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FUNCTIONAL CHARACTERISTICS OF MECHANORECEPTORS IN SINUS HAIR FOLLICLES OF THE CAT

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SUMMARY

1. The discharge of impulses in afferent fibres dissected from the infraorbital and ulnar nerves of anaesthetized cats was recorded during controlled movements of the maxillary and carpal sinus hairs.

2. Four main types of afferent units were identified. Two had slowly adapting responses characteristic of the epidermal type I, and dermal type II mechanoreceptors of the hairy skin. Two rapidly adapting responses to movement of the sinus hairs were found, one with a high velocity threshold and another with a low velocity threshold.

3. The slowly adapting units showed a power relationship between the degree of displacement of the hair and the mean interspike interval of the response. Slowly adapting units also exhibited a power relationship between the velocity of displacement of a hair and the mean interspike interval of the response.

4. The conduction velocities of all types of afferent units were measured and fell in the range of the Aα, fast myelinated fibres.

5. Movements of the carpal sinus hairs yielded both types of slowly adapting response recorded in fibres of the ulnar nerve directly innervating the carpal sinus hair follicles, and rapidly adapting responses from Pacinian corpuscles, found in close association with, but external to, these follicles.

6. On the basis of the findings in this study and the results of anatomical investigations of the receptor structures in the sinus hair follicle a correlation between the distinguishable afferent responses and the morphologically identifiable nerve endings has been proposed.

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INTRODUCTION

Cats and many other quadrupeds use their sinus hairs, especially their vibrissae, as tactile sense organs (Vincent, 1913; Schmidberger, 1932). Although our knowledge of the tactile sensibility of the skin has been enlarged widely in the past 20 years there is still uncertainty concerning the receptor physiology of sinus hairs. Fitzgerald (1940) reported that the nerve endings of sinus hairs were 'in the main slowly adapting' and that they had a directional sensitivity, preferentially towards the centre of the maxillary vibrissa group. This latter finding was recently challenged by Zucker & Welker (1969) and Hahn (1971) when they found that individual units from a given vibrissa responded to bending of the hair in several directions. For the rat vibrissae Zucker & Welker distinguished five categories of afferent vibrissa units on the basis of their response to specified stimulus parameters, whereas Hahn (1971) made two groups on the basis of the response of presumed slowly adapting receptors to sinusoidal stimulation. Both Hahn and Zucker & Welker found rapidly and slowly adapting responses but did not attempt to establish the particular types of receptors to which their units could be assigned. Afferent discharges from sinus hairs were recorded in the Gasserian ganglion (Kerr & Lysak, 1964), the trigeminal nuclei (Gordon, Landgren & Seed, 1961; Erickson, King & Pfaffmann, 1961; Kruger & Michel, 1962; Eisenmann, Landgren & Novin, 1963; Nord, 1967), in the ventrobasal thalamus (Waite, 1973) and in the cortex (Welker, 1971; Keidel, Keidel & Kiang, 1960) but in these investigations no attempt was made to differentiate the responses in detail. The existence of two rapidly and two slowly adapting mechanoreceptors in the sinus hair follicle of the cat reported in the present paper has been reported also by B. J. Pubols, P. J. Donovick & L. M. Pubols personal communication for the vibrissae of the opossum.

The older literature on the classical light microscopic studies of receptors in the sinus hair follicle was summarized by Vincent (1913), whose account was confirmed and extended by Andres's (1966) very thorough electron-microscopical investigation. Andres' description of the fine structure of four kinds of receptors in the sinus hair follicle of rats, rabbits and cats led to the suggestion that movement of a sinus hair may activate different sorts of receptors at the same time.

Using the technique of single fibre recording it was the aim of the present study to investigate the various types of afferent responses from the cats sinus hair follicle. On the basis of the electrophysiological results a correlation will be proposed between different discharge patterns of the afferent units and the nervous structures already identified by anatomical methods. A preliminary account of this work has been published (Gottschaldt, Iggo & Young, 1972).

METHODS

Preparation of the animal. The experiments were performed on forty-four cats of both sexes, weighing 1·7–4·5 kg. Anaesthesia was induced with ethyl chloride and ether, followed by chloralose 80 mg/kg I.V. If necessary, subsequent doses of pentobarbitone were administered through an I.V. cannula. The trachea was intubated and breathing supported with a pump if required. Rectal temperature was maintained at 36–38° C using a thermostatically regulated electric blanket.

A metal plate was mounted to the skull by self-tapping screws and dental cement. The head was rendered immobile by a steel bar fixed to the skull plate and the experimental table. This arrangement allowed unrestricted access to the right side of the forehead. The infraorbital nerve was exposed in the right orbit and single fibres were dissected in a pool of warm paraffin oil using conventional techniques. In two experiments fibres were dissected from the ulnar nerve adopting a preparation similar to that described by Nilsson (1969*a*).

Mechanical stimulation. Due to its curved shape the movement of a sinus hair can consist of three components: bending in any direction, clockwise or anticlockwise rotation around the long axis and a longitudinal displacement. Depending on the size and the rigidity of a given hair shaft these three components participate in different proportions in any mechanical stimulus. In order to investigate the activation of given receptors by different mechanical components of a hair movement several stimulating devices were used.

(1) An 'angle stimulator' Fig. 1 was designed which provided an approximately natural hair movement and at the same time enabled an examination of the effects of its separate mechanical components. With this instrument the hair could be bent in all cardinal directions (forward, backward, upward, downward) as well as in any directions resulting from the combination of adjacent cardinal directions. In addition, the hair could be rotated in either direction independently of the angular deflexion, or displaced longitudinally (for detailed description see legend of Fig. 1). A 'calibrator' determined the actual deflexion angle of the hair at any attachment position of the angle stimulator along the hair axis.

(2) An electro-mechanical stimulator (Brown & Iggo, 1967) could either be attached directly to the hair or, by means of a coupling, to the angle stimulator, making it possible to superimpose electrically controlled movements of up to 8 degrees on to the angle stimulator. The maximal velocity of an angle movement was equal to 160°/sec.

(3) Sinusoidal stimulation was achieved by driving the electromechanical stimulator or a piezoelectric bender element (Brush-Clevite, polymorth) with a sinewave generator. Since the necessary sinewave frequencies lay far above the limits of the available amplitude control systems, we were not able to measure the amplitudes of an oscillatory movement satisfactorily.

(4) Electrical stimulation, using a Grass SIU stimulator, was achieved by placing the tips of a sharp bipolar electrode on either side of the sinus body. The conduction velocities of single afferent fibres were calculated from the conduction times and measurements of the conduction distances.

A particular sinus hair giving rise to unitary action potentials was first identified by manual exploration of the face. The surrounding small hairs of the common fur were clipped off and neighbouring sinus hairs were pulled aside. If the source of the response was uncertain the sinus hair follicle was dissected free from the surrounding

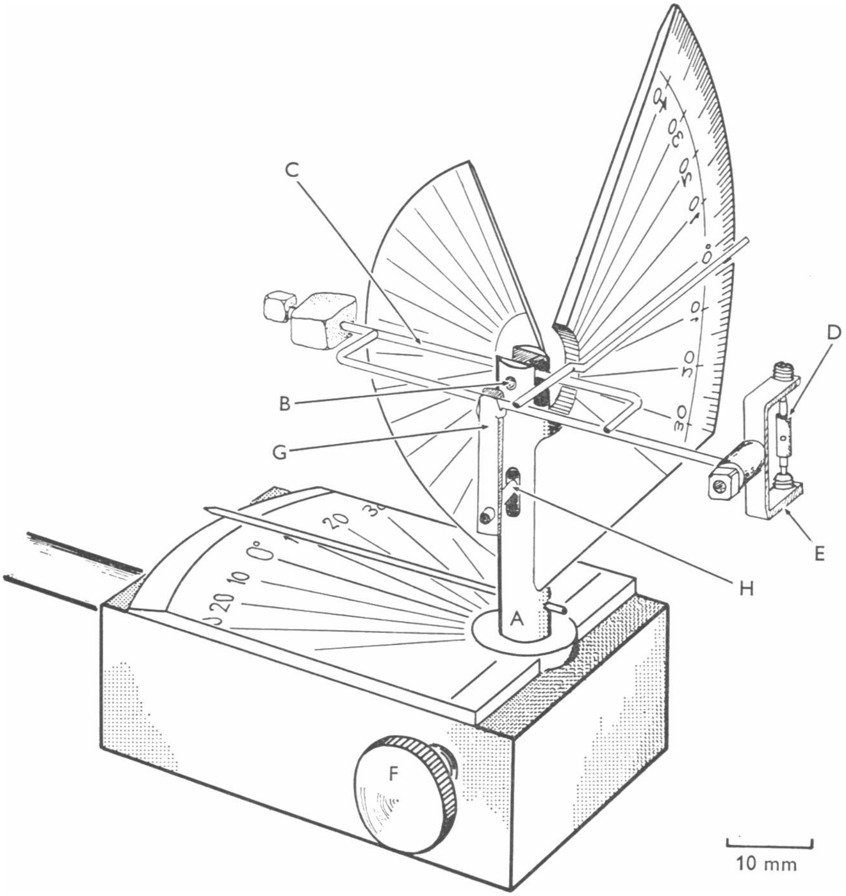

Fig. 1. The 'Angle Stimulator'. Rotation around the vertical axis (A) produced movement in the horizontal plane; around the horizontal axis (B) a movement in the vertical plane; and around the longitudinal axis (C) an axial rotation of the hair. The head of the stimulator consisted of a spindle (D) with a central eye through which the hair was passed. The spindle rotated freely in a yoke (E) which itself could rotate perpendicularly to the spindle axis. This arrangement ensured that the orientation of the spindle eye remained at right angles to the axis of the hair shaft, thus minimizing friction and buckling of the hair during application of a movement.

Movement around any given axis could be prevented independently by the locking devices F, G and H. The angular movement in any plane was measured on the appropriate scales. The electromechanical stimulator could be attached at any point on the horizontal arm, and was used to apply controlled movements, within a maximum amplitude of ± 8°.

skin under microscopical observation, while continuing to record the afferent discharge, in order to confirm the location of the receptor within a particular follicle.

Recording methods used are described by Brown & Iggo (1967) and Chambers, Andres, Duering & Iggo (1972) and the same precautions and criteria were adopted to ensure that single unit responses were analysed. Interspike interval data were collected and analysed using a PDP-12 computer. The methods of Perl (1960) were used in the analysis of the time course of adaptation of firing frequency.

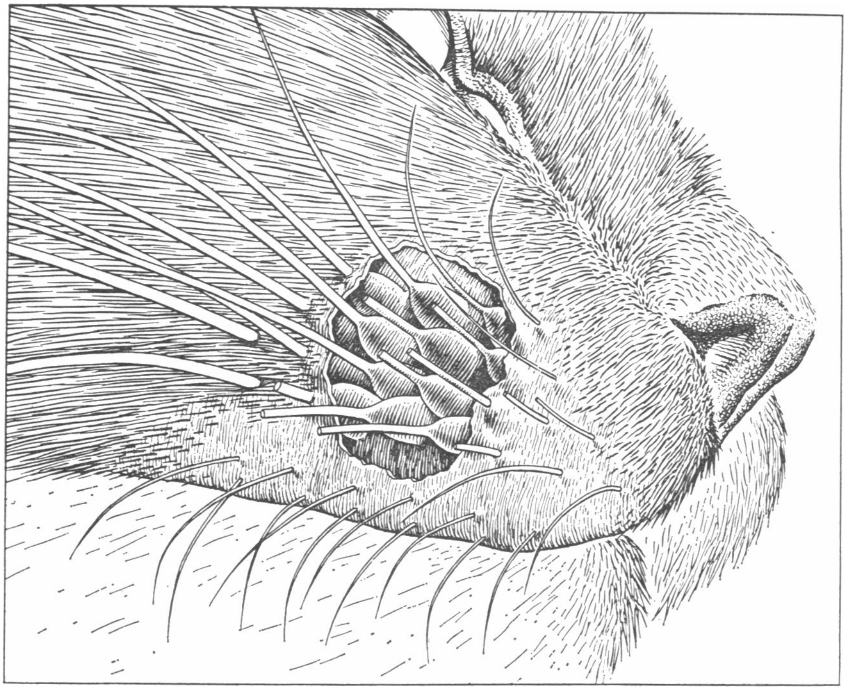

Fig. 2. Drawing of the cat face with overlying skin removed to show the arrangement of the upper labial and maxillary sinus hairs and some of the sinus bodies, exposed by dissection. For the internal structure of the follicles refer to Andres (1966).

RESULTS

Anatomical findings

The cat has two kinds of sinus hairs, the facial and the carpal. The *facial sinus hairs* lie above the eye brow, at the mouth angle and (the majority) in the maxillary area where they are arranged regularly in four rows of four to eight hairs (Fig. 2). Only the longer (4–7 cm) more backward situated maxillary sinus hairs are the vibrissae proper. Along the upper lip there is a double row of less conspicuous, shorter (1·5–3 cm) sinus hairs. The size of the sinus hair follicles (sinus bodies) varies with the size of the hair shaft, ranging from just visible structures (0·2 mm in diameter) to a maximum of 4 mm in length and 2 mm in diameter. The upper half of the sinus body is embedded loosely in the subcutaneous tissue while the lower half is enclosed by striated muscles attached to the tough follicle capsule. The receptors, described in detail by Andres (1966), are situated in the external root sheath and the inner hair follicle, both of which are surrounded by a cavernous or a circular blood sinus. *Carpal sinus hairs* and their follicles are smaller than the vibrissae. They are regularly associated with touch corpuscles which are seen as small elevations beside the orifice of the hair channel and the follicle bases are surrounded by numerous Pacinian corpuscles which can be exposed by dissection as tiny pearly beads. Carpal sinus hairs are supplied by smooth muscles.

Physiological findings

A total of 141 unitary responses from facial sinus hairs were investigated. Invariably a single afferent fibre innervated only one sinus hair follicle. About two thirds of the units were slowly adapting, while the remainder had rapidly adapting responses.

A. Slowly adapting responses

The one hundred slowly adapting units formed two principal groups as regards discharge pattern, adaptation behaviour, excitability characteristics and stimulus–response relationships. The groups had response characteristics similar to either the type I (SA I) or the type II (SA II) slowly adapting cutaneous receptors previously described (see Chambers *et al.* 1972) and we therefore refer to them as sinus type I and sinus type II (St I and St II).

Differences in the discharge pattern of slowly adapting sinus hair units

The steady discharge of an St I unit is characterized by irregular interspike intervals in contrast to the St II units which have highly regular interspike intervals (Fig. 3). This difference is independent of the stimulus applied. Besides the two clear-cut groups a third slowly adapting response has been recognized which, depending on the applied stimulus, may have regular or irregular interspike intervals. In the discharge of this last kind of unit a modal regular interspike interval is often present, around which shorter and longer intervals are scattered. Since these units otherwise displayed most of the response characteristics of the St II units they have been assigned to a subgroup of the Sinus type II units and therefore we called them slowly adapting St type II(*b*) (St II(*b*)) and refer to the more regular units as St II(*a*). Fig. 3 shows typical examples of the firing patterns, at similar mean firing rates, of the three kinds of slowly adapting units. In the left side of Fig. 3 the regular modal interspike intervals of the

St II (*b*) discharge, as well as the constant interspike intervals of the St II (*a*) response are illustrated. The St I discharge exhibits the characteristic feature of both long and short interspike intervals even at low firing rates, a distinct difference from the irregular discharge of the St II (*b*) response.

Sixteen interspike interval histograms of the slowly adapting discharges were compared with theoretical distribution functions using parameters derived from the experimental data, and the goodness of fit to these distributions was tested using the χ-square test. The distribution of interspike intervals of an St I response appears to be random, outside a variable functional refractory period (dead time) of several milliseconds. The distribution of these intervals should be that of an exponential distribution of the form $f(x) = \lambda\, e^{-\lambda x}$, where x is the interspike interval and λ a rate parameter. Fig. 3*A* shows the interval distribution histogram (mean $= 47{\cdot}76 \pm 34{\cdot}97$) for that part of the response (10th to 100th second) of an St I unit to maintained displacement, during which adaptation was minimal. The superimposed exponential distribution (⊙) fits the observed histogram closely ($P = 0{\cdot}05$) over the range of intervals from 14 to 100 msec. Deviations from the theoretical distribution presumably arise from a slow long-term trend in interval lengths. Fig. 4*B* shows the interval distribution histogram of an St II (*a*) unit during steady spontaneous discharge (mean $= 22{\cdot}0 \pm 2{\cdot}3$ msec) over a period of approximately 260 sec. A Gaussian distribution of the same parameters (⊙) fits the observed distribution with a high degree of accuracy ($P = 0{\cdot}01$). When shorter samples are taken (50 sec) the fit to a Gaussian distribution is even better. The differences in goodness of fit between the long and short collection periods may be attributed to cyclical rate variations of low amplitude, with a period of about 50 sec, but which do not constitute a monotonic increase or decrease of the discharge frequency. The distribution of intervals of an St II (*b*) unit, Fig. 4*C* (mean $= 48{\cdot}97 \pm 19{\cdot}38$) does not fit either exponential or Gaussian distributions of the same parameters. Using a different stimulus a discharge with a normally distributed interval histogram was obtained for the same St II (*b*) unit illustrated in Fig. 4*D*. A comparison of Fig. 4*C* and *D* suggests that the underlying distribution of interval lengths of the St II (*b*) unit is normal, with some variability introduced from a source other than that which causes the generation of regularly spaced impulses.

Another observation indicating the close relationship of St II (*a*) and St II (*b*) units is illustrated in Fig. 5. During the adapting St I response Fig. 5*A* the standard deviation of consecutive interval lengths increases as the mean firing rate becomes slower. In contrast, the discharge of the St II (*b*) unit (25101) started off with short but irregular interspike intervals (mean interval length: 35·1 msec; S.D.: ± 10·5 msec; C.V., coefficient of variation: 0·29) Fig. 4*C*. After about 10 sec, while the response was adapting, the discharge became more and more regular in spite of the decreasing firing rate. Eventually the response stabilized with a small standard deviation (mean interval length: 40·8 msec; S.D.: 3·6 msec; C.V.: 0·08), thus exhibiting the essential characteristics of an St II (*a*) unit,

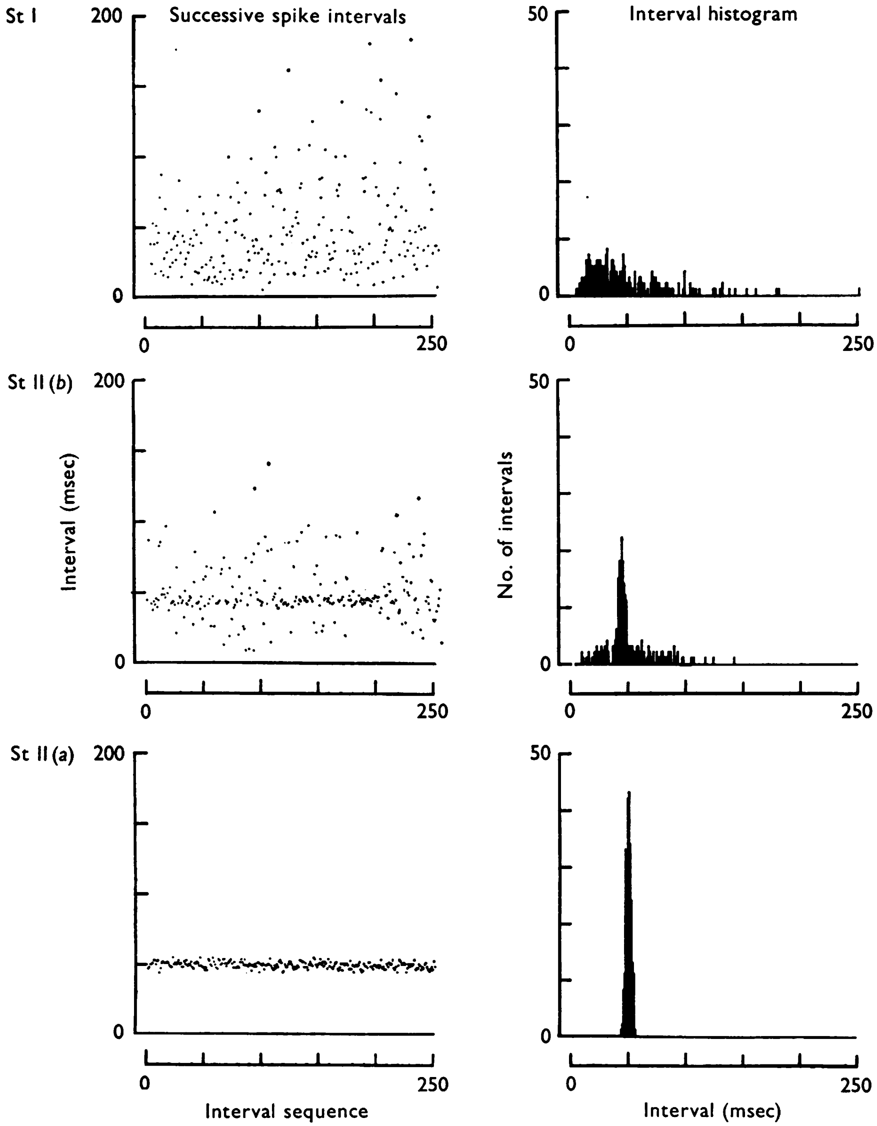

Fig. 3. For legend see opposite page.

an example of which is shown in Fig. 5*B*. At greater deflexion angles of the hair the St II (*b*) unit revealed the typical modal spike interval in an irregular discharge which was maintained for a long period at a constant level.

Adaptation of slowly adapting responses

In response to a sustained displacement the rate of discharge of an St I unit declines over a few minutes, until either the firing ceases completely or a very low firing rate ($<$ 5 impulses/sec) is reached. In contrast, the time courses of both St II responses differs from the St I in that the units, after an initial phase of adaptation, reach a steady discharge which can be maintained for a long period; e.g. St II (*a*) unit (0722) immediately after bending the hair by 10 degrees had a mean firing frequency of 10 impulses/sec. Two hours later, after a continuous firing of more than 72000 spikes, the unit was still discharging at the original firing rate.

In cutaneous SA I (Iggo & Muir, 1969) and SA units (Chambers *et al.* 1972) up to four phases of adaptation have been reported ($\tau_1 - \tau_4$). In the present study an early rapid adaptation period of St I and St II responses was seen but only the later phases ($\tau_3 + \tau_4$), recording the responses to larger hair displacements continuously up to 250 sec, were analysed.

The time courses of the adapted discharge curves shown in Fig. 6 indicates that in the period from 10 to 180 sec after the initial deflexion of the hair there were two time constants for both the St I and St II units. This data satisfies an exponential of the following form, which assumes independent and additive time constants;

$$f = f_1 . e^{-t/\tau_3} + f_2 . e^{-t/\tau_4},$$

Legend to Fig. 3.

Fig. 3. The discharge patterns of slowly adapting sinus hair follicle receptors (St I, St II (*a*), St II (*b*)) during sustained discharge. The three graphs to the left show the lengths of 250 successive intervals with each interval length, in msec, represented by the height of the point above the base line. The three graphs to the right are the interval distributions of the same data where the abscissae show the interval lengths and the ordinates the numbers of intervals within each bin (bin width 1 msec). The mean frequency of discharge of the three units is nearly the same but the distribution of intervals is substantially different. The upper pair of graphs is that of an St I unit (81101) showing the typically irregular discharge with interval lengths of between 2 and 250 msec (mean = 47·7 ± 34·9 msec). The centre pair of graphs shows the discharge characteristic of the St II (*b*) unit (25017) with a modal interval around which both long and short intervals are scattered (mean = 48·9 ± 19·3 msec). The third pair of graphs is that of an St II (*a*) unit (17811) showing a periodic discharge of low variability (mean = 49·5 ± 2·3 msec).

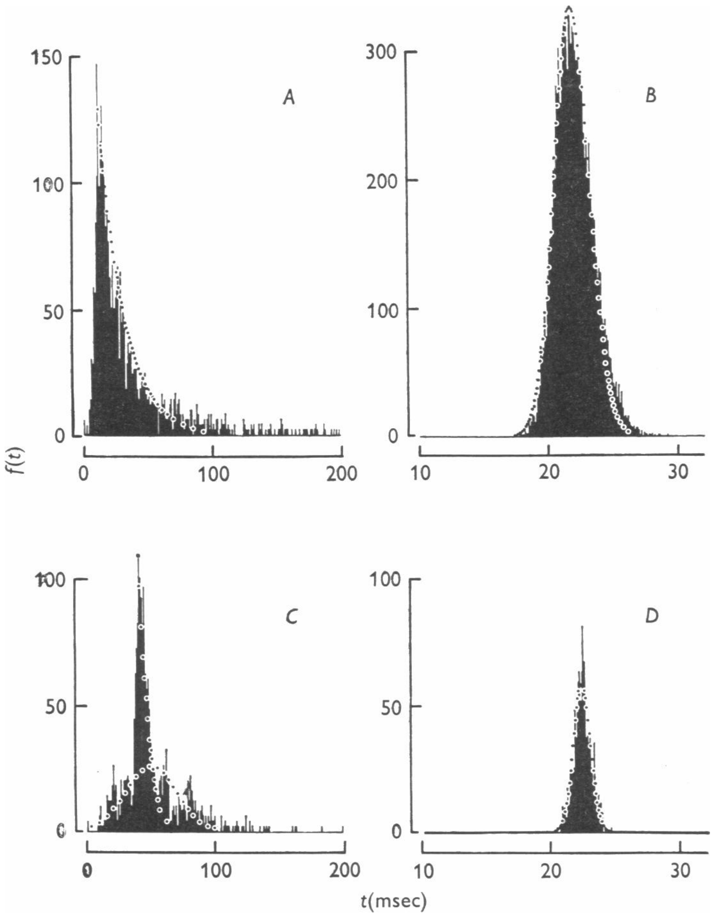

Fig. 4. Theoretical and observed distributions of intervals between impulses in the discharge of the slowly adapting sinus hair follicle receptors. Each graph shows an observed interspike interval histogram with a theoretical distribution of the same parameters superimposed upon it (○), and the goodness of fit has in each case been tested by chi-square.

A. The observed histogram of an St I unit (8111) fits an exponential relation ($f(x) = \lambda\, e^{-\lambda x}$ where λ is the rate parameter and X the interspike interval) for interval lengths between 14 and 100 msec.

B. The interval distribution histogram of an St II(*a*) unit (1541–1) collected over approximately 240 sec (mean $= 22{\cdot}0 \pm 1{\cdot}4$, $n = 11879$). The theoretical normal distribution, $f(x) = 1/\text{S.D.}\sqrt{(2\pi)}.\exp \tfrac{1}{2}\, (X - \bar{X}/\text{S.D.})^2$, fits the observed distribution to a high degree of accuracy ($P = 0{\cdot}01$).

C. The interval histogram of the St II(*b*) unit (25101–1) fits neither Poisson or normal distributions of the same parameters, suggesting that the population of intervals is not homogeneous.

D. The interval histogram of the St II(*b*) unit shown in (*C*) with the hair deflected in the opposite direction and held. The distribution of intervals is normal ($P = 0{\cdot}01$).

where f is the frequency at any time t sec after the initial displacement, f_1 and f_2 are the components of the initial frequency (at $t = 0$) determined by the time constants τ_3 and τ_4. In the early phase of the adaptation the effects of τ_3 and τ_4 are additive but as t increases τ_3, the shorter time constant, becomes negligible, and the exponential decline is governed only by τ_4. The earlier time constant τ_3 has been calculated by subtracting the extrapolated line of the later part of the curve from the early part and the new curve for τ_3 replotted as shown in the inset to Fig. 7. This is a standard 'peeling off' procedure (Perl, 1960). The early time constants for the St I units range from 20 to 70 sec (corresponding to TCA 3 of Chambers *et al.*

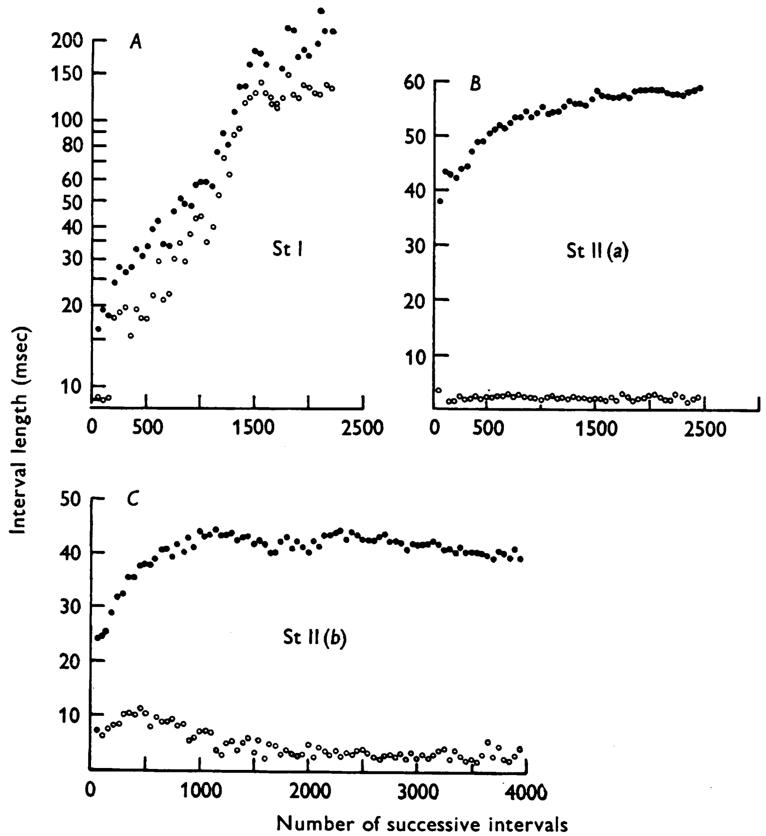

Fig. 5. Relationship between mean interval length and standard deviation in discharges of (*A*) St I, (*B*) St II(*a*) and (*C*) St II(*b*) units immediately following movement of the hair to a new fixed position. For each fifty intervals of a continuous number of successive intervals, plotted on the abscissa, each point represents the mean interval length (●—●) or the S.D. (○—○) of the appropriate fifty intervals. The graph of the St I unit is plotted on semilogarithmic axes, the graphs of the St II units on linear axes.

(1972), and the later time constant from 100 to 200 sec. The corresponding values for the St II units are from 40 to 500 sec and a late time constant approaching infinity, indicating that no adaptation occurred.

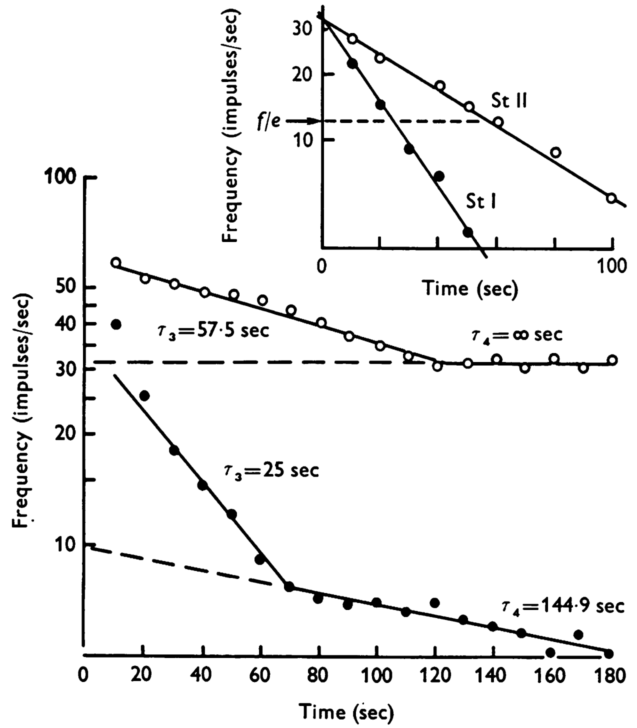

Fig. 6. The time course of the adaptation of the discharge of slowly adapting sinus hair receptors (St I = ●—●, St II = ○—○). The points represent average frequencies calculated over periods of 10 sec and are plotted on semi-logarithmic axes. Straight lines were fitted by the method of least squares using the relation $\log_e f = \log_e f_0 - t/\tau$, where f is the firing frequency, f_0 the initial frequency at stimulus onset, t the time after stimulus onset and τ the time constant of the exponential decline. Both type I and type II units show two time constants in the period of recording from 20 to 180 sec. The inset shows a replot of the early portions of both the St I and St II curves after subtracting the extrapolated lines of the late portions of the curves. This procedure enables the early time constant τ_3 to be calculated accurately.

In a recent comparison of the two types of slowly adapting cutaneous receptors (Chambers *et al.* 1972) the adapted discharge of SA I units had coefficients of variation of spike intervals greater than 0·50. A similar result was obtained in the present study for slowly adapting sinus hair follicle units. In ten St I units the coefficient of variation averaged 0·75 (range 0·52–0·86), for twelve St II (*a*) units it was 0·085 (range 0·02–0·17) and for nine St II (*b*) units it was intermediate (average value 0·49; range 0·07–0·83).

Excitability of slowly adapting receptors

The St I and St II units all responded to different mechanical components (i.e. bending, rotation or longitudinal displacement) of a hair movement. Individual units, even in the same follicle, were affected by a given stimulus component to a varying extent. In addition, the excitatory stimulus components for a particular unit could participate in a given hair movement in either a complementary or in an antagonistic manner. This is the basis for the finding that units, responding predominantly to one rotational component, could be activated by hair deflexion in opposite directions at the tip and at the base of the hair shaft, for, due to the curvature of the hair the rotational movements are in opposite directions at these points. In general the actual response of a slowly adapting receptor not only depended on the extent to which the receptor terminal was excitable by the different components of a hair movement but also on the extent to which the excitatory movement components participated in a particular stimulus situation.

Directional sensitivity

In our experiments the specification of the effective bending direction alone was insufficient to establish directional sensitivity. Directional sensitivity is defined as a response to movement of the hair in a given direction combined with the cessation of any discharge after a reverse movement. This requirement was only, but consistently met, by St I units. This kind of unit responded normally to a hair bending towards two adjacent cardinal directions while the discharge stopped immediately if the hair was bent back wholly or partly towards its original position. In addition, a positional effect was seen, i.e. bending of a hair in the sensitive direction towards the resting position of the hair was less effective than bending the hair in the sensitive direction away from its resting position.

Many of the St II (*a*) and St II (*b*) units responded to a deflexion of the hair from its resting position towards three or even four cardinal directions. In contrast to St I units the St II units never fired if the hair was moved towards the resting position from an insensitive direction, that is, they lacked the positional sensitivity of the St I units.

Fig. 7 illustrates the different directional sensitivity of a St I and an St II (*a*) unit. Both units were recorded from the same sinus hair follicle in the same experiment. In both cases identical hair movements were achieved using the angle stimulator. The high frequency discharge of the St I unit ceased almost immediately after the reversal of the movement direction (directional sensitivity) while the much lower frequency discharge of the St II(*a*) unit continued for further 500 msec, but with decreasing firing rate after the direction of the movement reversed (no directional sensitivity).

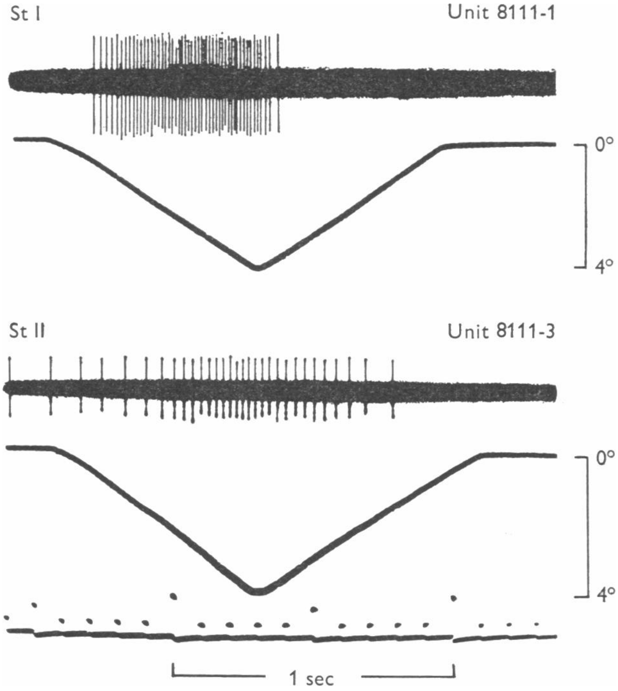

Fig. 7. Impulses recorded from a strand of the infraorbital nerve and illustrating the responses of slowly adapting type I and type II(*a*) units to an angular movement of the sinus hair. The downward going slope represents a 4° movement in one direction, the upward-going slope the return movement to the zero position at the same velocity. *A* shows the high frequency St I response which ceases almost immediately after the direction of movement has reversed, whereas in *B* the St II (*a*) response to the same stimulus shows the persistence of the discharge at a declining frequency for 500 msec after reversal of the movement.

St II(*a*) and II(*b*) units often behaved like null indicators, with a hair position at which the firing rate was at its lowest frequency. Movement of the hair in any direction away from this position caused an increase of the firing rate and vice versa. In these instances a *silent period* (i.e. an interval following movement during which there was no discharge, with gradual re-emergence of a continuous discharge) always appeared when the hair was moved towards the minimum position. The duration of a silent period was not related to the number of impulses discharged at a constant stimulus amplitude, as suggested by Fitzgerald (1940) but depended on the intensity of a stimulus was in terms of the amplitude and velocity of a hair movement.

Spontaneous activity, defined as a discharge in the resting position of the hair in absence of any experimentally applied stimulus, was present in only two out of the thirty-five slowly adapting St I units. The firing rate was very slow (2 impulses/sec) and irregular. Thirteen of thirty-nine St II(*a*) units were spontaneously active, as was a similar proportion of St II(*b*) units (five units among fourteen). Nine units of both kinds of response in the type II class, which were originally silent at the resting position, became 'spontaneously active' only after various manipulations on the hair and in some cases such activity could virtually be 'switched on' by a strong stimulation of the hair. The rate of the spontaneous activity could both increase and decrease during the recording period and occasionally the firing rate changed very abruptly. Since in some animals hardly any St II units were spontaneously active while in others almost every unit carried a resting discharge we conclude that the presence of a resting discharge in St II units depends on the influence of undefined factors.

Critical amplitude

If a sinus hair was bent by controlled movements of the angle stimulator, a relationship was found between the velocity of the angle deflexion (varying the rise time, keeping the final deflexion angle constant) and the 'critical amplitude' at which the first spike was elicited (Fig. 8). For the St II units (both *a* and *b*) the critical amplitude increased at higher movement velocities while for St I units the 'critical amplitude' tended to decrease, i.e. at higher movement velocities smaller amplitudes were needed to cross the threshold for the first spike. The extent of the change of the 'critical amplitude' differed in individual units but among the twenty-one units tested we found no exception to the rule. The test of the 'critical amplitude' was therefore a valuable help to decide the class of a slowly adapting response.

Stimulus–response relationship of slowly adapting units

Static S/R. Differences between the two types of slowly adapting unit were also found in the quantitative analysis of the responses of most of the units where either bending or rotating was the predominant excitatory stimulus component. The relationship between the mean interval length and the deflexion amplitude in a St I unit is plotted in Fig. 9*B*. On log–log axes the interval length is linearly related to the angular deflexion of the hair, i.e. the stimulus response relationship can be adequately described

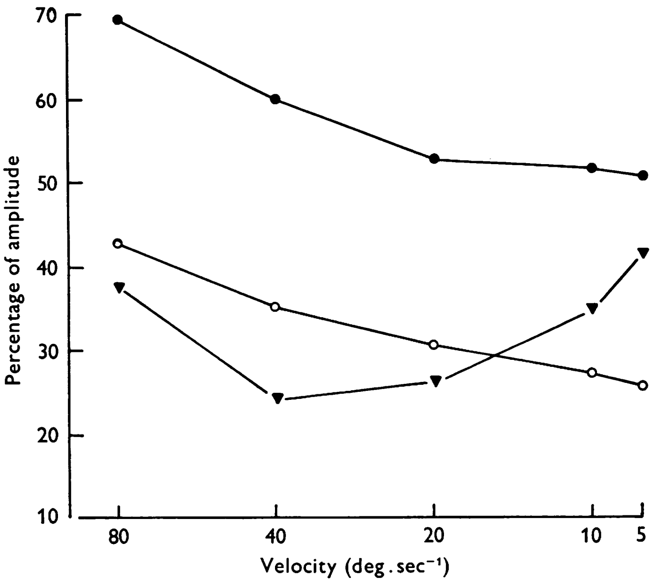

Fig. 8. The relationship between the velocity of angular movement of the hair (to a fixed angular deflexion of 4°) and the threshold amplitude (expressed as a % of the final amplitude) for the first spike in St I, = ▲, St II (*a*) = ●, and St II (*b*) = ○, units measured at rise times from 50 to 500 msec. Each point is the mean response amplitude for four different units. When the hair is moved through a constant angle at different rise times the 'critical amplitude' is defined as that percentage of the total angular movement at which the first spike occurs.

Legend to Fig. 9.

Fig. 9*A*. The stimulus–response relationship of an St I unit (2132-2). The angular deflexion of the sinus hair is plotted against the mean of the first 50 spike intervals during the static phase of the stimulus response. A straight line relationship holds when the data are plotted on log–log axes indicating a power function of the form $R = -k.S^n$, where R is the response expressed in mean interval length, S is the angular deflexion of the hair, K is a constant and n is the exponent determining the slope of the power functions plotted on log–log axes.

B, the response of slowly adapting receptors to a moving stimulus (dynamic response) plotted on logarithmic co-ordinates. Each point represents the mean interspike interval length during the last 10 % of the dynamic phase of the stimulus (St I = ●—●, St II = ○—○). The fit to a straight line relationship indicates that the stimulus velocity (measured on the abscissae as the rise time to a constant amplitude) and the interspike interval of the response are related by a power function ($R = -k$ (rise-time)^n).

by a power function of the general form $R = -kS^n$, where R = response expressed as mean interval length, S = deflexion angle of the hair, k is a constant and n is the exponent determining the slope of the power function plotted on log–log axes. On semilogarithmic axes (not illustrated) the stimulus–response curve had a distinctly curvilinear shape.

Fig. 10 shows the relationship between the spike interval length of an St II (a) unit and axial rotation of the hair which formed in this case the

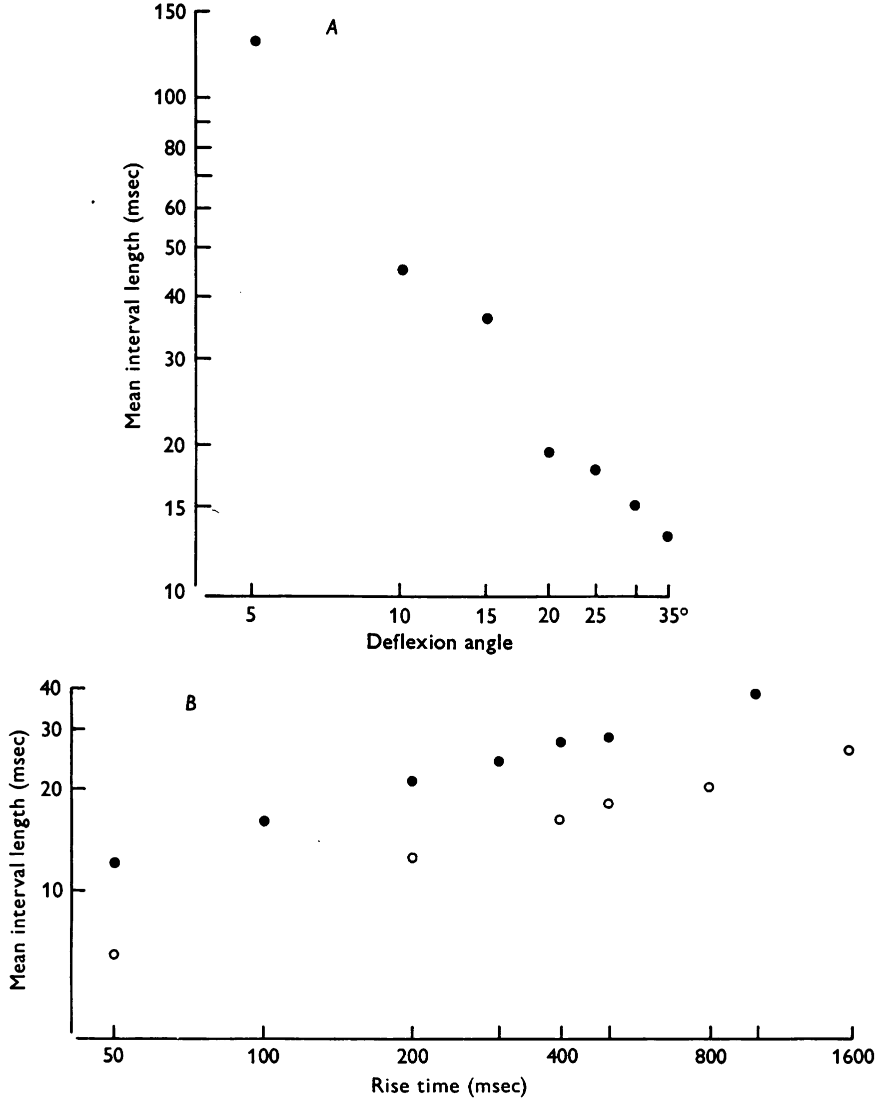

Fig. 9. For legend see opposite page.

major excitatory input. The stimulus–response relationship could be described by either a power function ($R = -kS^n$, Fig. 10*A*) or, in the range of 10–50 degrees, by a logarithmic function (Fig. 10*B*) of the general form $R = k - p \log S$, where p determines the slope of the function plotted on semilogarithmic co-ordinates. Thus, in contrast to St I units, the stimulus–response relationship for St II units can be described equally well within certain limits by a power or a logarithmic function. A similar result was reported for cutaneous SA I and SA II units (Chambers *et al.* 1972).

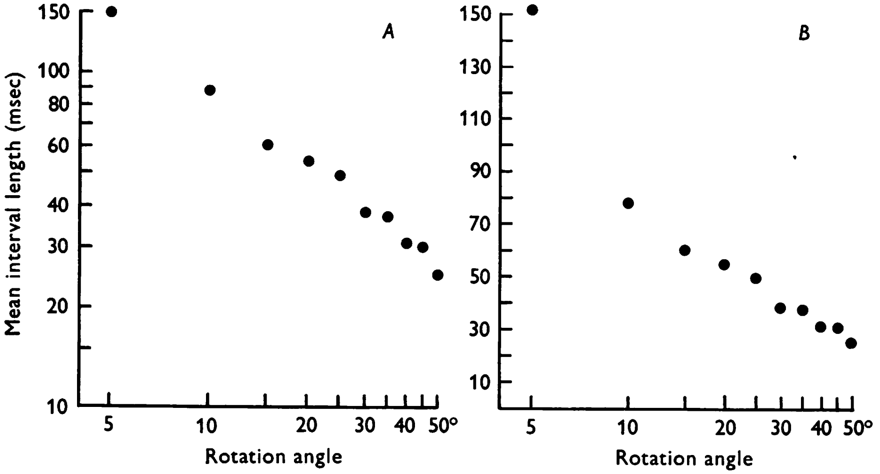

Fig. 10. The response of an St II (*a*) unit (3032-2) to rotation of the hair shaft. Each point represents the mean interval length of the first fifty intervals of the static phase of the response. *A*, the relationship between the log of the interspike interval and the log of the rotation angle is linear, suggesting a power relationship between the two variables. *B*, the same data plotted on semi-log axes shows a linear relationship over the range of rotation from 10 to 50° suggesting that over this range a logarithmic relationship may also hold between the interspike interval and the degree of rotation.

Dynamic S/R. In general, though not invariably, St I units had a higher dynamic sensitivity than the St II units. Nevertheless, the discharge rates of both types as a function of the velocity of an angular movement could be described by a power function (Fig. 9*B*).

Responses from the isolated sinus hair follicle

Nineteen sinus bodies were isolated by microdissection during continuous recording of the afferent discharge. The disconnexion of the sinus hair follicle from the surrounding skin caused a marked reduction in the directional response but no qualitative change in the directional sensitivity of St I units. Isolation of the sinus bodies almost invariably caused, in units of the St II (*a*) and (*b*) group, a high 'spontaneous discharge', or, if a resting activity existed before, an increase of the firing rate. This basic discharge from the isolated sinus hair follicle was little affected by bending the hair in any direction. All slowly adapting units could be excited by touching the upper half of the exposed sinus body capsule with a fine probe. While the side of the most sensitive spot of the sinus body capsule was variable for St II (*a*) and (*b*) units, for the St I responses it was always found to be situated on the side opposite the most effective bending direction. Extraction of the sinus hair from the follicle often abolished the mechanical excitability of St I units, but never led to a sustained discharge activity as was the case in many St II units. On the other hand, opening of the follicle capsule did not affect the excitability of St I units but stopped or diminished the response from St II receptors. Externally applied pressure on the sinus body increased the discharge of St II units while it had little effect on the activity of the St I units. These various results suggest that the St I receptors and the nerve endings which give rise to both kinds of St II responses are located at different places in the sinus hair follicle.

Stimulation of the facial nerve

In a few instances the branch of the facial nerve innervating the muscles attached to the sinus hair follicles was freed for electrical stimulation. At tetanizing stimulus frequencies (40–45 Hz), the sinus hairs rose and spread out, standing perpendicularly to the surface of the skin. Neither the St I units nor the St II units responded with a sustained discharge to the change of the hair position caused by the tetanizing stimulation, nor was their excitability substantially affected. Single shocks at low frequencies caused short twitch movements of the sinus hairs which were accompanied by short bursts of impulses if the quick movement caused the hair shaft, due to its inertia, to bend in the sensitive direction of the recorded unit.

B. Rapidly adapting units

Thirty per cent of the afferent responses from sinus hair follicles were rapidly adapting. Two kinds of units could be distinguished: the *'high velocity threshold' rapidly adapting* (*high velocity*) units discharged only a few impulses when the hair was flicked briskly. Slow hair movements, sufficient to activate slowly adapting units, often failed to excite these high velocity units and they therefore escaped notice unless high velocity stimuli were used. The most effective stimulus for this kind of receptor was vibration of the hair, as achieved by scratching the hair shaft with the serrated side of dissecting forceps or touching it with a vibrating tuning fork (440 Hz). A given high velocity unit was activated with small displacements of only one sinus hair. Responses could be obtained from surrounding structures only by using very much higher stimulus intensities. Isolation of the sinus bodies by dissection established that the high velocity receptors were located inside the follicle.

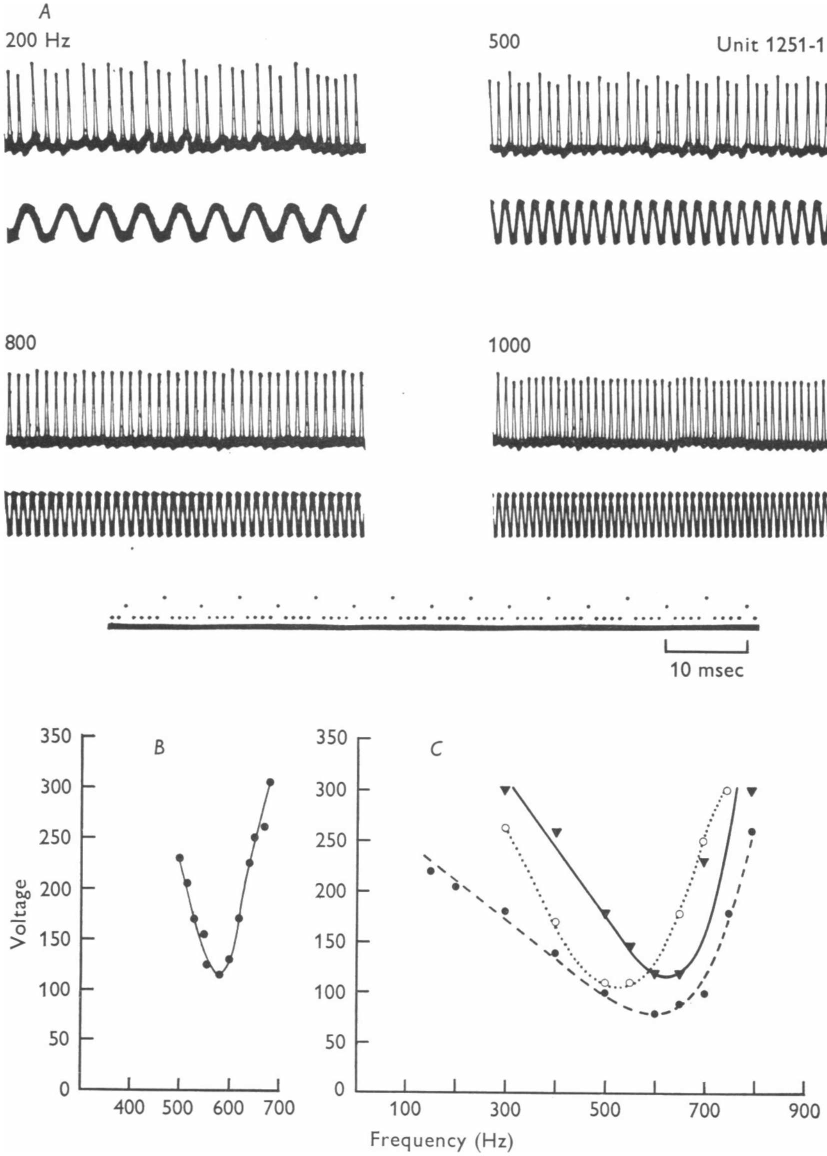

Fig. 11. For legend see opposite page.

Fig. 11*A* illustrates the response of a high velocity unit to sinusoidal stimulation at 200, 500, 800 and 1000 Hz with 1:1 following at the highest frequency. For some units the range of the frequency response was much narrower and it depended not only upon the response characteristics of the individual unit but apparently was also determined by resonance properties of the hair shaft. Fig. 11*B* shows the tuning curve of a high velocity unit at the 2:1 response level (1 impulse coupled consistently to two sine wave cycles). The width of the U-shaped response curve is much narrower than it is in another unit shown in Fig. 11*C*, for which three 1:1 tuning curves were obtained at distances of the probe of the electro-mechanical stimulator from the skin of 3, 14 and 24 mm. The threshold at a given frequency varied with the contact point of the oscillating probe on the hair shaft and in different units the lowest threshold point could lie at different parts of the hair. The direction of the vibratory stimulus had no effect on the discharge characteristics of high velocity units.

The '*low velocity threshold*' *rapidly adapting* (*low velocity*) units were relatively uncommon (6·5 % of the sample). Each unit was excited from only one sinus hair follicle unless much higher stimulus intensities were applied to surrounding tissue. The origin of low velocity units from inside the hair follicle was established for four units by isolating the sinus body. The rapidly adapting response could in each case be elicited by touching the sinus body capsule or by moving the tip of a needle inside the hair follicle. The response always disappeared after the sinus nerve was cut. The low velocity units were excited only by the dynamic part of a hair displacement. Both the number of impulses and their frequency increased with rising movement velocities and amplitudes. The velocity thresholds

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Legend to Fig. 11.

Fig. 11*A* the discharge of high velocity threshold rapidly adapting unit (1251-1) at the indicated frequencies of stimulation. For each record the upper tracing is the spike train recorded from a strand dissected from the infraorbital nerve, the lower trace is the output from the sinewave generator used to drive the electro-mechanical transducer. The records show a response of 1 spike per movement cycle over the range of frequencies from 800 to 1000 HZ, whereas at the lower frequencies several spikes were initiated during each cycle.

B, *C*, tuning curves of high velocity threshold rapidly adapting units. *B*, high velocity unit (19101-4) response to sinusoidal movement over the range 500–700 Hz. The ordinate is the amplitude of the movement of the hair represented as the voltage driving the mechanical stimulator, adjusted so that 1 spike was evoked with every second cycle of movement. The unit is maximally sensitive to vibrations at approximately 600 Hz.

C, high velocity unit (8101-6) plotted as *A*, but for three attachment points of the probe to the hair (●—● = 3 mm, ○—○ = 14 mm and ▲—▲ = 24 mm from base of hair), 1:1 responses.

lay one or two orders of magnitude below the velocity threshold of high velocity units. A single low velocity unit responded to movement of the hair in all directions but the sensitivity was normally greatest in one particular direction. Low velocity units were also distinguished from high velocity units by their responsiveness to vibration of the hairs. Only one low velocity unit was able to follow the vibration frequency of the tuning fork (440 Hz) and then only briefly. In the other eight units the band width of the response ranged from 5 to 200 Hz.

Conduction velocities

For forty-one afferent units of all types of response the conduction time of an impulse travelling from the hair follicle to the proximal recording electrodes never exceeded 1 msec. The calculated conduction velocities established that the afferent impulses from facial sinus hair receptors are transmitted via large myelinated fibres (> 6 μm diameter). Electrical stimulation of the whole nerve emerging from the sinus body revealed no slowly conducted component in a multifibre response.

The various kinds of units differed only slightly in their conduction velocities, the fastest unit being a high velocity unit. The mean values for the various units are given in Table 1.

TABLE 1. Conduction velocities in sinus afferent units

Type of unit	Number of units	Conduction velocity mean (± S.D.)	(m/sec) range
	Slowly adapting		
St I	9	53·9 ± 10·2	33–77
St II (*a*)	10	56·4 ± 14·9	44–72
St II (*b*)	3	57·5	47–68
St II	13	56·6 ± 13·5	44–72
	Rapidly adapting		
High velocity threshold	13	61·3 ± 24·2	34–104
Low velocity threshold	4	58·4 ± 17·1	42·5–82·5

Temperature sensitivity was not tested systematically. Preliminary experiments in which the skin surface was cooled, showed no alteration in the response of any type of unit from the sinus hair follicle as would have been predicted from properties of intracutaneous receptors.

Carpal sinus hairs

The structure of carpal sinus hairs and the function of their specific or associated receptors have been investigated by Nilsson (1969*a*, *b*) who reported one general kind of slowly adapting responses as well as a few rapidly adapting units originating from the carpal sinus hair follicle. Some of his illustrations (Nilsson, 1969*a*, Figs. 5 and 6) suggest that the innervation by slowly adapting units is similar in all sinus hairs.

In two experiments we recorded from the ulnar nerve ten slowly adapting units originating in the carpal sinus hair follicle. Three of them carried a typical St I discharge with irregular interspike intervals, including short intervals, even at low mean firing rates. In response to a steady hair deflexion the units adapted more rapidly than in facial St I units. Isolation of the sinus bodies revealed that these St I discharges did not derive from the touch corpuscles which are regularly associated with the carpal sinus hairs and give rise to SA I responses (Nilsson 1969*b*).

In four cases we recorded St II(*a*) responses and three units were classified as St II(*b*). Of these units, three had a spontaneous activity. The carpal St II units, like their facial counterparts, adapted very slowly, showed no real directional sensitivity and had silent periods when the hair was bent towards a less sensitive position. In one case an St II (*a*) unit with a regular resting discharge of 12·4 impulses/sec, increased to 45·3 impulses/-sec after the sinus body was isolated from the surrounding tissue. The carpal St II units, as with the facial, often had a much higher rate of discharge after the sinus was dissected away from surrounding tissue.

Rapidly adapting discharges originated from the clusters of Pacinian corpuscles surrounding the carpal sinus hairs and persisted after all sinus hair follicles were removed. The Pacinian corpuscles followed oscillatory movements up to 800 Hz with 1:1 responses. No rapidly adapting units from inside the sinus hair follicle were found in our two experiments.

DISCUSSION

Throughout the present paper we used, in agreement with Merkel (1880), the term *sinus hair* because (1) it emphasizes the distinctive structure of the hair follicles, (2) includes vibrissae and other facial sinus hairs as well as the carpal sinus hairs, and (3) does not anticipate the functional properties of the structure. The study has established that movement of a sinus hair activates four different types of mechanoreceptors, each corresponding to one of the four principal kinds of mechanoreceptors found in the skin. Ordinary hairs give rise only to rapidly adapting, or velocity responses (Adrian, 1926; Hunt & McIntyre, 1960; Brown & Iggo, 1967; Burgess, Petit & Warren, 1968), that do not originate from lamellated Paciniform corpuscles. The sinus hairs, movement of which activates two kinds of slowly and two kinds of rapidly adapting units, therefore form unique sensory structures. Although there is a certain morphological similarity between the general structure of tylotrich follicles (Straile, 1960; Mann & Straile, 1965) and the sinus hair follicles, they are functionally quite different and in our opinion are not homologous structures.

Zucker & Welker (1969) distinguished in rats five kinds of response to different stimulus parameters which on the basis of the similar morphology of sinus hair follicles in rats and cats can now be accommodated within the four types of response established in the present work. Nilsson's finding (1969*a*) of a single kind of slowly adapting unit from the carpal sinus hair follicle has been extended by the recognition of the two major groups of St I and St II units. We have also continued the reinterpretation of Fitzgerald's (1940) results in showing that (1) directional sensitivity exists only in St I units, (2) that the duration of silent periods, which occur only in the discharge of St II units, is related to the strength of the applied hair movement and (3) we could not confirm in our material that slowly adapting receptors were little sensitive to longitudinal displacements of the hair.

The response characteristics of both types of slowly adapting units have been shown to be essentially the same as those described for slowly adapting cutaneous units in mammals, primates and reptiles (Iggo, 1968; Iggo & Muir, 1969; Chambers *et al.* 1972; Merzenich & Harrington, 1969; Kenton, Kruger & Woo, 1971). The general dynamic sensitivity of St I units and their comparatively fast adaptation suggests that precise information transmitted by these units is probably confined to the dynamic part of the response, a conclusion also put forward by Merzenich & Harrington (1969) for cutaneous SA I units. A static hair displacement can only be signalled over a long period by the slowly adapting St II units, although their response also exhibits a marked dynamic proportion. A similar complementary function can be expected from the two kinds of rapidly adapting units in which high frequency oscillations of the hair are registered alone by the high velocity units.

On the basis of the distinctive properties of both types of slowly adapting units we propose that the St I and St II receptors are located at different places in the sinus hair follicles. Probably the glassy membrane forms the boundary between them. Generation of the St I response is attributed to the Merkel cells in the external root sheath. The two forms of the lanceolate nerve endings, situated on the other side of the glassy membrane, we suggest are the receptor terminals of both forms of the St II units. Although they are closely apposed to the glassy membrane in a position similar to the rapidly adapting palisade endings in pelage hair follicles (Yamamoto, 1966; Cauna, 1969), the latter are much smaller and simpler in structure and apparently lack the axoplasmatic processes which are in contact with nearby collagenous fibres, typical of the lanceolate nerve endings (Andres, 1966). The characteristic suspension of the lanceolate nerve endings suggests that tension on the collagenous fibres acts upon the cellular processes of the nerve terminal to set up a generator potential, as proposed for the morphologically similar terminals of cutaneous SA II receptors (Chambers *et al.* 1972).

According to Andres (1966) there are in the cat two variants of lanceolate nerve endings. The two variants of the St II discharge (i.e. the St II (*a*) and (*b*)) can be attributed to the straight and branched lanceolate nerve endings respectively. The straight lanceolate endings, innervated individually by a single afferent fibre, presumably form the source of the regular St II (*a*) discharge. The single endings of the branched form are orientated irregularly in respect to the glassy membrane. The dependence of the irregularity of the discharges of St II (*b*) units on the applied stimulus raises the possibility that under certain stimulus conditions more than one receptor terminal, connected to a single afferent fibre, can participate in generating the variable interspike intervals characteristic of St II (*b*) units. The presence of multiple generator regions converging upon the afferent axon might be expected to introduce some degree of irregularity into the lengths of interspike intervals (Chambers *et al.* 1972). The differences in the degree and nature of the irregularity in the discharge patterns of St I and St II (*b*) units, which probably arise from Merkel cell clusters and branched lanceolate nerve endings respectively, may reflect the different number of terminals served by one axon or substantially different generator and spike initiation processes.

Wrobel (1965) has demonstrated that bending of the sinus hair shaft results in a plastic deformation of the soft tissue of the inner hair follicle. The location of Merkel cells between the hair shaft and the relatively rigid glassy membrane could cause small but relatively rapid movements of the hair to deform the composite receptor terminal. The softer tissue in which lanceolate nerve endings are suspended and the surrounding blood sinus will exert the least resistance to movements of low velocity and render the receptor terminals particularly sensitive to slow movements of the hair. These considerations are supported by the finding of the 'critical amplitude' tests for both types of slowly adapting responses at different stimulus velocities (p. 301 and Fig. 8). Curving of the external part of the hair shaft should cause a greater movement of its internal part at the lower root enlargement. Consequently, smaller movements of the external hair should be sufficient to exceed the amplitude threshold of receptors situated at the lower root enlargement which is in line with the observation that the absolute 'critical amplitude' Fig. 7 was clearly smaller for St II (*b*) units than for St II (*a*) units, the proposed receptors of which are situated opposite the lower and upper root enlargement respectively.

The mechanism of directional sensitivity of slowly adapting sinus hair afferents was recently discussed by Waite (1973) who did not distinguish between different types of units. In our opinion the directional sensitivity of the St I units does not reflect an inherent feature of the St I receptors. Like cutaneous SA I receptors (Iggo & Muir, 1969) the St I receptors seem to respond to a stimulus applied perpendicularly to the plane of the epidermal surface. Due to the invagination of the epidermis into the sinus hair follicle, forming the external root sheath, the plane of the epidermis is shifted by 90° in respect to the surface of the skin. This causes the internal hair shaft, by movement of its external part in a given direction, to press perpendicularly on to the Merkel cells in the external root sheath and thus produces the reported directional sensitivity of the receptors. Accordingly, one should expect to find the receptors of St I units in the sinus hair follicle on the side opposite to their most effective bending direction, where in fact they were located in the isolated sinus body.

Physiologically the carpal sinus hair follicles differ from facial sinus hair follicles by the absence of the high velocity threshold response. Instead, high velocity transients are detected by the numerous Pacinian corpuscles surrounding the carpal hair follicle. Anatomically the carpal sinus hair follicles lack the lamellated nerve endings (Golgi–Mazzoni corpuscles) (Nilsson, 1969*a*) of the facial sinus hair follicles and we conclude that the high velocity discharges from facial sinus hair follicles derive from their Golgi–Mazzoni corpuscles (their lamellated structure implies sensitivity to vibratory stimuli (Pease & Quilliam, 1957; Munger, 1971). Sakada & Aida (1971) reported vibratory responses of similar properties from Golgi–Mazzoni corpuscles in the periosteum of the cat's jaws. The high velocity units of sinus hair follicles were not activated by stimulation of periosteal structures.

The source of the low velocity units is difficult to assess. The rapidly adapting responses bore many similarities to discharges from ordinary hairs (Brown & Iggo, 1967) which are thought to derive from palisade nerve endings as described by Yamamoto (1966) and Cauna (1969). One could imagine that there are in the sinus hair follicle some terminals which lack the characteristic suspension of the lanceolate nerve endings and thus resemble the palisade endings in pelage hairs. Another possibility is that in the course of transformation or growing processes the lanceolate nerve terminals lose their contact with the auxiliary structures, and so lose their slowly adapting properties. This is supported by the frequent observation that St II units lost their slowly adapting discharge after opening the sinus body capsule while a rapidly adapting response was often still obtainable during hair movement. Our original suggestion (Gottschaldt *et al.* 1972) that the low velocity responses are derived from the free nerve endings observed by Andres (1966) and Nilsson (1969*a*) remains a possibility.

The complex information from numerous receptors in different sinus hairs probably forms only part of the physiological basis of the functional significance of the sinus hair system. The actual response from a particular unit depends to a great extent upon the interaction of single stimulus components. Moreover, the slowly adapting receptors in the sinus hair follicle seem to signal a displacement of the hair shaft relative to the follicle rather than relative to the head. This latter information must be provided by other mechanisms controlling the actual position of the hair. The finding that a large variety of mechanical stimuli activate the receptors of sinus hairs must not necessarily mean they served a tactile sensation exclusively. Schmidberger (1932) has demonstrated that blind cats and cats in the dark use their vibrissae for orientation and Vincent (1913) concluded that the vibrissae of rats provide guiding sensations which assist in locomotion and equilibration, compensating for the poor vision of these animals. She also assumed links to the emotional system.

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