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ELECTRORECEPTOR MECHANISMS: THE RELATION OF IMPULSE FREQUENCY TO STIMULUS STRENGTH AND RESPONSES TO PULSED STIMULI IN THE AMPULLAE OF LORENZINI OF ELASMOBRANCHS

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The ampullae of Lorenzini of elasmobranch fishes present a number of unsolved problems of sensory function; for example, their true role in the life of the fish remains uncertain; their receptor mechanisms at the level of the sensory cell and nerve endings are unknown; and there is doubt about their relation with the lateral-line organs.

The function of the ampullae is not yet fully established because the natural stimuli to which they respond have not yet been identified. However, they seem to be electroreceptors of some kind: in electrophysiological tests they are sensitive to very weak electrical stimuli (threshold voltage gradient in the water is 1 μV/cm) (Murray, 1962), and this sensitivity has been confirmed by behavioural evidence (Dijkgraaf & Kalmijn, 1963) for the dogfish *Scyliorhinus canicula* shows responses to weak, localized, electrical stimuli which are abolished by cutting the ampullary nerves. Moreover, the morphology of the organs, including their ultrastructure (Barets & Szabo, 1962), is very similar to that of presumed electroreceptors in teleosts (Mullinger, 1964) and is unlike that of the lateral line organs (see Dijkgraaf, 1963). The high thermal and mechanical sensitivities which are also shown in electrophysiological experiments (Sand, 1938; Murray, 1960; Loewenstein, 1960) are presumably side effects of some kind. Adequate temperature changes may not occur in the life of the fish, and the mechanical responses, which must occur to the fish's own movements, for example, may be discounted centrally. The sensitivity to ionic changes in the medium which the ampullae show (Murray, 1962; Loewenstein & Ishiko, 1962) may be a part of the electroreceptive system.

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The properties of teleost electroreceptors have been studied by behavioural analysis in *Gymnarchus niloticus* (Lissmann & Machin, 1958; Machin & Lissmann, 1960; see also Machin, 1962) and in *Clarias* (Lissmann & Machin, 1963), and electrophysiologically in *Hypopomus* (Hagiwara, Kusano & Negishi, 1962), in *Gymnotus*, *Stenarchus* and *Eigenmannia* (Hagiwara & Morita, 1963) and in various Mormyrids (Szabo, 1962).

The impulse code of the ampullae in rays in response to electrical stimulation is further described in this paper, in particular when brief pulses or very strong stimulating currents are used. The results are relevant to the problems of the receptor mechanisms in the system: sea water—jelly—sensory cell—nerve ending—nerve axon.

METHODS

Most of the experiments were done with preparations of the mandibular capsule of *Raja ocellata*, left *in situ* in the isolated lower jaw, with minimal dissection consistent with seeing and cutting the lateral-line branch of the mixed ampullary and lateral-line nerve, as in Murray (1962) (Fig. 1). Single units were obtained by shredding the cut end of the nerve bundle with scissors and forceps. When necessary during dissection the nerve was kept moist with fluid drawn from the rostral cavity of the skull, and the nerve and sometimes the whole preparation was kept under liquid paraffin. Room temperature was 20–25° C, but the fish had been kept in tanks in the laboratory at 17–19° C for varying lengths of time, so the transition from the fish's environmental temperature was not sudden.

Conventional a.c. recording was used, with C.R.O., loud-speaker and camera. Appropriately small stimulating currents were obtained by attenuating the isolated output of a Tektronix stimulator and were applied to the preparation through a high series resistance (100MΩ) and a small Ag/AgCl electrode; this minimized artifacts from the electrode potentials. However, the high resistance meant that the stray capacities of the stimulating circuit were significant, that below 1 msec duration the stimulus pulses were not square, and below about 0·1 msec they could not be reliably monitored.

RESULTS

The relation of impulse frequency to d.c. stimulus strength

When a single unit in an ampulla is stimulated electrically by channelling weak direct currents down the jelly-tube from a small electrode at the opening, the time course of the changes in the resting impulse frequency is as shown in Fig. 4*B* (see also Fig. 2*A*). A cathode on the opening results in a partly-adapting increase in frequency, with an inhibitory after-effect at break, and an anode on the opening inhibits, with a rebound at break (Murray, 1959, 1962). However, there remained a question concerning the form of the relation between the current strength and the impulse frequency, for Ishiko & Loewenstein (1961) stated that the response depended on the logarithm of the stimulating current, while Murray (1959) had found that the response was linear (the methods of applying the current were in fact different in these two experiments).

To resolve this ambiguity and as a basis for further experiments the stimulus–response relation was again determined, using currents applied through one electrode (Teflon-coated silver wire, diameter 0·2 mm) resting on the opening of the tube of the ampulla, and an earth elsewhere on the preparation. The stimulating circuit and a sample curve are shown in Fig. 3, where the frequencies plotted represent the average over the first half-second from the start of the current flow. This curve is typical in that the response is approximately linear with current, between the resting frequency and about 70–100 imp/sec, where it begins to flatten out (see also Fig. 4*A*, ●). So, if strong currents are used, the curve will look logarithmic, but in fact, over what may be called the working range of the sense organ, the relation is more nearly linear. At frequencies below the resting level (i.e. with an anode at the tube-opening) the linear relation

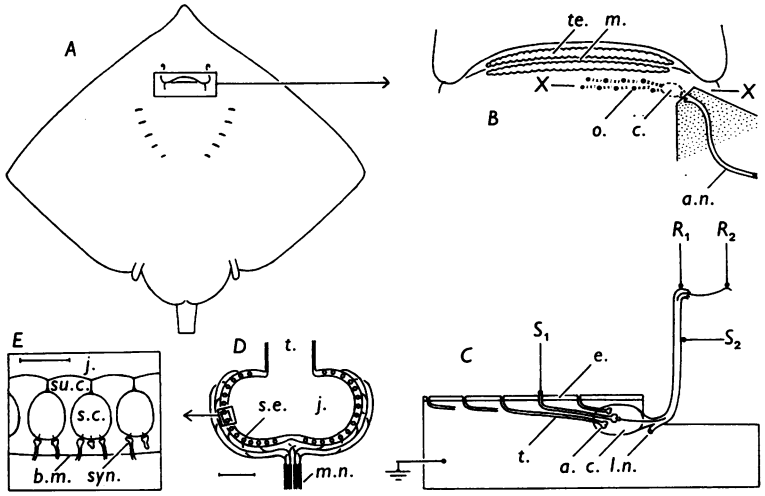

Fig. 1. Diagrams illustrating the location and anatomy of the mandibular group of ampullae of Lorenzini. *A*. Ventral aspect of *Raja*, showing mouth and gills. *B*. Location of the mandibular capsule and tubes just posterior to the mouth; the stippled area indicates the extent of dissection required. *C*. Section through the preparation along the line × - - - × in diagram *B*. This section illustrates the way in which the jelly-filled tubes run from the openings through the epidermis to the ampullae proper in the connective-tissue capsule. The recording electrodes R_1 and R_2 and the stimulating electrodes S_1—earth, or alternatively S_2—earth, are also shown. *D*. L.S. ampulla, showing the sensory epithelium and the innervation; there are normally about six fibres per ampulla, and the branching of the non-myelinated terminals is much more extensive than is shown. Scale approx. 100 μm. *E*. Detail of sensory epithelium of *Torpedo*, showing sensory and supporting cells and the synaptic terminals of the sensory nerves (after Barets & Szabo, 1962). Scale 10 μm. *a*. ampulla; *a.n*. ampullary nerve; *b.m*. basement membrane; *c*. capsule; *e*. epidermis; *j*. jelly; *l.n*. lateral-line nerve, cut in dissection; *m*. mouth; *m.n*. myelinated nerve (stem axon); *o*. opening of tube; *s.c*. sensory cell; *s.e*. sensory epithelium; *su.c*. supporting cell; *syn*. synapse; *t*. tube; *te*. teeth.

is usually maintained down to zero frequency, but in some preparations, especially at the end of an experiment, the curve flattens off again without ever reaching zero, again giving an impression of a logarithmic relation. It is probable that such preparations were in poor condition.

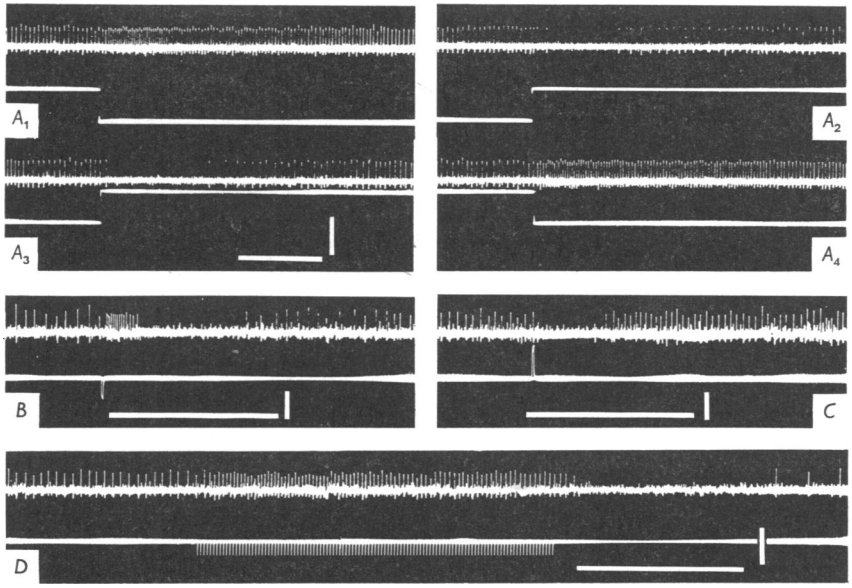

Fig. 2. Impulse activity in single units from the ampullae of Lorenzini (upper traces) in response to electrical stimuli applied via an electrode on the skin at the opening of the tube (S_1 in Fig. 1*C*) (lower traces). A_{1-4}. d.c. stimuli; the four records are consecutive, with 4·5 sec between 1 and 2, 8·5 sec between 2 and 3 and 6·5 sec between 3 and 4. *B*. 5 msec cathodal pulse. *C*. 5 msec anodal pulse (the same unit as in *B*). *D*. 0·5 msec cathodal pulses repeated at 100/sec. Calibration: all times 0·5 sec; stimulus monitor traces: *A*, 5×10^{-10} A; *B*, *C* and *D*, 2×10^{-7} A.

No special attempts were made to look for units with very low thresholds, but values down to about 5×10^{-11} A for a detectable change in frequency were obtained. This is ten times more sensitive than Murray (1962) reported when he had tested this type of stimulation, and is in line with his other methods of stimulation; for this value is close to that for the current which can be calculated to flow down a tube, given the threshold gradient in the water of 1 μV/cm and the known dimensions and conductivity of the jelly.

In Fig. 3 it can be seen that stimulating currents of approximately 10^{-6} A (roughly $1000 \times$ threshold) result in a falling-off of the response. This 'overstimulation' effect is described more fully on p. 600.

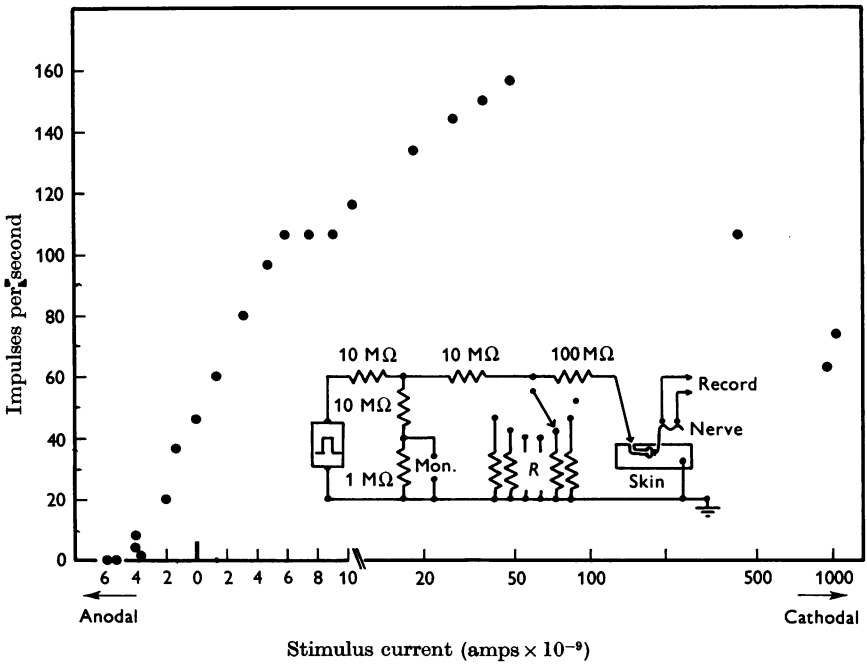

Fig. 3. The initial response frequencies of a single unit from the mandibular ampullae, subjected to sudden changes of stimulating current applied through the jelly-filled tube (averaged over the first half-sec). Note that the scale for the current strength is linear over the lower part, but logarithmic for high strengths. The inset shows the stimulus attenuation and monitoring circuit (values of $R = 1K\Omega - 2M\Omega$).

The response to single short pulses

The word 'pulse' is used to refer to a brief stimulus, while the word 'impulse' refers to an action potential in the nerve. A single, short, cathodal pulse (i.e. 1–10 msec) is followed by a burst of impulses (the first phase of the response) and then by a period of lowered frequency (second phase of the response) before the resting frequency is re-established (Fig. 2*B*); an anodal pulse results in inhibition followed by a period at a raised frequency (Fig. 2*C*). The lowest three records in Fig. 5 also illustrate these responses, with pulses of increasing strengths. The time scale of the responses is given in Table 1. The change of frequency in the first phase is about 7–10 times greater than the opposite change in the second phase, and therefore the second phase can only satisfactorily be demonstrated with pulses so strong that the first phase reaches beyond the linear working range of the unit—i.e. cathodal pulses result in maximal frequency of impulse firing in the burst, and anodal pulses result in complete inhibition.

If an anodal pulse is applied to a preparation which is silent, there can, naturally, be no further reduction in the frequency which is already at zero, but the second phase shows as a low-frequency burst of impulses after a latency of perhaps 400 msec. The second phase is not therefore the result of the changed frequency of impulse discharge in the first phase.

TABLE 1. Time course of the frequency changes following brief current stimuli (times in msec)

	Stimuli	
	Cathodal	Anodal
Latency with weak stimuli (the latency is reduced with stronger stimuli)	10–60	10–60
End of first phase (i.e. frequency crosses resting level)	100–240	150–500
Peak of second phase	—	360–1100
End of silent period	450–1200	—
Return to resting frequency	700–1500+	600–2500

The conduction time for the impulses in the nerve between the sense organ and the recording electrode is about 2 msec.

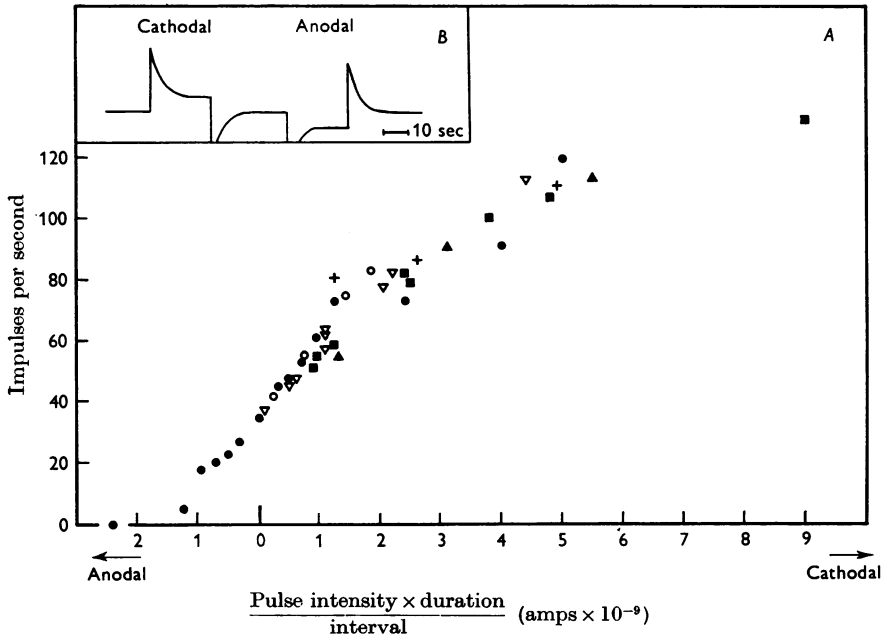

Fig. 4. *A*. Impulse frequencies in response to trains of pulses at various intensities, frequencies and durations, compared with the response to d.c. The stimuli were applied with an electrode on the skin and the impulse frequencies were averaged over the first half-sec after the onset of the stimulus (d.c. or pulse-train). The ratio of pulse-duration to interval ranged from 1:4 to 1:40. Pulse-durations: ●, d.c.; ○, 0·5 msec; ▽, 1 msec; ■, 2 msec; +, 4 msec; ▲, 10 msec.

B. Diagram of the sequence of impulse frequency changes when an ampulla is stimulated through an electrode on the opening of the jelly-tube.

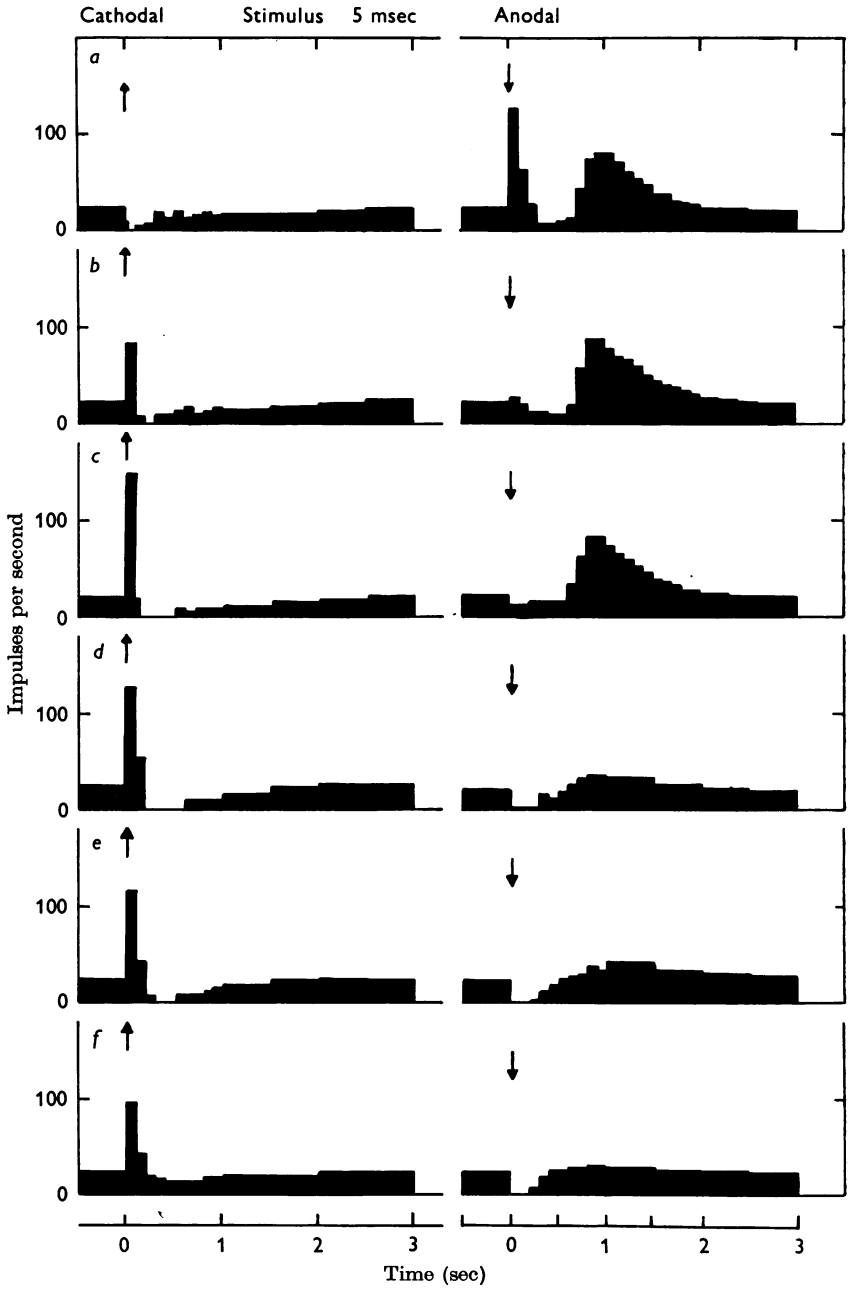

Fig. 5. Histograms of impulse frequencies from a single unit during stimulation and overstimulation by 5 msec pulses; weak pulses at the bottom, strong at the top. *a*, $2{\cdot}5 \times 10^{-5}$ A; *b*, $1{\cdot}2 \times 10^{-5}$ A; *c*, 4×10^{-6} A; *d*, $3{\cdot}3 \times 10^{-7}$ A; $1{\cdot}8 \times 10^{-7}$ A; *f*, 7×10^{-8} A.

(A similar situation is found when longer d.c. stimuli are used, for the post-inhibitory rebound at break occurs even when the unstimulated unit is silent, and inhibition therefore has no visible effect.)

In two preparations, the single stimulus-pulse set off a series of damped oscillations of frequency (mirror images of each other for the two polarities of stimulation) the interval between successive maxima being about 1·5 sec (Fig. 6). In this connexion one may note that complicated rhythmic oscillations in resting frequency are often recorded from ampullary nerves (as Sand, 1938, first described), with a periodicity between 0·5 sec and

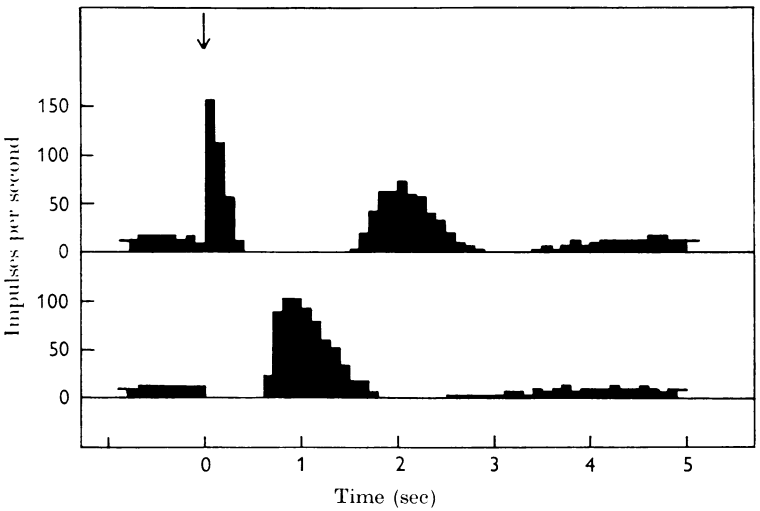

Fig. 6. Impulse frequencies in a single unit which showed a damped oscillation of frequency following a single short pulse (1 msec; 2×10^{-6} A). Upper record, cathodal stimulus; lower record, anodal. The arrow indicates the time of delivery of the stimulus.

about 30 sec. The fluctuations are associated with and presumably result from fluctuations of a generator potential (as recorded by close electrodes in an isolated preparation); they are synchronous in the several fibres running from one ampulla (Mendelson, personal communication). Generator potentials and synchronized impulse activity can also be elicited in the undissected, just-dead fish, by inserting a recording electrode wire suddenly about 1 mm into the opening of one of the ampulla tubes; low-frequency oscillations of potential of a few millivolts can be detected, which die out in about half a minute, and these are synchronized with bursts of impulse activity which can also just be detected by the electrode. It is of course possible that such a vigorous stimulus may cause some damage to the ampulla.

The response to repeated pulses

When trains of stimulus pulses are used, the ampullae respond as if the stimulus is d.c. of equivalent charge per sec, over a wide range of pulse durations and intervals (e.g. Fig. 2*D*). At the lower limit of duration, 0·1 msec pulses are fully effective (shorter stimuli could not be used in a quantitative experiment because of the stray capacities in the stimulating circuit). At the upper limit, above pulse intervals of about 200 msec, the impulse discharge becomes grouped after each pulse, and no longer maintains its smooth frequency. This is in agreement with the time course of the impulse discharge following a single pulse, described in the previous section. But between these two limits, as Fig. 4*A* shows, impulse frequency depends on stimulus pulse intensity, multiplied by pulse duration and divided by repetition interval (pulse : interval ratios ranged from 1 : 4 to 1 : 40).

If pairs of pulses are used, whether of the same or of opposite polarities, their effects are added. A weak excitatory pulse falling in the inhibitory second phase of a previous excitatory pulse results in an increase in frequency which is the same as usual, but merely starting from a lower level. If the stimuli are weak, so that the response frequencies lie on the linear part of the stimulus–response curve, simple summation of the frequency changes can occur. But if one of the stimuli is for instance strong enough to cause complete inhibition, then an arbitrary allowance must be made for 'how far below the line' it is, an estimate which can be made on the basis of the frequency change with the opposite polarity of stimulus.

'Overstimulation'

An example of a strong stimulus being less effective than a weaker one was described on p. 595. In fact, this process goes further, and a very strong stimulus may even cause a response which is in the opposite direction to that given to weaker stimuli. This phenomenon is called 'overstimulation' and is described in more detail here because it seems to clear up an apparent discrepancy in the direction of responses between ampullae and lateral-line organs (see Discussion).

When the intensity of cathodal stimuli is increased (Fig. 5), the impulse frequency in response to each also increases, up to a maximal initial frequency of about 150 imp/sec—but of course if the stimulus lasts longer than a few tenths of a second this high rate soon adapts, or if the stimulus is short, the burst is followed by the inhibitory effect described on p. 596. Throughout this range, stronger stimuli result in more prolonged responses as well as in higher frequencies. But when the stimulus is increased still more, first the duration of the high-frequency response is sharply reduced (for example, down to 100 msec in the experiment illustrated in Fig. 3

at 4×10^{-7} A) and then its amplitude as well, until the cathodal stimulus results only in inhibition (Fig. 5, top record). If the stimulus is a maintained one, there is a rebound at break instead of the normal inhibition. Corresponding but opposite effects occur after anodal stimuli. The stimulus strength at which reversal of response occurs can be expressed as a multiple of the current strength required to cause doubling of the resting frequency (measured over the first half-sec); in five preparations the value of this multiple lay between $\times 300$ and $\times 2000$. This represents at least $2000 \times$ threshold, or more.

The results were consistent in that different preparations all responded in essentially the same way, and weak stimuli presented at the end of a series of increasing intensity gave responses comparable with those at the start. However, the relatively enormous current strengths appeared to cause some damage. For example, one preparation which had a linear response curve running down to zero frequency with anodal currents at the start of the series ended with its response curve flattening off below the resting frequency so that virtually no inhibition occurred with weak anodal currents.

Currents applied via the sensory nerve

In earlier experiments (Murray, 1959) a stimulating current was passed through an electrode on the dissected nerve adjacent to the recording electrodes, through the sense organ, to an indifferent electrode elsewhere on the preparation (Fig. 1); under these conditions an anode on the nerve causes an increase in frequency, and a cathode inhibits. This method of stimulation has been repeated and compared directly (consecutively and concurrently) with stimulation through the jelly-tube, in case there should be differences which could be attributed to the part that the sensory cells, for example, play in the transduction chain.

However, only slight differences could be found. Stimulation through the jelly resulted in a more rapid build-up to maximal frequency at make and in a rather more rapid and complete adaptation. It is probable that these differences were the result of the apparently square stimulus being rounded-off when applied through the nerve by the capacity of the membrane, for it was not, of course, possible to monitor the stimulus as it reached the nerve endings in the ampullae.

DISCUSSION

Concerning the possible function of the ampullae as electroreceptors

In their experiments which showed that dogfish use their ampullae of Lorenzini in the detection of weak electrical stimuli, Dijkgraaf & Kalmijn (1963) used currents which passed from one electrode to another 1 cm

away alternately in either direction, the polarity being reversed every 0·1 sec. My results show that such a duration should be very effective, for 0·1 sec is long enough to allow the maximal frequency of discharge to be reached, i.e. the same as if a longer d.c. stimulus had been applied, but not so long that adaptation has had time to become significant. When the thresholds are compared, it is satisfactory to find that the electrophysiologically determined value of 1 μV/cm gradient for the most sensitive units (Murray, 1962) falls between the behaviourally determined values of 0·1 μV/cm for the whole fish and 3 μV/cm for restricted areas; lowering of threshold by integration over large areas is of course a general property of many sensory systems.

One cannot say much about the possible function of the ampullae from a study of the impulse code, except that it seems unlikely to be navigational in the way that the electric organ–electroreceptor system in Gymnotids is. For there are two requirements in the receptor of such a system, which can be seen to be fufilled in *Hypopomus* (Hagiwara *et al.* 1962), but which are not so in *Raja*. First, the small changes in the intensity of the detected pulses are important, and the normal strength of the pulse in the absence of external objects is relatively large; high absolute sensitivity is not required. The stimulus–response curve for *Hypopomus* receptors matches this requirement, for there is a relatively high threshold below which no impulses result, but then over a narrow range small increments of stimulating current result in progressively more and more impulses per burst, to a maximum after which no further increase in stimulus makes any difference. Now the normal strength of the electric-organ pulse falls approximately in the middle of the working region of the curve. Secondly, it is only the intensity of the pulse which is significant, and not its polarity, for the normal pulse, undistorted by external objects, causes inward currents at some receptors and outward at others; only in the narrow region between them would the value of the distortion be comparable to the strength of the normal pulse and the chance of a polarity reversal due to the object in the vicinity be significant. In *Hypopomus*, both inward and outward current pulses result in a similar impulse discharge, the one at 'on', the other at 'off'. Neither of these requirements is met in *Raja*. First, the response curve rises straight from the resting frequency, with theoretically no threshold; in practice, in a number of units the threshold is very low compared with the electric-organ discharge of those species which possess one. Secondly, opposite polarities of stimulus result in mirror-image changes of frequency within the working range of the receptor. It seems therefore much more probable that the ampullae serve to detect electrical stimuli which originate *outside* the fish, though what these stimuli may be under natural conditions remains unknown.

Concerning the receptor mechanism

The stimulus:impulse frequency relation, or 'characteristic curve' (as Groen, Lowenstein & Vendrik, 1952, have called it, by analogy with the triode valve) is clearly an important item in the full description of the functioning of a sense organ. But it is less useful to argue about linearity, or logarithmic or power-law shape, unless the hypothetical receptor mechanisms predict one or the other curve, which is not the case here. So the mere description remains, that the ampullae have characteristic curves which are roughly linear on each side of zero stimulation, and which flatten out at the top as maximal frequency is approached, and also at the bottom, more or less suddenly, at zero.

The responses to brief stimuli underline an aspect of sense-organ function which is of more general application. It is possible, from several lines of evidence, to postulate the existence of an intermediate state or process lying between the stimulation and the changes in impulse frequency. For example, the phenomena of adaptation and rebound appear to depend on processes which continue in varying degree and with characteristic time courses even in silent preparations; similarly, the responses to brief stimuli appear to involve a complicated sequence of changes in some process which long outlasts the stimulus and which in turn results in changes of impulse frequency. The changes in the intermediate process are mirror-images of one another when stimuli of opposite polarity are presented. But the changes may be too great to be linearly represented by impulse frequency since the working range of the unit is limited, especially on the inhibitory side of the resting frequency. So the changes of impulse frequency will only be mirror-images of each other on application of stimuli of the two polarities if those stimuli are weak.

The shape of the response to single short pulses of current (Figs. 2*B*, *C*, 5) is unusual in the symmetry of the responses to opposite polarities of stimulus and in the long time scale, both of which must be important as clues to the underlying mechanisms; but there is as yet too little evidence on which to base a definite hypothesis. So further discussion of such matters as the presence or absence of chemical transmission between sensory cell and nerve ending and the nature of the intermediate processes referred to earlier must be deferred.

However, there is one small point of general interest: in records of the response of a unit to a single pulse it can be seen that under appropriate conditions an excitatory stimulus (i.e. cathodal) results in fewer impulses than would have been provided by the resting discharge; conversely, an inhibitory, anodal pulse may result in more impulses than usual. The high-frequency burst after a cathodal pulse lasts, for example, 100 msec,

but since the unit cannot fire faster than at 150 imp/sec, the maximal number of impulses in the burst will not exceed fifteen, and during that time there would normally have been, say, two impulses in the resting discharge. So there are thirteen extra impulses. However, in the second phase, total inhibition may last longer than the 650 msec needed to balance this thirteen (i.e. 0·65 sec × 20 imp/sec). The effect is even more marked with anodal pulses for the inhibition lasting 100 msec only means a deficit of two impulses, which can readily be more than compensated for during the increased frequency of the second phase. It is reasonable to suppose therefore that the central nervous processing of the information from the ampullae must be affected by the temporal patterning of the discharge, and not merely by the number of impulses per second.

The way in which pulsed stimuli are as effective as d.c. of equivalent charge per unit time is very similar to the results obtained by Machin & Lissmann (1960) in *Gymnarchus*, but both are unlike *Hypopomus* (Hagiwara *et al.* 1962), where intensity only compensates for brevity in pulses shorter than 2–5 msec; with pulses longer than this the response is the same whatever the duration.

Stimulus polarity

The overstimulation results make possible the resolution of a problem concerning stimulus polarity. In *Xenopus* and non-electric teleost lateral-line organs (Murray, 1956; Katsuki & Yoshino, 1952) when a current is passed through the skin in which the sense organ lies, it is an anode outside (inward current) which excites, and an outward current inhibits. The ampullae, on the other hand, are excited by weak outward currents and it is only during overstimulation that the polarity is the same as for the lateral line. Moreover, the sensitivity of the lateral line in *Raja* is 10^3–10^4 times lower than that of the ampullae (Murray, 1962; also by behavioural tests in *Scyliorhinus*, Dijkgraaf & Kalmijn, 1963) and this means that the lateral line organs are responding at stimulus intensities comparable to the overstimulation of the ampullae.

The polarity of the stimulus for excitation of the lateral line is one which would cause relative hyperpolarization of the membrane of the nerve endings and depolarization of the stem axon, and I have previously suggested that this supports the hypothesis of impulse initiation at the stem axon, or first node, rather than in the non-myelinated nerve terminals; lack of electrical excitability in the terminal membrane is implied by this. In 1956 this hypothesis was coupled with an 'electrical' theory of transmission whereby the sensory cells transduced the mechanical stimulus into a generator potential, and the currents associated with the latter were

channelled into the nerve endings. But a theory of chemical transmission from sensory cell to nerve ending would fit equally well.

In the ampullae there must be a further process involved, to account both for the reversal and for the sensitivity. The nature and site of the electrical sensitivity involved in this additional process cannot yet be determined, but evidence favouring chemical transmission between cell and nerve is discussed by Machin (1962). But whatever the process, it will presumably work linearly on each side of its resting state and will reach a limit with larger stimuli. If the stimulating current is further increased beyond this limit up to the threshold corresponding to that of the lateral-line organs it can then begin to affect directly the impulse-initiating mechanism at the stem axon and produce an opposite change in impulse frequency; the antagonism between the effects of current at the two sites, terminal and subterminal, could account for the phenomena of over-stimulation. There are of course resemblances to the 'overstretch' of the crustacean-muscle receptor organ, but the phenomena are distinct, especially in that the ampullae show 'overinhibition' as the mirror-image to overstimulation.

In the electrically-sensitive lateral line organs of *Hypopomus* (Hagiwara *et al.* 1962) it is inward current which gives 'on' excitation; this is in agreement with the polarity for excitation of mechanically-sensitive lateral line organs and overstimulation of the ampullae, and so is opposite to the polarity for the threshold excitation of the latter.

SUMMARY

1. Under electrical stimulation through the skin (d.c.) the ampullae of Lorenzini show an approximately linear response curve from zero through the resting frequency to about 70–100 imp/sec above which the curve flattens off (frequency averaged over the first half second, i.e. before adaptation).

2. In response to single brief pulses of current there are two phases of change of impulse frequency, the first in the same direction as the response to d.c., but lasting about 100–500 msec, and the second in the opposite direction, about 10 times smaller, but up to 10 times as prolonged.

3. Repeated pulses are as effective as d.c. of equivalent charge per second, so long as the interval between pulses does not exceed 200 msec; above this interval the response follows each stimulus and is no longer at a smooth frequency.

4. Stimuli larger than about 1000 times threshold cause a reversal of the direction of the change of frequency (i.e. cathodal stimuli inhibit). This is

interpreted as due to the saturation of the receptor mechanism and direct electrical stimulation of the impulse-initiating site in the sensory nerve.

5. No direct evidence is presented concerning the biological use of the organs, but the results are consistent with an electroreceptor function.

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