J. Physiol. (1959) 145, 1–13

THE RESPONSE OF THE AMPULLAE OF LORENZINI TO COMBINED STIMULATION BY TEMPERATURE CHANGE AND WEAK DIRECT CURRENTS

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(*Received* 18 *March* 1958)

In certain sense organs an increase in frequency of nerve impulses occurs on cooling, and a decrease on warming, but no satisfactory general account has yet been given of the way in which cooling speeds up the rate of initiation of impulses at the nerve endings. The experiments here described are intended to provide more evidence concerning this problem. They involve a comparison between one stimulus, temperature change, whose mode of action is unknown, and another, electrical polarization by direct currents, whose mode of action is known, or can at least be fairly confidently deduced from first principles. The comparison is made by applying one stimulus first by itself and then in the presence of the other; the way in which the presence of the second stimulus affects the response given to the first shows whether the two stimuli operate at the nerve endings in like or unlike ways. The direct current used as the stimulus is routed to the sense organ through one electrode on the nerve and another on the surrounding tissues, and thus directly affects the membrane at the nerve endings. Evidence for the course of the current, and earlier references, are given by Murray (1956*a*).

The ampullae of Lorenzini of elasmobranchs are the sense organs under consideration; their great sensitivity to temperature change has been known for some time (Sand, 1938), and they are generally held to be temperature receptors. Recently, however, their possible mechanoreceptive function has been suggested (Murray, 1957) and thus in the absence of behavioural experiments it is not possible to state definitely what function the organs perform in the living fish. But the sensitivity to temperature change is so great that it is of interest in its own right, and the sensory mechanisms involved are almost certainly similar to those of the 'cold' receptors in the mammalian tongue (Hensel, 1955). During the course of the investigation certain new aspects of the response to temperature change were observed and are also described.

METHODS

The ampullae of Lorenzini consist of long, jelly-filled tubes which open by small pores through the skin and end in the head region in clusters of irregularly shaped swellings (the ampullae themselves) at the base of which are the sensory nerve endings. In the rays the ampullae are all located in a small number of tough connective-tissue capsules.

One of the mandibular capsules of *Raja clavata* was dissected out with as great a length of ntact, jelly-filled tubes as possible and with 2–4 cm of nerve. To prevent drying the dissection was where necessary performed under fluid drawn from the cavity of the skull in front of the brain: about 10 ml. could be obtained from a medium-sized fish. When cleared of connective tissue the nerve was draped over a series of chlorided silver wire electrodes in a moist chamber; similar electrodes were placed against the side of the capsule or the tubes. A single active unit was obtained by thinning the nerve with scissors between two of the electrodes; further preparations could be obtained later by thinning the nerve nearer to the capsule. Some of the preparations lasted for longer than 12 hr if not over-stimulated, maintaining a basic discharge all the time.

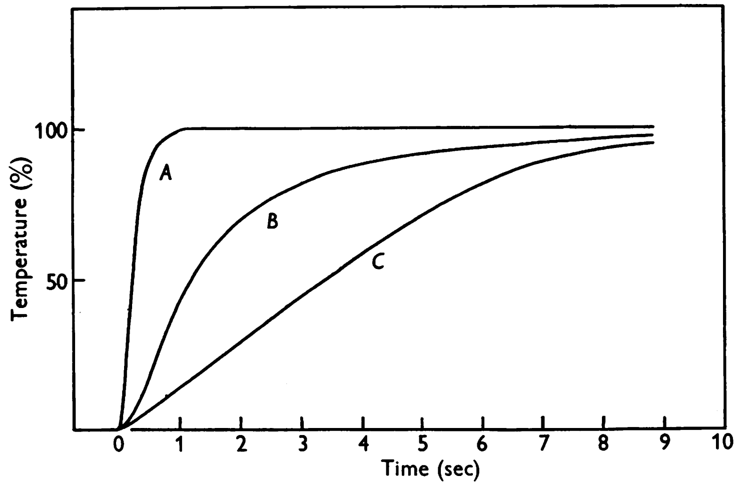

Fig. 1. Rate of change of temperature in the experimental apparatus. The curves represent the temperatures (measured by thermocouple) between the capsule and the thermode diaphragm (*A*) and within the capsule at distances of 1 mm (*B*) and 2 mm (*C*) from the diaphragm. The temperatures are expressed as percentages of the final change of temperature. The external water temperature was changed suddenly at 0 sec.

Action potentials were recorded from the electrodes on either side of the thinned region of the nerve, using a conventional a.c. amplifier feeding a cathode ray oscillograph, loudspeaker, tape-recorder and at times a pulse-interval meter (Andrew & Roberts, 1954) whose output could be displayed on a meter or on the second beam of the cathode ray oscillograph.

The capsule was laid against a diaphragm (of glass or silver foil) in the wall of the moist chamber, and two jets of water of different temperature were directed against the outside of this diaphragm; rapid changes of temperature were effected by diverting first one jet, then the other, by interposing a movable scoop in their paths. Temperatures in different parts of the preparation were measured by miniature thermocouple junctions whose potentials were recorded by a mirror galvanometer, or amplified and displayed on the second beam of the cathode ray oscillograph. Fig. 1 shows typical rates of change of temperature at different depths in the preparation when the temperature of the water outside was changed suddenly. It can be seen that for about 8 sec there was a marked spatial gradient of temperature across the capsule.

Electrical stimuli were applied to the preparation through an electrode on the outside of the capsule and one or other of the electrodes on the nerve. The stimuli were produced by a simple circuit containing a battery, a high variable resistance and a change-over switch, or by means of the smoothly variable constant-current stimulator described by Lowenstein (1955). When the nerve is anodal the direction of current is called 'ascending', and when the capsule is anodal, 'descending'.

Analysis of results

In the main experiments a standard thermal stimulus was applied while maintained direct currents held the preparation in an abnormal condition, with the discharge frequency either higher or lower than the basic discharge rate. The changes of impulse frequency due to the temperature change under these conditions have to be compared with each other and there exists no *a priori* standard for the comparison of an increase in frequency from, say, 5/sec to 15/sec, with an increase from 60/sec to 70/sec. To state that these increases are the same is possible only if it is known that the behaviour of the sense organ is linear. The standard for comparison which will be used here is based on the response to direct-current stimulation alone. This choice is justified by the fact that d.c. stimulation produces changes of membrane potential and changes of membrane potential are known to be intimately involved in nerve-impulse initiation. There is, therefore, no question of the intervention of an intermediate process such as occurs when a generator potential mediates between stimulus and impulse initiation. Thus the relationship between impulse frequency and strength of stimulating current obtained in this type of experiment can be said to represent the characteristic behaviour of the organ, in the same way as the characteristic curve represents that of a thermionic valve (Groen, Lowenstein & Vendrik, 1952). For instance, a certain temperature change is found to result in a certain increase in discharge frequency. The characteristic curve shows what d.c. stimulus would be required to produce the same change of frequency; that is, what strength of current may be assumed to be equivalent to the temperature change. A d.c. equivalent can be obtained in this way, whatever the range of frequencies the experiment involves, even if the response curve is non-linear.

RESULTS

The response to thermal stimulation is as described by Sand (1938) and by Hensel (1955). Cooling produces a transient increase in the basic firing frequency, the rate then declining to a constant value which is lower than that before the temperature change; corresponding but reverse effects occur on warming. The terms 'unadapted frequency' and 'unadapted response' will be used to refer to the period of maximal response which occurs up to 20 sec after the change of outside temperature, according to the size and arrangement of the individual preparation; the 'adapted frequency' after a temperature change is of course the same as the basic discharge frequency at the new steady temperature.

Electrical stimulation

The effects of electrical stimulation alone will be discussed first. Fig. 2 shows the result of a typical sequence of current changes. On 'make' of an ascending current there is a sudden increase in discharge frequency, followed by a process of adaptation to a new level of frequency higher than that obtaining before 'make'; the term 'time constant of adaptation' is not appropriate here because the process is not exponential, but the average time for adaptation to be three-quarters complete is 15 sec at 15° C. Even after several minutes some adaptation continues, but very slowly, and so it is not possible to give a time for the completion of adaptation. On 'break' of the ascending current there is an inhibitory after-effect, with a similar time course to that of the adaptation. Corresponding but reverse effects are obtained on 'make' and 'break' of a descending current. In Fig. 2 the changes of current are sudden; when the changes are gradual the immediate changes of frequency are less pronounced. The extent of both the post-excitatory and post-inhibitory after-effects varies not only with the strength of the stimulating current and the suddenness with which it is stopped but also with the duration of current flow.

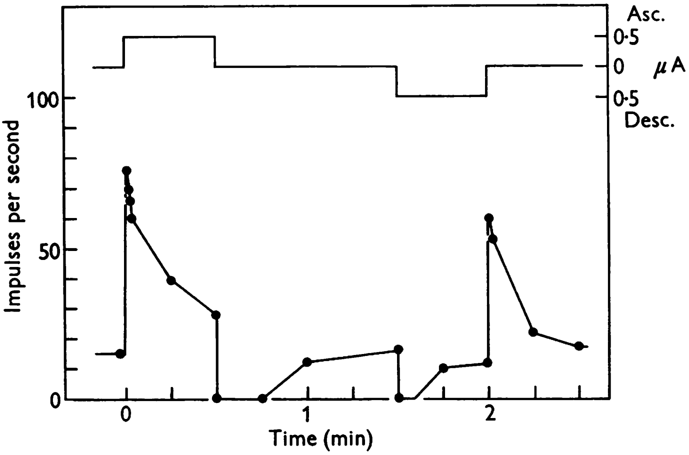

Fig. 2. Discharge frequencies in response to electrical stimulation alone. Upper graph, current; lower graph, frequency.

The terms 'unadapted frequency' and 'unadapted response' will be used to refer to the maximal or minimal frequency immediately after a sudden change of current, and the terms 'adapted frequency' and 'adapted response' will refer to a time, usually about 30 sec after 'make' of current (whether sudden or slow), when the discharge frequency has reached a nearly constant level.

Stimulus–response relationships can be studied by plotting either the unadapted or the adapted frequencies against the current strengths that caused them. In the majority of preparations both relationships are approximately linear. Exceptions to this linearity occurred at low frequencies, for a sudden 'cut-off' below about 5/sec was common (Figs. 4 *D*, 5 *A*) and at high frequencies (approx. 80/sec) when the maximal firing frequency was approached. For technical reasons such high frequencies could not be recorded in response to maintained currents, but maximal frequencies obtained in response to sudden electrical stimuli or to combinations of stimuli were consistent with this interpretation. Further departures from linearity, affecting the middle of the range, were found in about one quarter of the preparations (Fig. 6); this non-linearity occurred in both adapted and unadapted responses. There is, however, no sharp and significant distinction between linearly and non-linearly responding preparations.

An asymmetry of response to temperature change is often found; that is to say, the immediate change in frequency on changing the temperature from t_1 to t_2 has not the same magnitude as that found on changing back from t_2 to t_1. For instance, the preparation illustrated in Fig. 6 responded to cooling 3·5° C by an increase in frequency of 19 impulses/sec from 22 to 41/sec; but when warmed the same amount (after adaptation had taken place) the change in frequency was only 4/sec, from 23 to 19/sec. In this preparation the asymmetry of the thermal response can be explained in terms of a non-linear characteristic, but this is not always possible.

The strength of current required to produce a given effect depends on the position of the stimulating electrodes, as also does the height of the recorded spikes. Spikes recorded from near the anode are larger than normal, from near the cathode, smaller. Both these effects are similar to those described by Murray (1956*a*).

When the same stimulus was repeated, the changes of frequency resulting from it were consistent to within 10% in the majority of preparations, although the ensuing resting discharge might vary more than 10% from the pre-stimulation value, especially after prolonged electrical stimulation. The slope of a response curve was more consistent than its absolute position.

Combined electrical and thermal stimulation

The possible interaction of the two types of stimulation was investigated by applying a standard thermal stimulus under different conditions of electrical polarization. Twenty-seven preparations were tested in this way. In a typical experiment (Fig. 3) the standard sequence of temperature changes was a fall of 2·5° C followed by a rise of 2·5° C to the original temperature after 1–2 min when the adaptation was effectively complete. When this sequence had been recorded, an ascending current of 4 μA was applied and time was allowed for the frequency to adapt to its new steady level. The thermal stimulation was then repeated; and again also after an increase of current to 6 μA. The whole procedure was now repeated with descending currents, but in the case of the experiment analysed in Fig. 3 the position of the stimulating electrode had to be changed to a point nearer the cut end of the nerve because strong descending currents would have made the height of the recorded spike too small. With the new electrode position descending currents increased the height of the recorded spike whilst ascending currents reduced it. The strengths of current used in the second part of the experiment are therefore not comparable with those used in the first half, a different proportion of the total current being routed through the axon of the active unit. Normally the currents applied were not strong enough to necessitate such a change of electrode position. The frequency following the application of 4 μA descending current (Fig. 3*E*) was near the cut-off point, and in fact the discharge did not return after warming until the current was reduced at the end of the experiment.

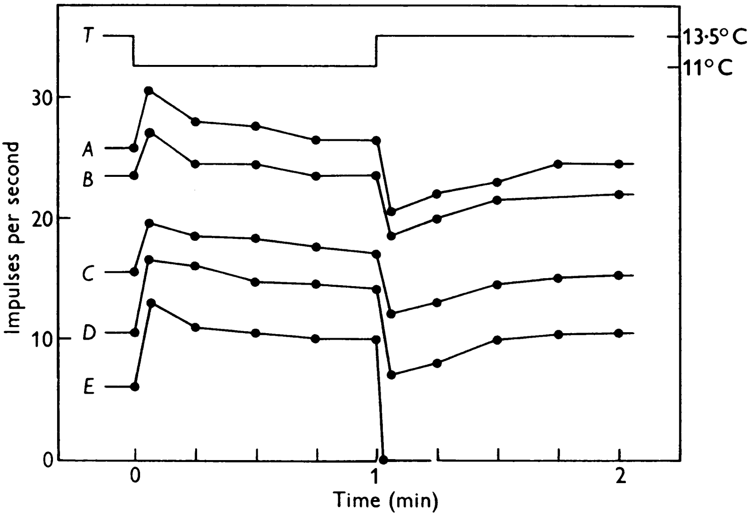

Fig. 3. Discharge frequencies in response to a standard sequence of temperature changes applied during the passage of different steady currents. *T*, temperature; *A*, 6 μA ascending; *B*, 4 μA ascending; *C*, zero current; *D*, 2 μA descending; *E*, 4 μA descending. The position of the stimulating electrodes for *A* and *B* was different from that for *D* and *E* so the current strengths are not comparable.

In the two curves (Fig. 3*A*, *B*) which represent the results with ascending currents, the final frequency is lower than that before the temperature changes were made. This is so because slow adaptation to the applied current continued during the 2–4 min such a standard temperature sequence occupied. To avoid this change in the base line, and to obtain more numerous results, in the majority of the experiments the temperature was lowered for 10–20 sec only (Fig. 4). This was sufficient for the recording of the maximal frequency after cooling but a true minimum in response to warming was not obtained. However, as the result of warming in prolonged experiments was often complete inhibition, the lowered activity caused by the descending current did not appear on the record, so could not be used in analysis either. Fig. 4 shows the record of the whole experiment in progress, curve *A* having been obtained first, and *B*, *C* and *D* in succession after it, with progressively increased strengths of descending current.

Experiments like this can also be illustrated differently. In Fig. 5 the lower curve *A* represents the characteristic curve of adapted frequency under electrical polarization plotted against strength of current, obtained at a steady temperature, and the upper curve *B* represents the maximal or unadapted frequency after cooling by 3° C, at zero and at seven other strengths of current.

The three experiments just described are examples of preparations whose response to current was linear, and the results can be analysed in a straightforward way. The combined stimuli result in a change of frequency equal to the sum of the changes produced by each stimulus applied separately. The temperature change has in general the same effect, in terms of change of frequency, whatever the initial frequency. In Fig. 3 the increase in frequency on cooling is 4–6 impulses/sec over a range of initial frequencies from 6 to 26/sec; similarly in Fig. 4 there is an increase of 15–20/sec for initial frequencies from 0 to 29/sec, and in Fig. 5, an increase of 6–9/sec from 5 to 23/sec with a specially large increase from 0 to 12/sec due to the sudden cut-off when the current was 1 μA descending. The increases due to the cooling are not numerically the same at all current strengths, being slightly greater the stronger the descending current, but by comparison with the range of initial frequencies the differences are small and can be neglected. This point is made specially clear by the way cooling brings back the discharge under conditions when it has been completely inhibited by the descending current (Figs. 4*D*, 5). In view of the linearity of the preparations this general result means that the thermal stimulus can always be expressed in terms of the same change in current strength: thermal and electrical stimuli are equivalent.

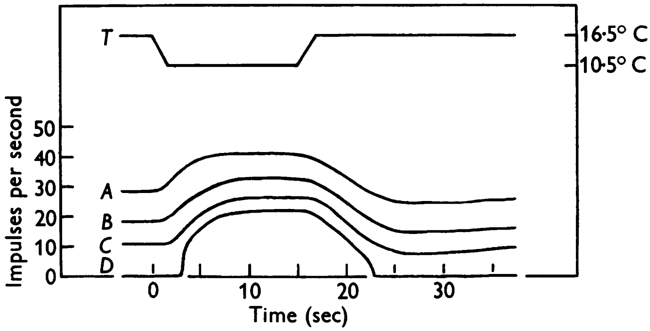

Fig. 4. Discharge frequencies in response to a standard sequence of temperature changes applied during the passage of descending currents, traced from photographic records of the output of the pulse-interval meter. *A*, zero current; *B*, 0·4 μA; *C*, 0·75 μA; *D*, 1 μA; *T*, temperature.

In preparations in which the response curve is not linear the analysis is more complicated, but the result is the same. In the preparation illustrated in Fig. 6, for example, although the drop of 3·5° C at 1 μA descending current did not produce nearly such a large increase in frequency as it did at zero current or with ascending currents, the d.c. equivalents of the temperature drop, found

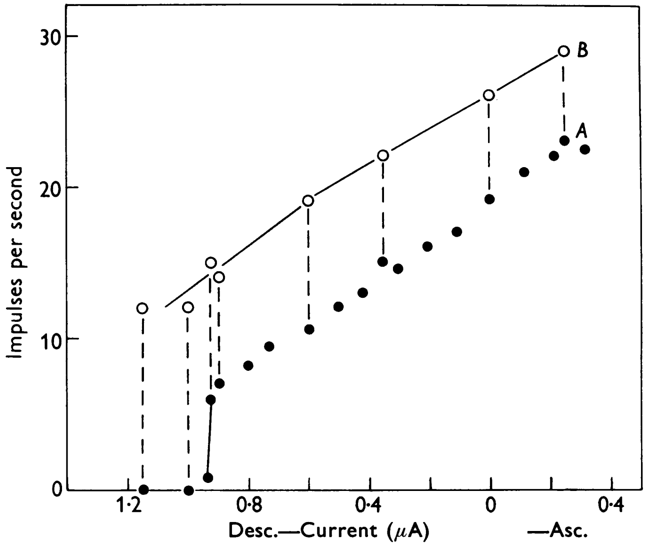

Fig. 5. The effect of temperature change superimposed on the adapted response to direct currents *A*, stimulus-response curve for electrical stimulation at 17° C, obtained by plotting the discharge frequency 1 min after 'make' against the strength of the stimulating current; *B*, maximal discharge frequencies after a fall in temperature to 14° C.

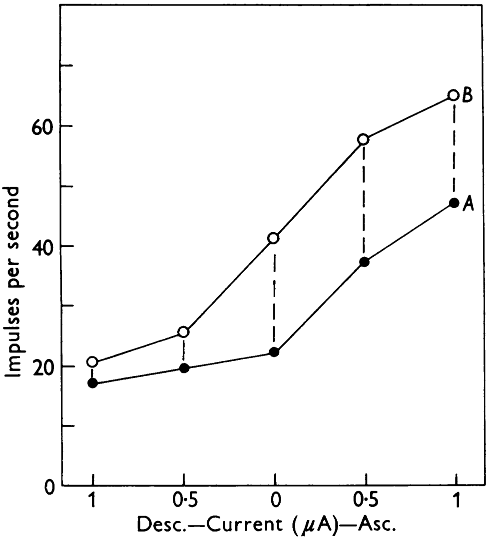

Fig. 6. The effect of temperature change superimposed on the adapted response to direct currents. *A*, curve of adapted responses to electrical stimulation at 16° C. *B*, maximal discharge frequencies reached after a fall in temperature to 12·5° C.

by reference to the characteristic curve 6*A*, were the same, namely 0·6–0·7 μA. At zero current the cooling produced the same increase in frequency as would have resulted from the application of 0·7 μA ascending; at 0·5 μA descending the cooling resulted in a frequency which would have been given by 0·1 μA ascending, i.e. 0·6 μA difference, and at 1 μA descending the cooling resulted in a frequency which would have been given by 0·3 μA descending, also a difference of 0·7 μA. Thermal stimulation is again equivalent to electrical. Thus both curves represent parts of the same characteristic curve of the unit, but over different regions, curve *B* representing the upper portion, curve *A* the lower. To obtain the complete characteristic, curve *B* must be moved to the right by an amount equal to 0·7 μA. The combined curve is effectively linear between frequencies of 25/sec and 60/sec, but flattens out below this.

In the experiments so far described, the thermal stimulus was applied some time after the make of the current, so that the unadapted response to temperature change became superimposed on the adapted response to d.c. Experiments have also been performed to investigate the possible interaction between the unadapted thermal response and the unadapted d.c. response by comparing the effects of brief electrical stimuli applied before and after changes of temperature. Compared with the simplicity shown in the previous experiments, the results here were more complex and variable, and no simple generalizations can be made. Fig. 7, for instance, illustrates an experiment in which a standard electrical stimulus was applied at various stages of a cycle of temperature change; the electrical stimulus consisted of sudden make of an ascending current, sudden reversal to descending current after 2 sec and then sudden break 2 sec later again; the strength of current initially was 0·1 μA and this was increased to 0·2 μA in a second series of tests. The standard electrical stimulus was first applied at a steady temperature of 15·5° C, and the resting, maximal and minimal frequencies are represented by the three points of curve *D*. The temperature was then lowered to 13·5° C, and, after 30 sec, the application of the standard electrical stimulus gave the results shown in curve *A*. Curve *F* refers to an application of the standard electrical stimulus 30 sec after a rise of temperature from 13·5 to 15·5° C. Curves *B*, *C* and *E* are the corresponding results of repeating the sequence with currents of 0·2 μA. The interval between changing the temperature and applying the standard electrical stimulus was chosen as long as 30 sec because in this particular preparation the latency of the thermal response was long and the frequency maximum was consequently reached slowly.

Apart from the flattening-off of the top of the *A*–*B* curve on approaching the maximal frequency of the unit, *A*–*B* is steeper than *C*–*D*, and *E*–*F* is flatter; that is, the effectiveness of the standard electrical stimulus was greater after cooling than at a steady temperature, and smaller after warming. These changes in effectiveness were confirmed by the responses to electrical stimuli applied 1 min after the temperature changes. Here the curves were still steeper and flatter respectively than the steady-temperature curve. The differences between the gradients of the curves are too great to be explained in terms of the slightly non-linear characteristic.

Of the nine preparations so tested, five showed enhanced effects after cooling, and reduced effects after warming. However, in three the response was the same at all phases of the temperature sequence, and in one the response was greatest after warming. The only associated character that could be found to distinguish between the preparations responding in these three different ways was the symmetry of the responses to increase and decrease of temperature. In the five preparations of the first type, the immediate increase of frequency which occurred when the temperature was lowered was greater than the immediate decrease of frequency which occurred when the temperature was altered back to its initial value after adaptation of the response had taken place. In the last one, the response to warming was the greater, and the other three were symmetrical.

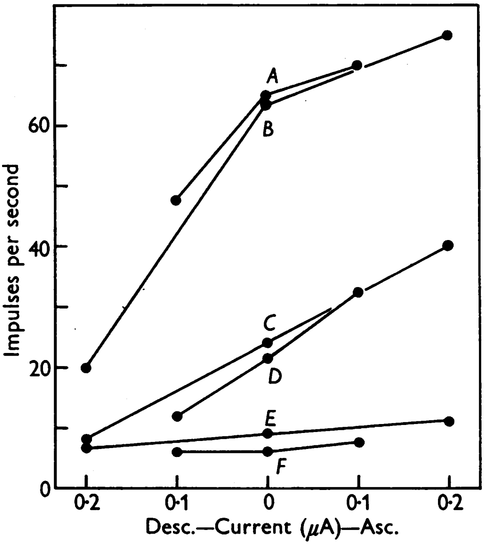

Fig. 7. The effect of sudden electrical stimulation applied before and shortly after changes of temperature; for full description see text. *A* and *B*, response to standard electrical stimuli 30 sec after a fall in temperature from 15·5 to 13·5° C. *C* and *D*, response to standard electrical stimuli at a constant temperature of 15·5° C. *E* and *F*, response to standard electrical stimuli 30 sec after a rise in temperature from 13·5 to 15·5° C.

Anomalous responses to temperature change

In the course of the investigation a number of anomalous responses to temperature change were found. In five preparations out of about a hundred an unusual and very transient change in discharge frequency was obtained each time the temperature was changed (Fig. 8): on cooling there was an initial decrease in frequency lasting 1–2 sec before the more normal increase, and conversely on warming there was a short increase before the slowing-down. In one preparation there was an even more complex response involving an increase, decrease and finally increase again on cooling. Both these types of anomalous response were shown equally when a polarizing current was flowing, the usual summation occurring.

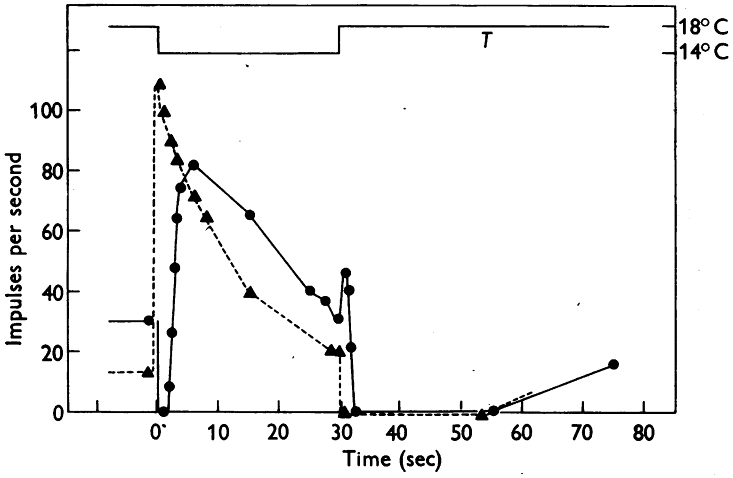

Fig. 8. The response of a single unit to changes of temperature applied from two different directions; between the recordings illustrated in the two curves the capsule was turned over. The continuous curve shows the anomalous response. *T*, temperature.

Response to direction of thermal gradient

In view of the possibility that the effective stimulus for cutaneous thermoreceptors in mammals is the spatial gradient of temperature, responses to standard temperature changes were recorded with the capsule arranged in different positions relative to the direction of the spatial gradient. In every position the sign of the response was the same, although the latency and sensitivity were affected, presumably because of the altered distance between the thermode and the active nerve ending. One particular preparation was arranged so that it only touched the thermode with one end or the other, with the tubes or with the region of the capsule wall through which the nerve emerged; in each position an increase in frequency was caused by cooling. In another experiment (Fig. 8) the anomalous response was altered to a normal one by turning the capsule over.

In a theoretical analysis (Tyrrell, Taylor & Williams, 1954) it was suggested that the existence of the resting discharge itself might depend on the presence of non-isothermal conditions at the nerve endings. However, in the present experiments the discharge continued under such different conditions and directions of temperature gradient that this hypothesis can be excluded.

DISCUSSION

A satisfactory explanation of the mechanisms by which thermosensitive nerve endings convert temperature change stimuli into changes of impulse frequency has not yet been proposed. Any such explanation must be able to account for the results described here.

First, the effective stimulus is the temporal gradient of temperature change and not the spatial gradient. This means that the hypothesis of Tyrrell *et al.* (1954, 1956) proposed for mammalian cutaneous sensory nerves cannot apply to the ampullae, nor to any of the other thermosensitive organs with a resting discharge in which it has been shown that the direction of the spatial gradient is unimportant (mammalian tongue 'cold' receptors, Hensel & Zotterman, 1951; lateralis organs of *Xenopus*, Murray, 1956*b*).

Secondly, in experiments in which thermal stimuli are combined with the adapted response to electrical stimulation, thermal stimulation is equivalent to electrical; the one is as effective in the presence of the other as in its absence. This result is relevant to a discussion of the way in which both electrical and thermal stimulation may effect the mechanisms which are involved in the maintenance of the repetitive discharge.

Thirdly, in experiments in which recordings are made of the non-adapted responses to electrical stimuli applied at a short interval after a change of temperature there are usually consistent changes in the effectivenesss of the electrical stimuli. These changes occur when the responses to warming and cooling are not symmetrical. The results cannot at the moment be explained but it is possible that there are two separate effects of the polarizing current, an electrotonic shift of membrane potential and a change in the depolarization rate between impulses; the two effects could be unequally affected by adaptation. The latter effect has been suggested by Hodgkin (1951, p. 389), and can be seen in the photographs in his earlier paper (1948) on the initiation of impulses in crab nerve by d.c. stimulation.

Fourthly, certain preparations show anomalous responses to temperature change. They are numerous enough to warrant a special explanation, but nothing can usefully be said at the moment, except that the alteration between excitation and inhibition is in some respects similar to that described by Bullock & Diecke (1956) from the facial pit thermoreceptors of crotalid snakes.

SUMMARY

1. The impulse discharge from the ampullae of Lorenzini has been recorded during electrical stimulation by direct currents applied alone and in combination with thermal stimuli.

2. The discharge frequency varies linearly with the applied current in the majority of preparations.

3. When temperature changes occur after adaptation to an electrical stimulus has taken place, the change of frequency due to the combined stimuli is the sum of the changes due to each stimulus separately.

4. The response to a brief electrical stimulus applied during the period of maximal response to a thermal stimulus is in some instances greater than, and in others less than the response in the absence of thermal stimulation.

5. The direction of the spatial gradient of temperature is unimportant in determining the response to temperature change.

6. Some anomalous responses to temperature change are described.

The work was carried out at the Laboratory of the Marine Biological Association at Plymouth, and I should like to thank the Director and Staff for their hospitality and for supplying the living material. The cost of part of my apparatus was met by a Royal Society grant. I should also like to thank Professor O. Lowenstein for his encouragement and for suggesting the use of cerebrospinal fluid in the dissections.

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