

AN ELECTROPHYSIOLOGICAL INVESTIGATION OF THE RECEPTOR APPARATUS OF THE DUCK'S BILL

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SUMMARY

1. The properties of receptors in the duck's bill have been studied by recording from units isolated by dissecting fine filaments from the maxillary and ophthalmic nerves.

2. The units studied were divisible into three groups, phasic mechanoreceptors responsive to vibration, thermoreceptive units, and high threshold mechanoreceptors.

3. Vibration-sensitive mechanoreceptors (113 units) had small receptive fields, showed a rapidly adapting discharge to mechanical stimulation of the bill, were sensitive to vibratory but not to thermal stimuli and showed no background discharge.

4. Temperature receptors (twenty-one units) were insensitive to mechanical stimulation and showed a temperature-dependent background discharge. Sudden cooling produced a transient increase in discharge frequency.

5. High threshold mechanosensitive units (eight units) gave a slowly adapting discharge to strong mechanical stimulation and were insensitive to vibratory and thermal stimulation.

6. It is concluded that the low-threshold, vibration-sensitive responses come from Herbst corpuscles. No specific function can yet be assigned to the Grandry corpuscles.

INTRODUCTION

The only previous electrophysiological studies of function in the somatic sensory apparatus of birds appear to be those of Dorward (1970), who described the discharge characteristics of receptors in the feathered skin of the duck's wing, and of Skoglund (1960) and Dorward & McIntyre (1971), who studied receptors in the interosseous region of the leg.

The skin covering the duck's bill contains large numbers of two kinds of morphologically specialized sensory end-organ: Herbst and Grandry

corpuscles. The large amount of structural work devoted to these corpuscles has been reviewed recently by Munger (1971); however, the extent to which free sensory nerve terminals are represented in the bill has not yet been studied (Quilliam, 1966).

Despite the considerable amount of histological work devoted to this interesting sensory array, including fairly recent studies by Quilliam and his co-workers (Quilliam & Armstrong, 1963; Quilliam, 1966), it has not previously been subjected to physiological investigation. This paper describes the results of an electrophysiological study of the functional characteristics of single sensory units in the duck's bill with fibres travelling in the ophthalmic or maxillary divisions of the trigeminal nerve. A brief account of some of the results has previously appeared (Gregory, 1968).

METHODS

Preparations. Domestic ducks (*Anas platyrhynchos*) of either sex were used, anaesthetized either with sodium pentobarbitone initially administered i.m. at a dosage of 60 mg/kg, followed by maintenance doses intravenously as required, or with ethyl carbamate 250 mg/kg plus α -chloralose 70 mg/kg, given i.p. All animals were artificially respired through a tracheal cannula, and 2 mg atropine sulphate was given i.m. to reduce secretion of tracheal mucus. The head and bill were fixed in position by clamps which did not impede access to the sensory surface. A dissection was carried out to expose either the ophthalmic or the maxillary nerve in the region between the brain and the proximal limit of the bill. The nerve was cut and the sheath removed from about 1 cm of the peripheral end, which was then subdivided to obtain filaments containing only a single functional sensory unit with a receptive field on the bill. Exposed tissues were covered with mineral paraffin oil.

Recording procedure. For recording purposes, nerve filaments were placed across bipolar platinum electrodes. Action potentials were recorded by way of a Tektronix 122 preamplifier, Tektronix 502A oscilloscope, and Grass Kymograph camera. An audio amplifier and loudspeaker provided auditory monitoring of the action potentials.

Mechanical stimulation. Mechanosensitive units were located by stimulating the bill surface with probes, brushes or the fingers. Receptive fields were plotted by exploring the skin surface with a probe made of thin monofilament nylon.

The discharge characteristics of mechanosensitive units were studied by using stimuli consisting of displacements of the skin in a direction normal to the surface by means of a 0.5 mm diam. probe, placed under microscopic control in contact with the bill surface. The probe was driven by a Goodman V 47 vibrator; its movements were monitored by a Grass FTO3C transducer the output of which was displayed on the second beam of the oscilloscope. Single rectangular, single sawtooth, and short periods of sinusoidally oscillating mechanical stimuli were used, the required wave forms being obtained from an Exact type 250 function generator, which drove the vibrator through a current amplifier. The strain gauge was calibrated both for steady displacements of the stimulus probe and for sinusoidal displacements over the range of frequencies used.

Thermal stimulation. Temperature sensitivity was tested by radiant heat, or by applying a few drops of ethyl chloride to the bill and allowing it to evaporate.

The behaviour of thermally sensitive units was further studied by applying water at various temperatures to the bill. The water was held either in a small plasticine dam built around the receptive field of the unit under study or in a watertight box surrounding the bill. The temperature of the skin surface was monitored by means of a small thermistor placed in contact with the bill surface in the receptive field of the unit concerned. The thermistor formed one arm of a Wheatstone bridge, the output of which was displayed on the second beam of the oscilloscope. The temperature-recording apparatus was calibrated against a mercury thermometer at the end of each experiment.

RESULTS

Because of their accessibility, units which had receptive fields on the outer surface of the bill were selected for detailed study. The total of 142 units isolated included a few whose receptive fields lay in the palate: these had discharge characteristics qualitatively similar to those of units on the outer surface of the bill, but were not studied in detail.

The population of units could be subdivided into three types: rapidly adapting, vibration-sensitive mechanoreceptors; temperature receptors; and high threshold mechanosensitive units.

Vibration-sensitive mechanoreceptors

One hundred and thirteen units were classified as vibration-sensitive mechanoreceptors (vibration receptors). They were found in all parts of the bill, including the dorsal skin, the palate and its bony tip. They showed no resting discharge in the absence of applied stimuli and were quite insensitive to thermal stimulation: even large temperature changes, such as could be produced by radiant heat or by applying ethyl chloride to the bill, did not evoke a response.

When weak stimuli were used to plot them, receptive fields on the dorsal bill skin were in most cases single small areas 0.5–2.0 mm in diameter. In a few cases they were larger, up to 5–6 mm in diameter. Careful exploration of the larger receptive fields did not reveal any consistent variation in sensitivity within their boundaries. Units with receptive fields on the bony tip of the bill tended to respond to stimuli applied anywhere in this region.

Ramp stimulation. Vibration receptors gave a rapidly adapting discharge to mechanical stimulation. To be effective, skin displacements had to exceed a particular minimum velocity, and no response occurred when the displacement was maintained at a steady value. The relation between stimulus displacement-velocity and stimulus amplitude at threshold was studied using sawtooth-shaped stimuli (Fig. 1*A*). At high velocities, threshold amplitude was independent of displacement velocity (Fig. 1*B*). Threshold values at high displacement velocities were used as a measure of the rheobase for a mechanical stimulus. Values of rheobase (Fig. 2)

measured in this way were between 0.6 and 76 μm . Rheobases were commonly less than 5 μm , and all but a few units had a rheobase of less than 20 μm . Rheobase values for three units were less than 1 μm . As the

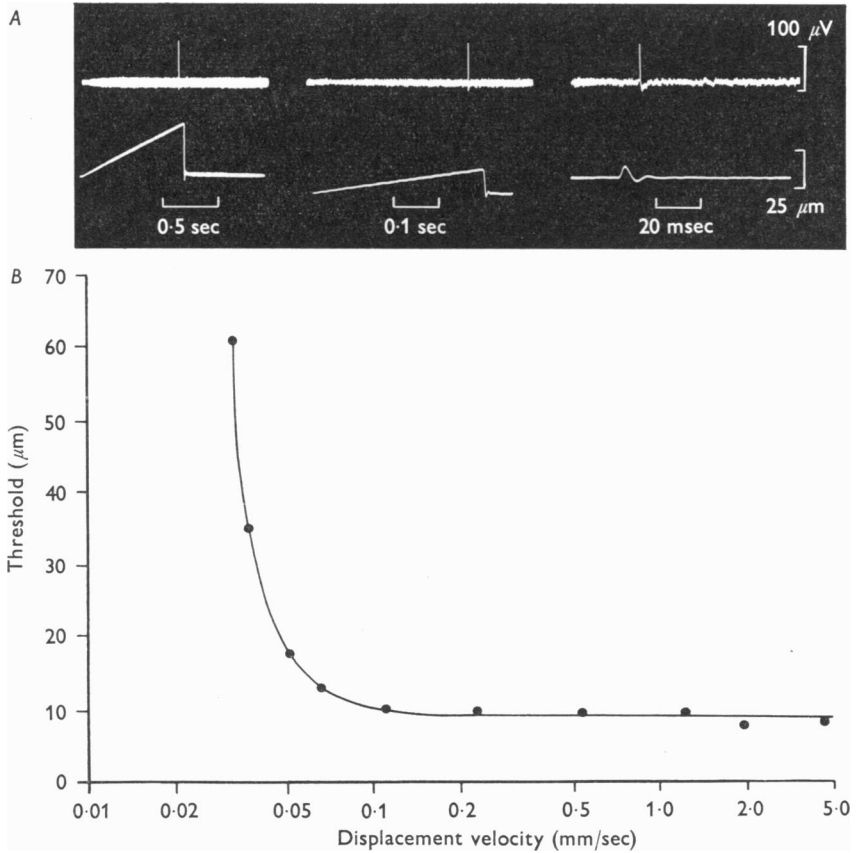


Fig. 1. *A*, part of a series of records from one vibration-sensitive mechanoreceptor, showing the minimally effective stimulus amplitude for each of three different sawtooth mechanical stimuli of differing displacement-velocity (note different sweep speeds). Response of the unit shown on upper trace in each record, stimulus on lower: upward deflexion indicates skin indentation. Records re-touched. *B*, relation between displacement-velocity and threshold amplitude of mechanical sawtooth stimuli plotted for one vibration-sensitive mechanoreceptor.

displacement velocity was reduced, larger amplitudes of displacement were needed for excitation (Fig. 1*B*). Values of the lower effective stimulus-velocity (critical slope) lay between 0.005 and 0.3 mm/sec.

The response of a vibration receptor to sawtooth stimuli at supra-

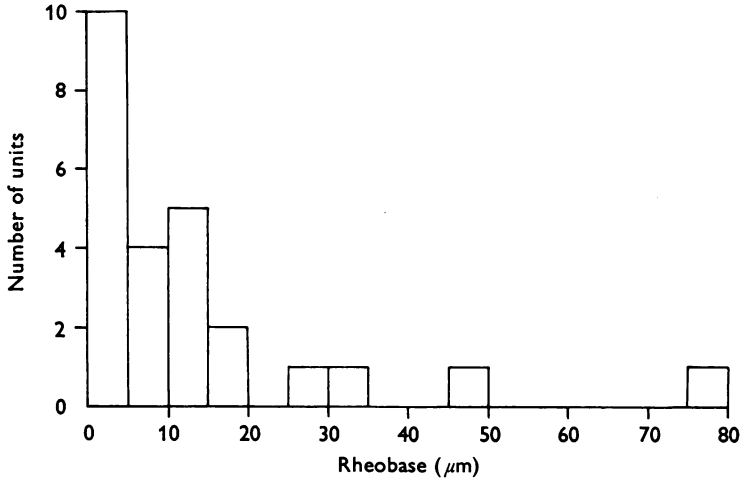


Fig. 2. Distribution of rheobase-values (threshold amplitude for rapid mechanical displacement in μm), measured for twenty-five vibration-sensitive mechanoreceptors.

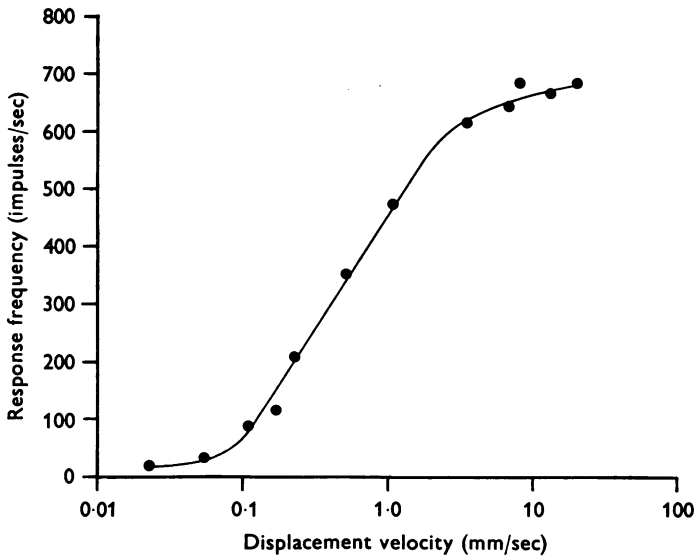


Fig. 3. Typical relation between the logarithm of displacement-velocity (abscissa) and response-frequency in impulses per second (ordinate), to suprathreshold mechanical sawtooth stimulation, plotted for one vibration-sensitive mechanoreceptor.

threshold amplitude was a train of impulses at a frequency which depended on the displacement velocity. Typically, discharge frequency was proportional to the logarithm of displacement velocity within a particular range (Fig. 3), the relation becoming non-linear outside this range. At high displacement-velocities, discharge frequency approached a maximum value which was not exceeded when displacement was further increased. As the initial slope was approached, discharge frequency declined towards zero. As a group, vibration receptors showed linear behaviour over a wide

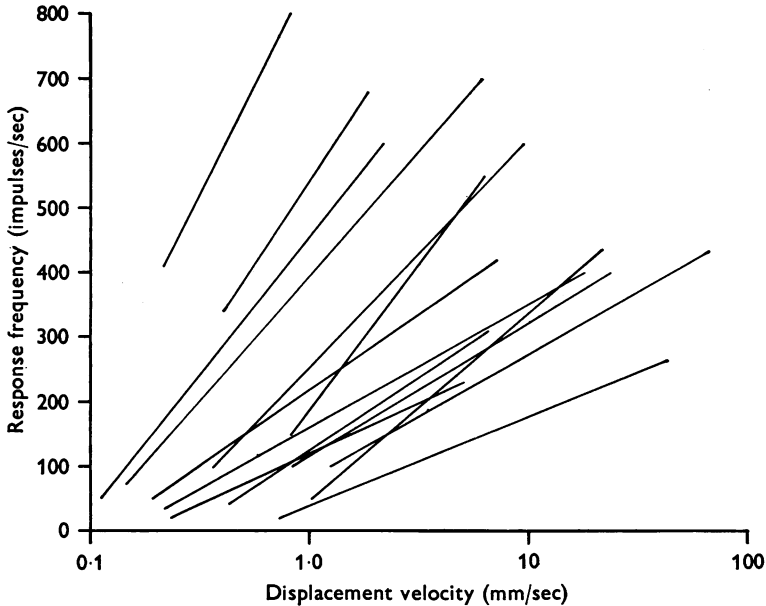


Fig. 4. Linear portions of curves such as the one in Fig. 3 relating logarithm of displacement-velocity to response-frequency, plotted for fourteen vibration-sensitive mechanoreceptors. The figure illustrates the range of response-characteristics of individual members of the population to saw-tooth mechanical stimuli.

range of discharge frequencies (20–800 impulses/sec) and displacement velocities (0.1–70 mm/sec) (Fig. 4). The sensitivity to a change in displacement velocity varied between units, as is shown by the differences in slope of the curves in Fig. 4.

Vibratory stimulation. The response to vibration was studied by measuring, at a number of frequencies, the minimum amplitude of a sinusoidal stimulus needed to produce a response. The response criterion adopted was one-to-one firing sustained for several seconds, except at the higher frequencies where 1:1 following for periods of less than 1 sec was accepted as indicative of response.

Fig. 5 shows some of the results obtained from one unit. The units studied responded to a range of frequencies within the values of 1 and 1075 Hz. Frequencies lower than 1 Hz were not used. In this sample of the population, the lowest frequency to which an individual unit responded varied from less than 1–40 Hz and the highest from 160 to 1075 Hz. The unit with the most restricted bandwidth gave a response only between 40 and 160 Hz, while the unit with the most extended bandwidth responded between 2 and 930 Hz. There was a rise in threshold towards either end of the responsive frequency-range and, typically, little change in threshold over a wide range of intermediate frequencies. Threshold-frequency curves are shown plotted for seven units in Fig. 6, which also illustrates the variation between units in their response to vibration.

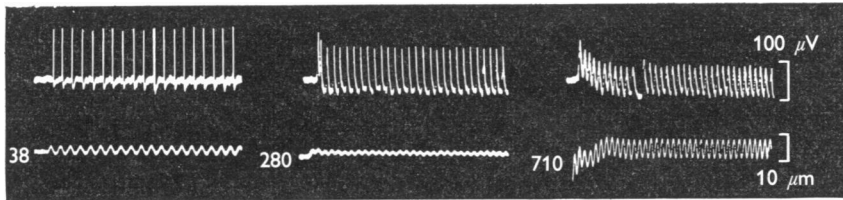


Fig. 5. Response (upper trace in each record) of one vibration-sensitive mechanoreceptor to sinusoidal mechanical stimulation at the frequencies (Hz) shown to the left of each pair of traces. At each frequency, the amplitude of the stimulus (lower trace in each record: upward deflexion equivalent to skin indentation) has been adjusted to the minimum effective value for a 1:1 response maintained for a brief period. Note reduction of unit spike amplitude at the two higher frequencies. Records retouched.

If the criterion for responsiveness of a unit to sinusoidal stimulation was changed to demand more prolonged following than the 'brief' period defined above, the maximum responsive frequency became lower and thresholds rose, especially at high frequencies. For example, the maximum responsive frequency of the unit which fired briefly to 1075 Hz dropped to 560 Hz when it was required to respond for 10 sec, and to 450 Hz when required to respond for 30 sec. This same unit showed a regular response to a maximum stimulus frequency of 1300 Hz but at this frequency discharge was limited to every alternate cycle of the stimulus (one-to-two firing).

Temperature receptors

A total of twenty-one temperature-receptive units was studied. Receptive fields for thermal stimulation were difficult to measure accurately, but appeared to be small, single areas with diameters of a few millimetres.

No response could be elicited by the mechanical stimulation procedures employed in this study.

The action potentials recorded from these units were on average smaller in amplitude than the impulses of vibration-receptors. It is likely, there-

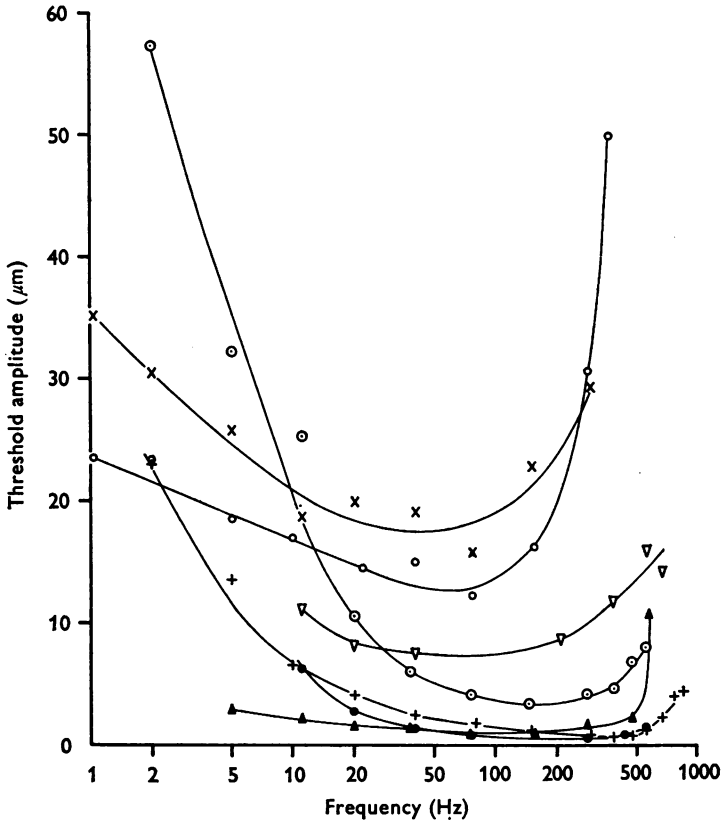


Fig. 6. Relation between logarithm of stimulus frequency (abscissa) and threshold displacement-amplitude (ordinate) plotted for seven vibration-sensitive mechanoreceptors. Values of sinusoidal stimulus frequency are plotted against values of the minimum effective stimulus amplitude for a 1:1 response maintained for a brief period, over the range of stimulus frequencies at which responses were obtained.

fore, that the afferent fibres of temperature receptors are generally of a smaller diameter than those of vibration receptors. However, direct measurements of conduction velocities were not made.

The response to thermal stimulation could be separated into static and dynamic components. When the surface of the bill was maintained at steady temperatures between about 2 and 40° C, temperature receptors

discharged at a frequency which depended on the temperature; outside this range they became silent. The firing rate was maximum at a temperature towards the centre of the range and decreased at higher and lower values (Fig. 7). Average rates of discharge at the optimum temperatures were between 5 and 8 impulses/sec for different units.

A dynamic component of the response to temperature became evident when the temperature of the bill was changed rapidly. During rapid

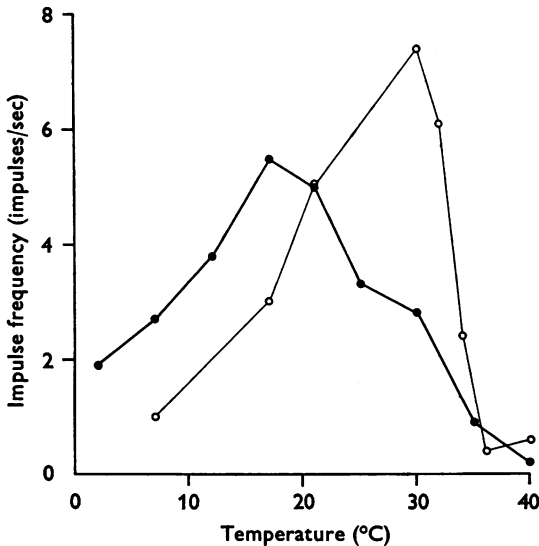


Fig. 7. Relation between steady temperature (abscissa) and mean impulse frequency (ordinate) plotted for two temperature receptors designated by open and filled circles.

temperature changes, the direction of the initial change in firing rate depended only on the direction of the temperature change and not on the values of the initial and final temperatures. Thus warming always caused a transient decrease in firing rate, or complete cessation of activity if the temperature change was rapid enough. The response to cooling (Fig. 8) consisted of a transient increase in firing rate; and if the unit had initially been silent, rapid cooling initiated a discharge. Values of instantaneous impulse frequency as high as 24/sec were recorded during rapid reduction in temperature. No units were isolated which responded to cooling with a transient decrease in firing rate.

High threshold mechanosensitive units

Eight high threshold mechanosensitive units were found. They responded only to mechanical stimuli of large amplitude, showed no resting discharge

in the absence of stimulation and were insensitive to vibratory and to thermal stimuli.

The receptive fields of most of these units could not be located accurately, and they responded only to deformation of the bill, or to squeezing one side of it firmly between finger and thumb. The receptive fields which could be located were all in the lip of skin forming the ventral border of the bill.

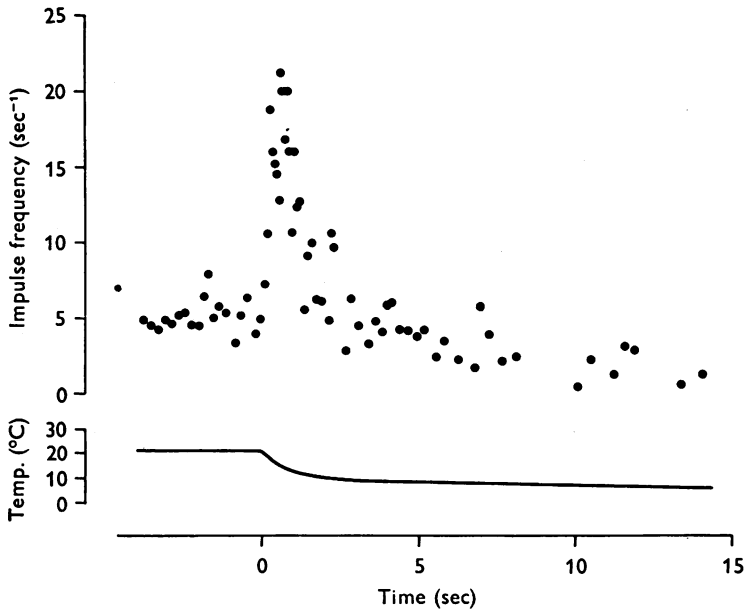


Fig. 8. Upper: instantaneous frequency of firing (reciprocals of successive spike intervals) of one temperature receptor during rapid reduction in temperature. Lower: temperature measured with thermistor in contact with skin surface. Initial temperature 21° C. Final temperature 6° C.

The response to a suddenly applied steady (rectangular) stimulus consisted of a discharge, initially at a frequency of up to about 50 impulses/sec, which declined rapidly to a low value maintained for the duration of the stimulus (Fig. 9). It was characteristic of these units that successive, identical stimuli delivered at intervals of a few seconds led to a progressive decline in response.

Experiments on the immersed bill. It was considered worth while to search for a type of receptor which might respond to some stimulus-parameter or combination of parameters occurring only with the bill immersed in water. To this end, a few experiments were carried out in which recordings were made from small bundles of fibres dissected from the maxillary or

ophthalmic nerves while the bill was enclosed in a watertight box. While recordings were being made from each bundle of fibres, the box was filled rapidly with water and the hydrostatic pressure at the bill surface was raised and lowered several times between 0 and approximately 50 cm H₂O. This procedure was repeated with water at a number of temperatures between 0 and 40 °C. In this way, conditions similar to those experienced by the bill as a result of immersion during diving were approximately reproduced experimentally. The only responses observed in these experiments were those of the temperature receptors described previously – and thermal stimuli delivered by any means were equally effective in stimulating these units.

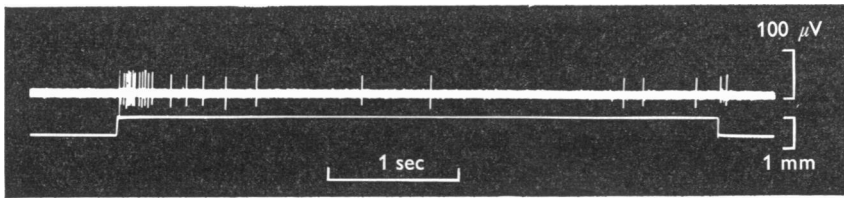


Fig. 9. Response (upper trace) of one high threshold mechanosensitive unit to a strong rectangular mechanical stimulus (lower trace). Records of action potentials retouched.

An attempt was made also to determine roughly the sensitivity of vibration receptors to waterborne vibration, which it might be supposed could provide the duck with significant sensory information about moving prey. The results, however, failed to indicate any special sensitivity of the vibration-receptors to this form of stimulation: waterborne vibration which could be felt quite readily by the experimenter's finger placed in the water near the bill did not evoke a response from any of the small number of units studied under these conditions. However, the rheobases of these units were not measured, and it is possible that they were not among the most sensitive units present.

DISCUSSION

The results indicate that the sensory apparatus of the bill – or, at least, that part of it which is supplied by myelinated fibres – consists almost entirely of rapidly adapting mechanoreceptors and temperature receptors, the only other units found being a few high threshold, slowly adapting mechanoreceptors, to which a nociceptive function can be tentatively assigned. The bill is unusual in that it does not appear to be equipped with sensitive, slowly adapting mechanoreceptors – at least, none were isolated

in this study. Receptors of this type have been found in other vertebrates in those situations where the cutaneous sensory apparatus has been studied, and they are present also in the feathered skin of the duck (Dorward, 1970).

Munger (1971) and others have noted the close epithelial cell-nerve terminal relationship in the mammalian Merkel ending and the Grandry corpuscle, and have suggested that the two types might be similar functionally. Since the Merkel-type ending is known to be a sensitive, slowly adapting mechanoreceptor with a degree of thermal sensitivity (Iggo & Muir, 1969), the failure to find such receptors in the bill does not support this suggestion. Although the high threshold mechanosensitive units are slowly adapting, they appear to be much less sensitive than Merkel endings, and have much lower maximum firing rates. Because of the small number of these units found, and because of their restricted distribution, it is also considered that they are unlikely to be responses of Grandry corpuscles, which are present in large numbers in most parts of the bill.

If, indeed, the bill does lack sensitive, slowly adapting mechanoreceptors, it is perhaps significant that critical slope values found for vibration receptors were generally lower than those reported for rapidly adapting receptors in other situations. The range of 0.005–0.3 mm/sec for receptors in the bill may be compared with values of about 1 mm/sec for mechanoreceptors, believed to be Herbst corpuscles, in the interosseous region of the duck's leg (Dorward, 1966), 1 mm/sec for Pacinian corpuscles (Gray & Matthews, 1951), 1.75 to 36 mm/sec for vibration-sensitive units, presumed to be Pacinian corpuscles, in the glabrous skin of the monkey (Lindblom & Lund, 1966), less than 0.08–3.5 mm/sec for other receptors in the glabrous skin of the monkey (Lindblom, 1965), and less than 0.08–40 mm/sec for receptors in the toad (Höglund & Lindblom, 1961). Although they could not respond in strictly tonic fashion to static stimuli, because of these low critical slope values vibration receptors in the bill would be able to supply much of the information about relatively slowly changing stimuli which in other situations could be obtained only by true slowly adapting receptors. It may also be that a slowly adapting receptor is more appropriate in other parts of the body subjected to steady stimuli, e.g. pressure on surfaces in contact with the ground, incorrect feather placement, air pressure on feathers during flight, to which the bill normally is not exposed.

Corresponding to their low critical slope values, many vibration receptors were found to respond to very low frequencies of sinusoidal stimulation, frequencies lower than those reported for vibration-sensitive units in the duck's leg (Dorward & McIntyre, 1971). The wide variation

between different vibration-sensitive receptors of the bill in their response to stimulation is obvious, and would be of value in enabling the receptor population to signal information about a wide range of stimulus conditions. However, in none of the properties studied (rheobase, threshold-frequency relationship, etc.) could any evidence be found of a division into more than one group: rather there is an even spread of unitary properties for each of these criteria. Although a few units were not conspicuously sensitive to vibration, it seemed better to regard all the rapidly adapting mechanoreceptors as a single group than to attempt a subdivision which could at best be arbitrary and probably misleading.

There is good reason for believing that at least some of the vibration receptors were Herbst corpuscles. The structural resemblance between Herbst and Pacinian corpuscles suggests functional similarity, and it is now well known that the Pacinian corpuscle is a rapidly adapting, vibration-sensitive, specific mechanoreceptor. More direct evidence comes from the work of Dorward (1970), who showed that visually identified Herbst corpuscles in the duck's wing functioned as rapidly adapting mechanoreceptors sensitive to at least moderate frequencies of vibration – properties shared by vibration receptors in the bill. Their presence in the tip of the bill also supports the view that at least some vibration receptors are Herbst corpuscles, since this region of the bill contains large numbers of Herbst corpuscle, but probably few Grandry corpuscles (Quilliam, 1966).

The only other receptors found in moderately large numbers in the bill were temperature-receptors. Their properties fit the definition of a cold receptor proposed by Hensel, Iggo & Witt (1960), but they appear to be less sensitive to thermal stimulation than some mammalian forms (Hensel 1966). The non-feathered skin of the bill is a favourable situation for a thermosensitive receptor array to respond rapidly to small changes in external temperature. By contrast, Dorward (1970) found no thermally sensitive units in the feathered skin of the duck. The possibility must be considered that the thermally sensitive units represent responses of Grandry corpuscles. This seems unlikely because of the small number isolated in contrast to the large numbers of these corpuscles known to be present; furthermore, the fibres serving thermo-receptors appeared to be considerably smaller than those of the low threshold mechanoreceptors, in contrast to the slight difference between sizes of fibres supplying Herbst and Grandry corpuscles indicated by histology (B. L. Munger, personal communication to A. K. McIntyre). It is more likely that the thermosensitive receptors are 'free endings', as seems to be the case in mammals. The particular sensory role of Grandry corpuscles remains a puzzle which can only be solved by further experiments.

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