QUALITATIVE ANALYSIS OF THE EFFECT OF THERMAL STIMULI ON THE SPONTANEOUS ACTIVITY OF TUBEROUS (*KNOLLEN-*) ORGANS IN *GNATHONEMUS* SP., MORMYRIDAE, PISCES*

By ANTON ROTH† and THOMAS SZABO

Laboratoire de Neurophysiologie Sensorielle Comparée, Centre d'Etudes de Physiologie Nerveuse‡, C.N.R.S.

The effect of changes in temperature on afferent nerve activity has been examined in many sense organs bearing secondary sensory cells (Sand, 1938, Hensel, 1955; Murray, 1955, 1956, 1965). In all of these investigations the thermal effect was studied in terms of the change in the number of impulses per second in the afferent nerve fibre connected to the sense organ, or more precisely to the sensory cells. It was shown that the frequency of afferent impulses changes when the temperatures at the receptor site varies, e.g. lowering the temperature ($-\Delta T^\circ$ C.) provokes a temporary increase of frequency ('paradoxical' thermal effect; see Sand, 1938) and the final frequency after this temporary effect is positively correlated with the decreased temperature ($-T^\circ$ C.) ('normal' thermal effect); $+\Delta$ °T C. and $+T^\circ$ C. provoke opposite effects.

To our knowledge no investigation has been carried out to ascertain which part of the complex sense organ structure or which of its functions mediates these effects on the discharge frequency of afferent impulses. The possible sites of action are the site of impulse initiation, the end-arborizations of the afferent fibre (Murray, 1965), the pre- or postjunctional membrane involved in transmission between sensory cell and nerve endings (see Machin, 1962) or, finally, the sensory cell itself (Roth & Szabo, 1969).

Mormyrid fish possess particular cutaneous sense organs, the tuberous ('Knollen-organ') of Franz (1920), which are identical with specific lateral line organs (Szabo, 1965) and which generate brief spike-like spontaneous receptor potentials (RP) of relatively large amplitude (0·5–2·0 mV.) (Szabo, 1962; Szabo & Fessard, 1965).

We have previously shown that the 'spontaneously' arising RP of the tuberous receptor recorded extracellularly at the skin surface does not represent the propagated potential (PP) of the afferent nerve fibre, but is a rapid phenomenon due to the receptor itself. This receptor potential triggers the action potential in one-to-one fashion and the relation in time between the RP and PP in steady conditions remains constant (Roth & Szabo, 1967; Szabo & Roth, 1967; T. Szabo & A. Roth, in MS.)

Using differential degeneration of the sense organ–afferent nerve complex obtained after transection of the afferent nerve, we were able to show (Roth & Szabo, 1969)

that the spike-like potential of the receptor is generated by the sensory cell itself. Thus, in this particular sense organ the effect of temperature on the secondary sensory cell (Fessard & Szabo, 1962) could be studied to determine whether the sensory cell activity displays characteristics similar to those observed in its afferent nerve (T. Szabo & A. Roth, in preparation). The results of these observations might also provide a basis for explanation of the temperature-related frequency behaviour found in the afferent nerves of other sense organs.

The characteristics of the spike-like receptor potential (RP) and the relationship between the RP and the propagated potential (PP) will be described in a subsequent paper.

METHODS

Two species belonging to the same genus of the family Mormyridae were used: *Gnathonemus petersii* and *stanleyanus*, both native to the Congo basin. The fish were kept for several months in Parisian tap water at 22–26° C.

The general experimental procedure has been described in previous papers (Szabo & Fessard, 1965). The fish was fixed with gauze bands to a wooden plate in the normal swimming position and placed in a water container; good gill movements were maintained by a water jet introduced into the fish's mouth.

Recording. The epidermal activity was recorded under water 'at distance' with a silver wire insulated to its tip and brought within 0·5–1 mm. of the skin surface. Activity 'out of water' was recorded by Ag/AgCl balls placed in contact with the epidermis close to the active points, while the water level was lowered to keep the dorsal skin surface just out of water, so that a thin water layer kept the surface moistened.

The activity was amplified with a conventional RC-coupled amplifier and displayed on an oscilloscope (Tektronix 365). The number of spikes was read directly from a counter device (type Rochard A 1211) whose illuminated panel was projected on to the oscilloscope screen and photographed with a Grass C4 camera. During rapid temperature changes spikes were counted for a period of 1 sec. at intervals of 3·17 sec. or 9 sec.

Temperature stimuli. For recording under water the water in the container was replaced by water of a different temperature which was measured directly with a thermometer. This procedure was used only for studying constant temperature effects.

Rapid temperature changes of the skin surface were produced by means of a U-shaped glass tube which formed a loop of inner diameter 1·85 cm. and outer diameter 2·91 cm. through which water of constant temperature (initially identical to that of the container) was continuously flowing. A double three-way tap system on the glass tube permitted rapid temperature changes of the skin surface. The rate of temperature change was controlled by varying the speed of the water flow in the tube. The system allowed us to apply temperatures from 10° to 40° C. and the rate of temperature change could be varied from 0·33° to 0·04° C. sec.$^{-1}$. Rapid changes of small amplitude (less than 1° C.) could not be obtained with this device. The non-isothermal conditions in which the receptor *in situ* was examined and the presence of air currents made it difficult to reproduce identical thermal stimuli.

The rapid changes of temperature were measured with a thermistor (100 K ohm) stuck to the tip of the recording electrode and lying 1·5 mm. lateral to it in such a way

that the thermistor, embedded in glass, touched the skin surface. The latency between the registered temperature change and the biological response was small and can be neglected in a qualitative analysis.

RESULTS

Frequency behaviour of the tuberous organs at room temperature (23–24° C.)

The tuberous organs are less numerous than the other specific lateral line organs and than the ordinary ones in mormyrids. In contrast to the head region, the dorsal skin surface shows a sparse distribution of tuberous organs and is, therefore, a convenient area for studying single organ activity. A spontaneous discharge is usually present in the tuberous organs, but silent organs are also found; in addition a fish in bad general condition shows little epidermal activity and it frequently happens that certain antimycelial drugs used by commercial dealers 'kill off' the cutaneous activity. The drug effect is not irreversible, however, and fish put for a few days in clean water regain normal cutaneous activity. Activity *post mortem* or in isolated skin can easily be preserved for 10–20 min., in contrast to the afferent nerve activity which disappears immediately or within a few minutes after the fish is decapitated.

As has previously been reported (Szabo, 1962; Szabo & Fessard, 1965) the frequency of the spontaneous activity (spikes/sec.) under water varies from organ to organ (Fig. 1): average frequencies up to 1500 were encountered commonly and frequencies of over 2000 spikes/sec. were occasionally found. The 16 organs observed showed the following firing patterns: single potentials (four organs), burst-like potentials (ten organs) and regular high frequency activity (two organs).

Care was taken to keep the fish entirely under water before and during the experiments (see Discussion) and the water was maintained at room temperature (23–24° C.). To avoid mechanical effects caused by the recording electrode, the recordings were made 'at distance' as described above.

If the electrode touched the skin immediately above an organ the pattern and frequency of its spontaneous activity changed. Light pressure always decreased the frequency and heavier pressure abolished it. The effect persisted during maintained pressure and no adaptation occurred, but with strong stimuli the return of activity was delayed after the pressure was released. Pressure applied on the whole fish by placing the fish in a closed water-filled container had no effect on the spontaneous activity.

Generally, the activity of two points was recorded simultaneously. The 16 organs were examined during a total observation time of 9·5 hr.; six typical examples from four fish are shown in Fig. 1. The frequency was measured at 21 sec. intervals and each symbol corresponds to a single measurement over 10 sec. The total observation times were 38, 73, 80 and 90 min. For several other organs recordings were performed for 7–8 hr. From the first 63 min. of recording, three consecutive periods lasting 3·5 min. (each containing 11 measurements) starting at zero, 28 and 59·5 min. are represented. Maximum and minimum frequency values covering the whole 63 min. period of measurements are given at the right of each curve.

The spontaneous frequency of any organ may change by up to 200 imp./sec., the

rate of change is slow (several minutes) and the variation irregular. However, some organs also present relatively rapid changes (see Fig. 1, in the first 3 min. of the uppermost curve). The frequency of the different organs varied under steady conditions between ±3·3 to ±17% of the mean frequency.

Accidental touching of the organs (with the electrode for instance) sometimes caused drastic changes in frequency; the frequency might drop below or rise above its normal maximum/minimum range and then generally re-establish in a new frequency range.
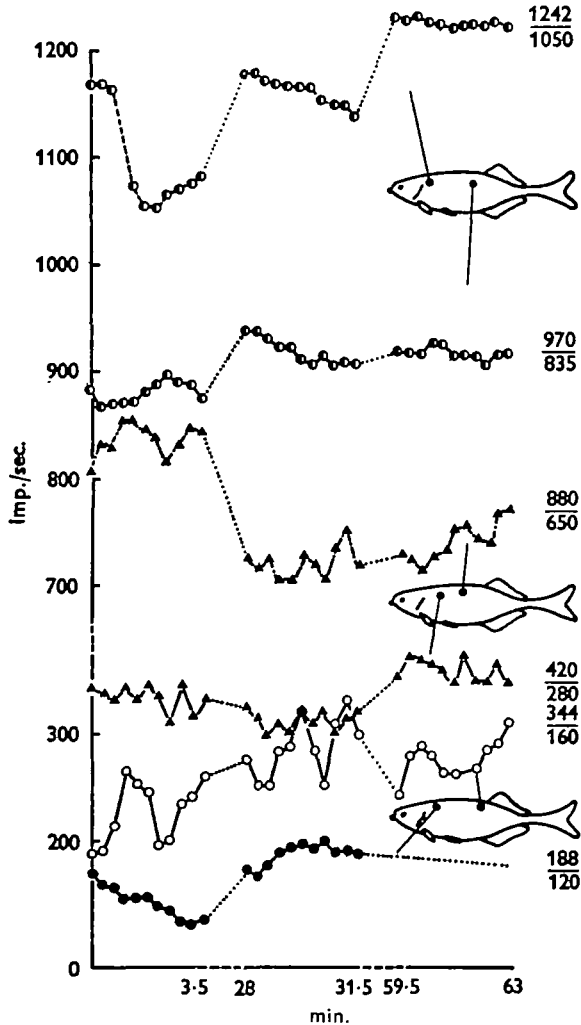

Fig. 1. Discharge frequencies of six tuberous organs recorded under water from four fish. Similar symbols indicate simultaneous recordings from the same fish (in 1st and 5th recording one point of measurement is lacking). Recording site is indicated in each fish. Figures on the right indicate max./min. frequencies for the whole 63 min. recording period. Mean frequencies for curves are 1180, 907, 750, 354, 250, 162 Hz. Coefficients of variation of the corresponding mean frequencies are 3·4, 3·3, 6·9, 9·3, 17·0, 12·5 %.

Effects of thermal stimuli

1. Frequency behaviour at steady temperature (T) was studied under two conditions: (a) While the fish remained fixed under water (recording under water); the temperature was changed by slowly replacing the water of the aquarium. (b) While the active epidermal point was maintained above water level (recording out of water) the organ site only was submitted to temperature steps (see Methods).

2. Frequency behaviour during temperature variations (Δ T) was studied in most of the cases, under the conditions (b) above.
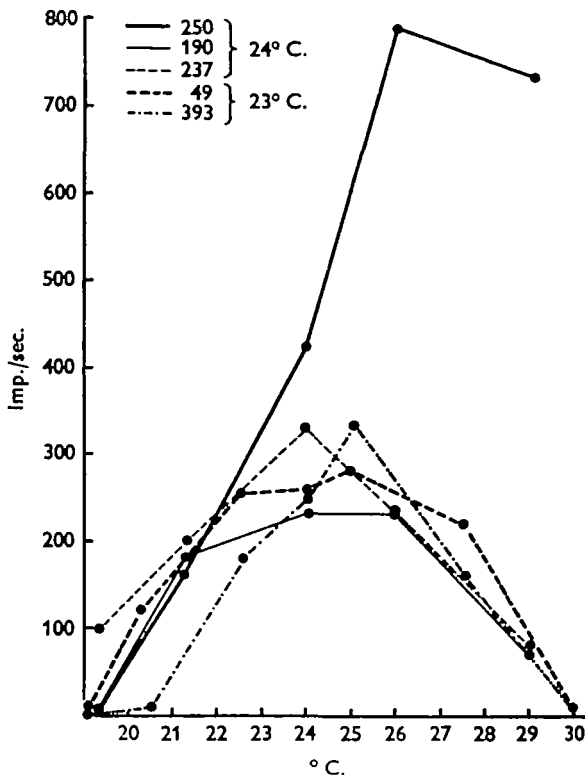

Fig. 2. Discharge frequencies as a function of temperature over the range 30–29° C. to 19° C. The temperature has previously been raised from an initial temperature of 24°–23° C. to 29°–30° C. Values correspond to the average of three measurements at 12 min. intervals, starting after 25 min. adaptation. Figures at top left indicate the frequency values of five (2+3) organs of two fish at the initial temperature.

1. Frequency behaviour at steady temperatures

Nine organs of two fish (6+3) were observed simultaneously while the water temperature was increased or decreased by steps of 2–3° C. between 19° C. and 30° C. The frequency was measured three times at 12 min. intervals starting 25 min. after each temperature step, thus, the effect of the temperature change appearing during the first minutes of the applied thermal stimulus was neglected in these experiments. Each point represents the average value of the three measurements.

The curves (in Fig. 2) illustrate the frequency variations of five tuberous organs as

a function of a sequence of temperature changes from 30° to 19° C. This sequence was recorded after the temperature of the water had been raised from 23 to 24° to 30° C. Each curve displays a maximum between 24° and 26° C, and, with one exception, two minima at 19° and at 30° C.

The frequency values are not identical for a given temperature on different occasions; they are generally higher when the final temperature level is reached by negative increments (see figures in left upper corner, Fig. 2).

In some similar experiments the frequency increased continuously with increasing temperature (thick solid curve in Fig. 2). In these cases the activity showed a regular firing pattern approximately 1000 imp./sec. and the spike interval diminished with increasing temperature; about 31–33° C., the amplitude of the spikes diminished until the activity disappeared. When the temperature was lowered the activity reappeared either starting with high-frequency and low-amplitude spikes or with the usual type of activity, i.e. with randomly occurring single spikes of maximal amplitude (Fig. 4A).

If spontaneous firing is considered as a sign of a 'normal state' of the tuberous organs (see T. Szabo & A. Roth, in prep.), it follows from Fig. 2 that the working range of the latter is between about 18 and 32° C. The critical temperature range of the water in which mormyrid fish live lies between 17° and 36° C. (see Discussion).

2. Frequency behaviour during temperature variations

The well known 'paradoxical' thermal effect was observed first by Sand (1938) in the afferent nerves of various sense organs and confirmed later by Hensel (1955), Murray (1956), Burckhardt (1959), Vuco & Todorovic (1962), J. Bernard & J. Boistel, unpublished observations).

The same effect has also been found for the receptor potential (RP) of the tuberous organs. Fig. 3A and D show typical paradoxial effects: a sudden fall of temperature 2° C. results in a temporary increase of frequency, while a rise of temperature has opposite effects. In both cases the paradoxical effect is followed by a further change in frequency, a decrease during cooling and an increase during warming (this effect corresponds to the dynamic component of the 'normal' thermal effect; for definition see under 'The normal thermal effect', below).

The paradoxical effect. The occurrence of the paradoxical effect is independent of the starting frequency of the RP. As the frequency of spontaneous firing is itself temperature dependent, it seems, therefore, also to be independent of the starting temperature over a large temperature range. Thus, the paradoxical effect can be produced if the organ is silent—for example at 19° C. (Fig. 4A)—as well as when the organ shows a relatively high-frequency initial discharge at 25–26° C. (Fig. 4B). In extreme cases, for example at high-frequency initial activity of the organ when no further increase can be obtained, cooling still provokes an effect which indicates that the process responsible for the paradoxical phenomenon is present. Thus at the start of the temperature decrease a 'plateau' (no change in frequency) appears, of duration similar to the paradoxical effect. This plateau is followed by a 'normal' thermal effect. The same phenomenon occurs during warming when the temperature is increased in an organ showing zero initial frequency; in this case the increase in frequency, the 'normal' thermal effect for warming, shows the normal delay with respect to the thermal stimulus.

The paradoxical effect can be obtained during the entire evolution of a thermal response (Fig. 3 B and C), including the paradoxical response.

The amplitude of the paradoxical response depends on the rate of temperature change, the greater the latter the larger the frequency change. The three paradoxical responses for cooling shown in Fig. 5 A were obtained by changing the temperature at different rates (0·33° C., 0·09° C. and 0·04° C. sec.$^{-1}$). The amplitude of the para-
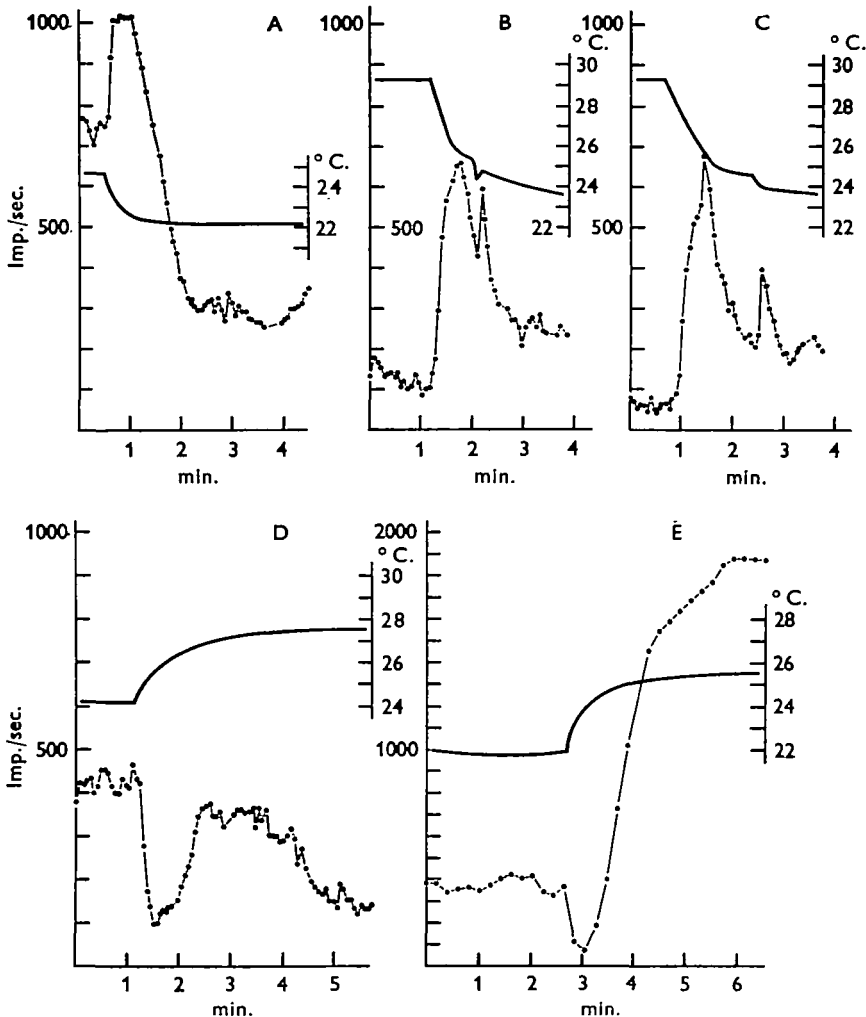

Fig. 3. Frequency variation of the RP in response to temperature steps. Dots, frequency curves; heavy lines, temperature curves. A and B from one organ, C and D from another.

doxical response is also dependent on the starting frequency at which a negative temperature stimulus is applied and seems to be inversely correlated to it (Fig. 6).

The peak of the paradoxical response always occurs at a fixed time relative to the onset of the stimulus. In other words, the rate of the temperature change has no effect on the time course of this response although it seems to influence the rate of frequency change. Since peak localization was difficult (Fig. 5 A) the time duration of the rising

phase of all the peaks observed (32 for cooling, five for warming) with different rate of temperature changes was measured (Fig. 5). The results confirm that the peak always appears during a limited period of from 20 to 50 sec. independent of the rate of temperature change.
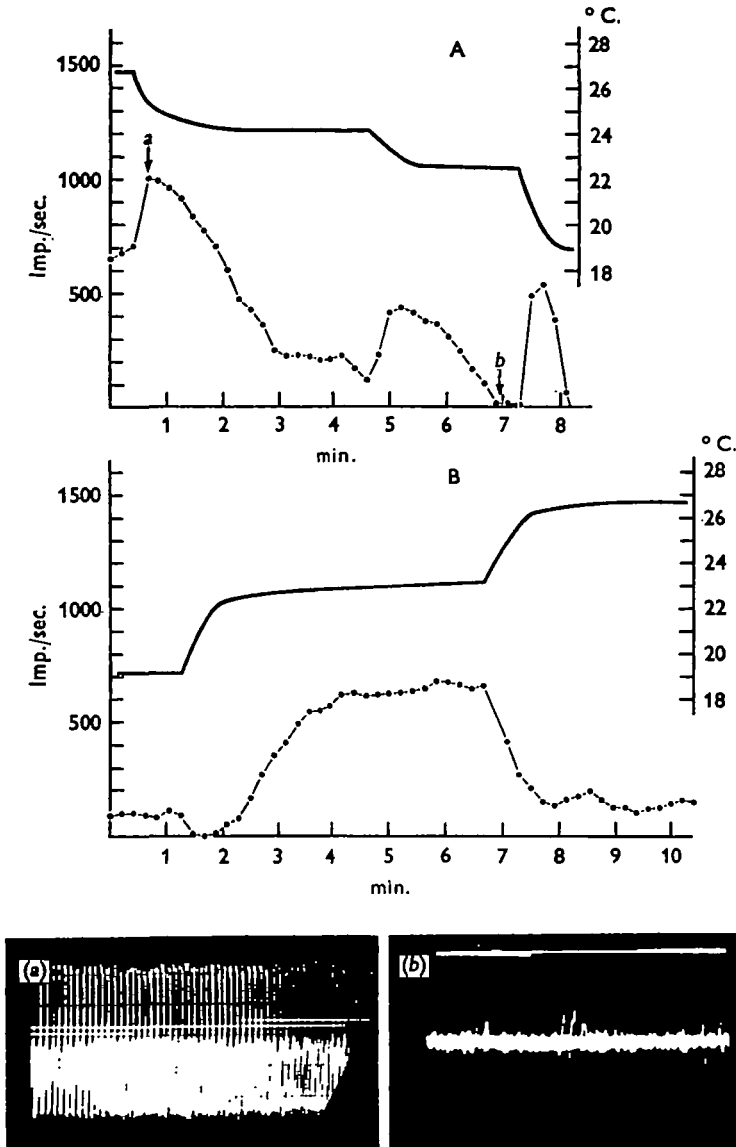

Fig. 4. Frequency variation of the RP in response to temperature steps. *a* and *b* oscillographic recordings indicated by arrows in A. A and B from the same organ.

The 'normal' thermal effect. In the 'normal' thermal response we can distinguish a dynamic component, the immediate transient frequency change following the para-doxical response and a static component, the sustained response.

The time course of the dynamic component depends on the rate of temperature

change. Fig. 5 A shows variations on the rate of frequency change provoked by three different rates of temperature change. The decrease of frequency in these three examples was 20·0, 7·2 and 5·0 Hz sec.$^{-1}$. The white symbols in Fig. 5 show that the smaller the rate of temperature change the longer tends to be the time course of the frequency variation*.
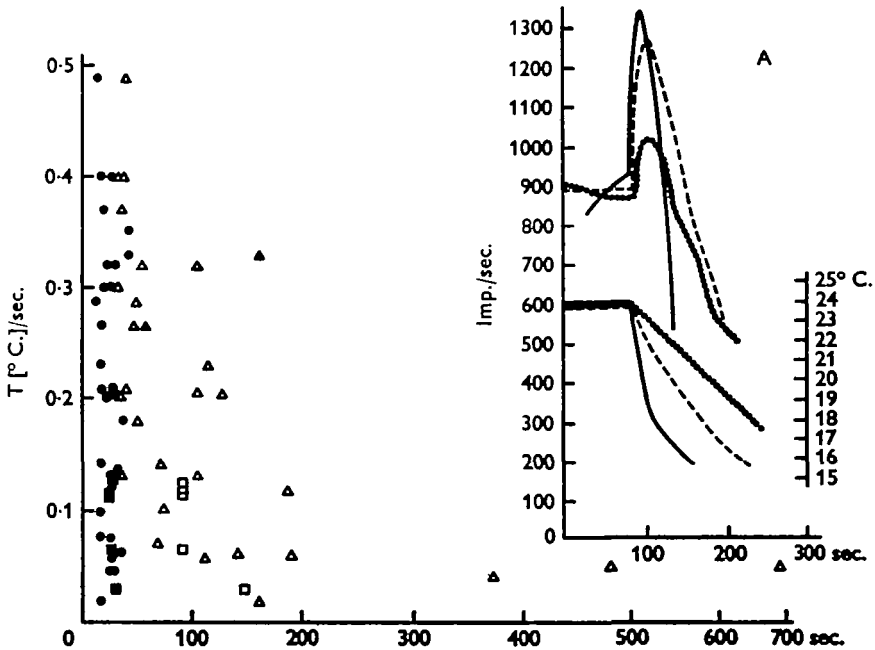

Fig. 5. Black symbols: time course of the 'paradoxical' thermal effects as a function of the rate of temperature change. White symbols: time course of 'normal' thermal effects as a function of the rate of temperature change. Dots, cooling; squares, warming.

Fig. 5A. Examples of frequency change of the RP during three rates of temperature change. Note the similar duration but the different amplitudes of the paradoxical response for the three different rates of temperature change. Above: frequency curves; below: corresponding temperature curves.
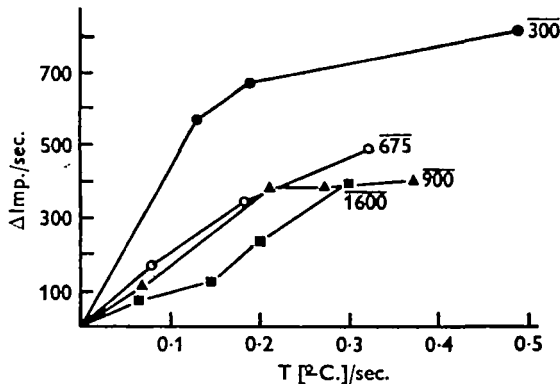

Fig. 6. Change in discharge frequency of RP as a function of the rate of temperature change. Figures indicate the mean starting frequencies.

---

* The values indicated by the triangles are calculated as follows: the mean frequency (1125 Hz) of the peak values of all paradoxical responses obtained were divided by the initial rate of change of frequency for each curve.

The static component of the 'normal' thermal response depends on the absolute temperature. It has a positive or a negative temperature coefficient depending on the temperature range at which the temperature change is applied (see Fig. 2). A warming step, for example from 19° to 23° C., will increase the frequency (first step in Fig. 4B) while a similar step from 23° to 27° C. decreases the frequency (second step in Fig. 4B). The dynamic component appears in the first case (see also Fig. 3E) while it fails in the second. Fig. 3 D illustrates a response of an intermediate type where an abortive dynamic component was observed.

DISCUSSION

The receptor potential (RP) of the tuberous organs shows behaviour to thermal stimuli similar to that described by Zottermann (1953) for mammalian cold fibres and, later, by several authors for other sense organs of poikilotherms. As the receptor potential not only precedes but also triggers the propagated potential (PP) in the afferent nerve (Szabo & Roth, 1967; Roth & Szabo, 1967) it appears at first sight that the frequency behaviour of the afferent nerve is explicable as a consequence of the thermal effect on the primary event, the receptor potential. However, this is true only within certain limits (see T. Szabo & A. Roth, in preparation).

The effect of thermal stimuli on the behaviour of the receptor potential, in terms of its frequency, is qualitatively the same as their effect on the afferent nerve activity of many sense organs with primary (Burkhardt, 1959; J. Bernard & J. Boistel, unpublished observations; Loftus, 1968) or secondary (Sand, 1938; Hensel, 1955; Murray, 1956) sensory cells, and similar behaviour has been observed in central neurone activity of a number of invertebrates (Kerkut & Ridge, 1962; Murray, 1966). The occurrence of the same effects in structures as different as central neurones and primary and secondary sensory cells suggests that the temperature effect is related rather to the dynamic properties of the physico-chemical process which determines the state of an 'excitable' membrane than to the specificity of one particular kind of membrane (the peripheral end-arborization of the sensory neurone; see Murray, 1955, 1965). We have indications indeed that the resting potential (Burkhardt, 1959; Murray, 1966), metabolic processes (Senft, 1967) and excitability threshold (Burkhardt, 1959; Bernard, Grahery & Boistel, 1964) are influenced by temperature.

Identical thermal stimuli applied to different organs in the same fish produce similar effects in or out of water. However, the fact that very high and very low frequencies occur at the same temperature suggests that one of them does not correspond to the physiological state of the organ (see T. Szabo & A. Roth, in preparation). Some explanation for this high-frequency behaviour may be found in the results of Späth (1967), who observed that mechanoreceptors of fish displaying 'cold-fibre properties' react differently in different conditions to identical thermal stimuli; the afferent nerve activity of this sense organ shows increases with rising temperature either continuously or to a maximum value followed by a decline.

Bennett (1965) observed high-frequency activity of the tuberous organs, over 800–1000 Hz, only when the organ was raised out of water. The thermal effect could partly explain such frequency behaviour: evaporation of water provokes cooling and thus an increase in frequency. However, the maintained high-frequency activity out

of water cannot be explained by the same reasoning. Our observations (see Methods) show that high-frequency activity also occurs under water even for several hours (Fig. 1). Our results as well as De Souza's (1969) recent experiments confirm that some organs maintain high-frequency activity when the fish is kept several centimetres (more than 5 cm.) below water level, while others, under the same conditions, show low frequency discharge. Thus, the high-frequency discharges cannot be explained solely by bad conditions (drying) of the skin.

The observed effect of temperature on the activity of the tuberous organ raises the question of the temperature variations to which *Gnathonemus* is exposed in its natural environment.
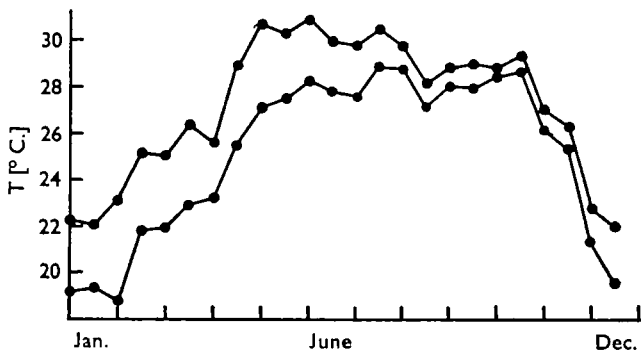

Fig. 7. Minimum and maximum values of the surface temperature of the river Niger at Diafarabe (Rep. Mali) in 1955. Temperature measured at 6 a.m. and 6 p.m. Dots indicate mean values over 15 days. Rainy season from end of May till October (from Blanc, Daget & d'Aubenton, 1955).

The temperature of the subtropical rivers where *Gnathonemus petersii* lives varies over the year between 19° and 31° C. (Fig. 7). During the rainy season, from May to October, the temperature remains high (28°–31° C.) while during the dry season it is low (19°–22° C.); daily variations are roughly 1°–3° C. In small pools the maximum temperature can be as high as 36° C. The temperature data compared with our results (Fig. 2) indicate that the spontaneous activity of the tuberous organ should be low (< 150 Hz) during almost the whole year because the temperature of the rivers tends to be either high or low. Considering on one hand the fact that the tuberous organs represent one type of electroreceptor of the fish (Szabo & Fessard, 1965; Roth, 1967) and, on the other hand, that their high-frequency discharge implies a low threshold (i.e. higher sensitivity) to electric stimulation (T. Szabo & A. Roth, in preparation), one would like to correlate the changes in sensitivity (see also Beatty, 1966) with some biological or ecological aspects of the fish behaviour; for example, improved communication between male and female in the breeding season (from June on) or schooling when the fish return to the river after the rainy season (in October). The temperature curves of the river show, however, that the increased sensitivity of these organs occurs only temporarily and thus cannot be essential to either of these types of behaviour.

SUMMARY

1. The effect of thermal stimuli on the spontaneous spike-like receptor potential (RP) of the tuberous (*Knollen*) organ in *Gnathonemus* (Mormyridae, Pisces) was examined.

2. The frequency of the spike-like receptor potentials varies from organ to organ even in the same fish; the mean frequency values observed lay between 162 and 1180 Hz.

3. The frequency of the RP discharge was related to steady temperature of the receptor site over a temperature range of 19° to 30° C. with a maximum at 24°–26° C. In some cases the frequency increased with increasing temperature over the whole range.

4. The receptor potential shows a temporary increase on cooling (paradoxical thermal response), followed by a decrease in frequency (normal thermal response); warming provokes opposite effects.

5. The amplitude of the paradoxical response depends on the rate of temperature change but its time course does not.

6. The time course of the dynamic component of the normal thermal response is related to the rate of temperature change. The static component of the normal thermal response depends on the absolute temperature value and displays positive and negative temperature coefficients in the 'cold' and the 'warm' temperature ranges respectively.

7. The receptor potential shows behaviour on temperature change similar to the mammalian cold fibre and the afferent fibres of several other sense organs. Thus, the results suggest that (within certain limits) the events occurring at the level of sensory cells could be responsible for the frequency behaviour of the action potential in the afferent nerves of sense organs.

8. The significance of the thermal effect under natural conditions is discussed.

REFERENCES

BEATTY, D. D. (1966). A study of the succession of visual pigments in Pacific salmon *Oncorhynchus*). *Can. J. Zool.* **44**, 429–55.

BENNETT, M. V. L. (1965). Electroreceptors in Mormyrids. In *Sensory Receptors. Cold Spring Harb. Symp. quant. Biol.* **30**, 245–62.

BERNARD, J., GRAHERY, Y. & BOISTEL, J. (1964). The effects of temperature changes applied to the cervical nerves and to the sixth abdominal ganglion of the cockroach (*Blabera craniifer* Burm.). In *The Physiology of the Insect Central Nervous System. Proc. XIIIth Congr. Ent.* London: Academic Press.

BLANC, M., DAGET, J. & D'AUBENTON, F. (1955). Recherches hydrobiologiques dans le bassin du Moyen Niger. IFAN, 17 A (3).

BURKHARDT, D. (1959). Die Erregungsvorgänge sensibler Ganglienzellen in Abhängigkeit von der Temperatur. *Biol. Zbl.* **78**, 22–62.

FESSARD, A. & SZABO, T. (1962). Effets des variations de température sur l'activité de certains récepteurs des Mormyrides. *C. r. hebd. Séanc. Acad. Sci. Paris*, **254**, 2084–5.

FRANZ, V. (1920). Zur mikroskopischen Anatomie der Mormyriden. *Zool. Jb. (Anat.)* **42**, 91–148.

HENSEL, H. (1955). Quantitative Beziehungen zwischen Temperaturreiz und Aktionpotentialen der Lorenzinischen Ampullen. *Z. vergl. Physiol.* **37**, 509–26.

KERKUT, G. A. & RIDGE, R. M. A. P. (1962). The effect of temperature changes on the activity of the neurones of the snail *Helix aspersa*. *Comp. Biochem. Physiol.* **5**, 283–96.

LOFTUS, R. (1968). The response of the antennal cold receptor of *Periplaneta americana* to rapid temperature changes and to steady temperature. *Z. vergl. Physiol.* **59**, 413–55.

MACHIN, K. E. (1962). Electric receptors. *Symp. Soc. exp. Biol.* **16**, 227–44.

MURRAY, R. W. (1955). Nerve endings as transducers of thermal stimuli in lower vertebrates. *Nature, Lond.* **176**, 698–99.

MURRAY, R. W. (1956). The thermal sensitivity of the lateralis organs of *Xenopus leavis* to electrical stimulation by direct current. *J. Physiol., Lond.* **134**, 408–20.

MURRAY, R. W. (1965). Receptor mechanisms in the ampullae of Lorenzini of Elasmobranch fishes. In *Sensory Receptors. Cold Spring Harb. Symp. quant. Biol.* **30**, 233–43.

MURRAY, R. W. (1966). The effect of temperature on the membrane properties of neurons in the visceral ganglion of Aplysia. *Comp. Biochem. Physiol.* **18**, 291–303.

ROTH, A. (1967). Propriétés fonctionnelles et morphologiques des différents organes de la ligne latérale des Mormyridés. *J. Physiol. Paris* **59**, 486.

ROTH, A. & SZABO, T. (1967). Corrélations entre potentiels locaux et propagés engendrés au niveau d'un organe sensoriel. *J. Physiol., Paris* **57**, 290.

ROTH, A. & SZABO, T. (1969). The effect of sensory nerve transection on the sensory cells and on the receptor potential of the tuberous (*Knollen*) organ in Mormyrid fish (*Gnathonemus* sp.). *Z. vergl. Physiol.* **62**, 395–410.

SAND, A. (1938). The function of the ampullae of Lorenzini with same observations on the effect of temperature on sensory rhythms. *Proc. Roy. Soc. Lond.* B **125**, 523–53.

SENFT, J. P. (1967). Effects of some inhibitors on the temperature-dependent component of resting potential in Lobster Axon. *J. gen. Physiol.* **50**, 1835–48.

SOUZA, DE P. F. (1969). Analyse des autoactivités des électropercepteurs d'un Mormyre et leur stabilité. *J. Physiol., Paris* **61**, suppl. 2, 266.

SPÄTH, M. (1967). Die Wirkung der Temperatur auf die Mechanorezeptoren des Knochenfisches *Lemiscus rutilus* L. *Z. vergl. Physiol.* **56**, 431–62.

SZABO, T. (1962). Spontaneous electrical activity of cutaneous receptors in mormyrids. *Nature, Lond.* **194**, 600–1.

SZABO, T. (1965). Sense organs of the lateral line system in some electric fish of the Gymnotidae, Mormyridae and Gymnarchidae *J. Morphol.* **117**, 229–50.

SZABO, T. & FESSARD, A. (1965). Le fonctionnement des électrorécepteurs chez les Mormyridés. *J. Physiol., Paris* **57**, 343–60.

SZABO, T. & ROTH, A. (1967). Comportement des potentiels propagés dépendants de la modulation des potentiels récepteurs autoactifs des Knollenorgans. *C. r. hebd. Séanc. Acad. Sci. Paris* **265**, 807–9.

VUCO, J. & TODOROVIC, B. (1962). Afferent discharge from the muscle spindle during the cooling of the muscle. *Arkh. biol. Nauk* **14**, no. 1–2, 95–9.

ZOTTERMAN, Y. (1953). Special senses: thermal receptors. *A. Rev. Physiol.* **15**, 357–72.