for the same receptor on which directionality experiments were performed. It will also be noted that, in equation (3), when $\theta = 0°$, $C = R$.

In Fig. 9 a composite plot has been made of these results, shown in Fig. 6, where complete directionality curves were obtained. In each case the 'most sensitive direction' and the frequency at this direction have been judged by eye. The 'most sensitive direction' has then been laid along the position 0°, and all responses from each curve have been reduced by a factor which brought their frequency at the 'most sensitive direction' to an arbitrary value of 100 units. Against these collected results, a curve has been drawn of equation (3), in which K has been taken as 350 and in which C must be 100. If values between 100 and 400 are given to K, curves can be drawn which fit any of the experimental curves reasonably well, since K determines the width of the base of the curve. The origin of skew in the experimental curves is unknown: perhaps the spiral shape of the rabbit incisor should be taken into account in equation (1).

Clark (1947) has suggested that the differing alignment of the receptors of the skin may be the basis of the perception of the direction of a mechanical stimulus applied to the skin. Boyd & Roberts (1953) have presented evidence that their 'slowly adapting' responses originate from stretch receptors whose directionality is a property of their individual orientation in the joint capsule, and not the result of their systematic arrangement round the capsule. Similarly, the directionality of periodontal mechanoreceptors could be a property of the orientation of individual receptors otherwise randomly distributed in the periodontium. Each such receptor must have an axis (impulses being initiated on deformation along that axis), whose direction would determine the direction of stimulation of the incisor crown to which the receptor would be sensitive. The axis of such a receptor need not be that of the nerve terminals themselves. Boyd (1954) has shown that the 'slowly adapting' sensory unit of the knee-joint consists of a number of nerve terminal sprays situated on a bundle of connective tissue fibres. Thus the receptor orientation could be that of connective tissue fibres. In such a composite the relation between discharge frequency and the magnitude of a stimulus might be more a property of the extensibility of the connective tissue than of the nerve terminals themselves.

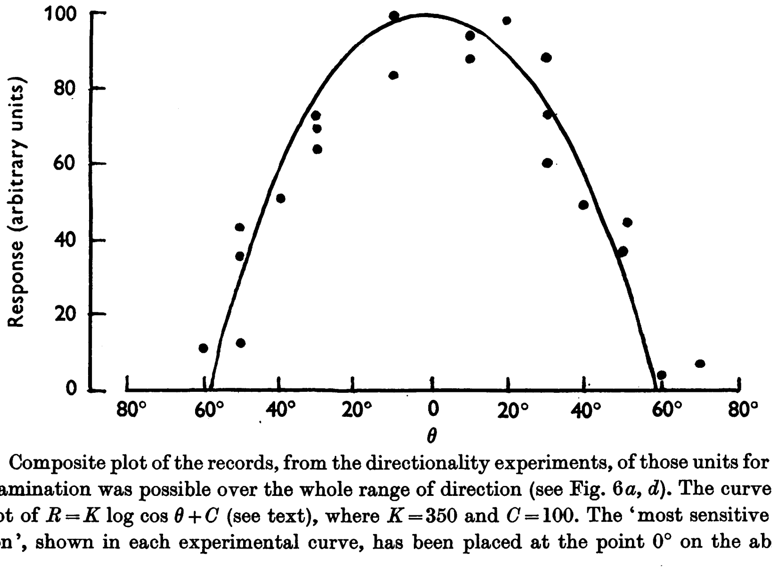

Fig. 9. Composite plot of the records, from the directionality experiments, of those units for which examination was possible over the whole range of direction (see Fig. 6*a*, *d*). The curve is the plot of $R = K \log \cos \theta + C$ (see text), where $K = 350$ and $C = 100$. The 'most sensitive direction', shown in each experimental curve, has been placed at the point 0° on the abscissa.

Such a model of the periodontal mechanoreceptors introduces a curious problem. If afferent information is to be of use to the central nervous system in the analysis of the changing environment, then the responses in sensory receptors must bear a constant relationship to a given stimulus. But, in the rabbit, the incisor periodontal membrane is in a state of continuous reorganization, the tooth being extruded from its socket at a rate of 0·3 mm/day, rising to as much as 0·9 mm/day if the tooth is taken out of occlusion (Herrmann, 1953; Ness, unpublished). Therefore, the maintenance of a constant orientation of the receptors appears a striking example of the general problem of the maintenance of the form of the organism when its component parts are continuously changing. Unless, that is, the 'glide plane' between tooth and socket could be shown to lie close to the tooth, thus leaving the bulk of the periodontal membrane relatively undisturbed by eruption; Sicher (1942), on histological evidence, placed the 'glide plane' in the middle third of the thickness of the periodontal membrane.

Continuous eruption would not present such a problem if directionality involved orderly arrangement round the circumference of the socket of pressure receptors responsive *either* to the compression *or* to the decompression which must be produced in the periodontal membrane, on opposite sides of the root, when pressure is applied to the tooth crown. Movement in the long axis of the tooth during eruption would not seriously affect such a receptor whose directionality arose from its position in the socket and not from orientation of an 'axis'. But since the responses recorded from the incisor nerve, when forces are applied in the labiad, linguad, mediad or laterad directions, are indistinguishable, directionality based on a non-orientated receptor carries the postulate of even distribution of receptors round the tooth circumference. Preliminary histological examination indicates that no nerve bundles course in the labial aspect of the periodontal membrane of the rabbit mandibular incisor: such a finding, if confirmed, explains the failure of attempts to locate receptors by pushing a spring down the labial aspect of the socket. Such uneven distribution of nerve fibres, and thus presumably of sensory endings, would rule out any model based on orderly arrangement of pressure endings; unless similar numbers of two groups of receptors of opposite 'polarity', evenly distributed round half the socket circumference, were postulated. Such a combination would seem unlikely.

It is possible that, instead of being randomly arranged, stretch receptors, such as are postulated in the first model above, might be systematically arranged round the socket with their axes lying radially across the periodontal membrane. Such a model would present the difficulties of both the previous models and involves a postulate of regular arrangement which is unnecessary to the explanation of directionality.

In the practice of orthodontics, forces are applied to the teeth of children to improve the form of the dental arch. In some cases teeth are made to rotate 90° or more round their long axes. It would be most interesting to test the ability of subjects to judge the quality and direction of a mechanical stimulus applied to the tooth before, during, and after such treatment.

SUMMARY

1. Sensory nerve impulses have been recorded from the whole incisor and mental nerves, and from dissected unit preparations of the incisor nerve, in the rabbit anaesthetized with urethane.

2. The mechanoreceptor distributions of the mental and incisor nerves have been plotted.

3. Slow-adapting, fast-adapting and spontaneously discharging types of response have been recorded from the incisor nerve, activated by mechanical

stimulation of the incisor crown: these responses appear to emanate from three distinct groups of receptors. In addition, movement of the mandibular symphysis has been shown to produce small bursts of impulses in the incisor nerve and to modify the frequency of spontaneously discharging receptors: the location of receptors so affected remains obscure.

4. The response of mechanoreceptors of the incisor nerve has been shown to be related to the direction of a stimulus applied to the incisor crown.

5. A simple mathematical relation between the response of slow adapting receptors and the direction of a stimulus has been developed. Receptor models which might show directionality have been proposed.

6. The problems of the maintenance of directionality of periodontal mechanoreceptors of the continuously erupting rabbit incisor, and of the teeth of patients undergoing treatment with orthodontic appliances, have been indicated.

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