Vol. 18, 1932

* It has, however, been shown by Du Buy that the curvatures obtained are reduced when higher concentrations of agar are employed. Our value of K/v applies to 1.5% agar.

Bonner, J. F., Biol. Zentr., 52, 565 (1932).

Boysen-Jensen, P., Biochem. Zeit., 236, 205 (1931).

Boysen-Jensen, P., Biochem. Zeit., 250, 270 (1932).

Du Buy, H., Proc. Kon. Akad. Wetensch. Amsterdam, 34, 1 (1931).

Dolk, H. E., Diss. Utrecht (1930).

Dolk, H. E., and Thimann, K. V., Proc. Nat. Acad. Sci., 18, 30 (1931).

Kögl, F., and Haagen-Smit, A. J., Proc. Kon. Akad. Wetensch. Amsterdam, 10, 1 (1931).

Nielsen, N., Jahrb. wiss. Bot., 58, 406 (1930).

Thimann, K. V., and Dolk, H. E., Biol. Zentr. (in press).

Went, F. W., Rec. trav. bot. néerl., 25, 1 (1928).

Wey, H. G. van der, Diss. Utrecht (1932).

IMPULSES FROM SENSORY NERVES OF CATFISH

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Using a Matthews¹ amplifier and oscillograph in conjunction with a loud speaker, a standing wave screen and a camera, electrical responses were recorded from various sensory nerves of the catfish *Ameiurus nebulosus* (Les.) in response to mechanical, thermal and chemical stimulation of the receptors which these nerves supply. The nerves tested were lateral line nerves, spinal nerves supplying the skin of the flank, and branches of the facial nerve supplying the tactile endings and tastebuds of the lips and barbels. Some 52 nerves were examined in 32 fishes.

After severing the medulla oblongata (in some cases brain and cord were pithed), the nerve to be tested was exposed at a point as near its region of emergence from the central nervous system as was anatomically convenient, and freed from surrounding tissues for a suitable length. It was then tied proximally with a thread, cut and drawn across silver, silver chloride electrodes connected to the recording system. The preparation was generally so arranged that the receptive areas were kept immersed in water while the nerve and incision were out of water and bathed with Ringer solution.

Maps of skin areas supplied by spinal and facial nerves were made by stroking the skin with the tip of a feather and listening to the bursts of impulses from the loud speaker. In this way it was possible to ascertain the particular skin areas supplied by a branch of nerve. By means of the volume of sound, it was also possible to determine the relative distribution of tactile sensitivity of the skin. The impulses set up in facial and spinal nerves in response to touching the skin were typically the A-type impulses of Erlanger and Gasser²—rapid impulses of from 10 to 20 microvolts. The lips and barbels were found to be very much more sensitive to mechanical stimulation than was the skin of the flank. Bursts of impulses were initiated from the lips and barbels in response, not only to direct contact, but also to small ripples in the water bathing the skin. Impulses were initiated by a stream of water a few centimeters per second projected toward the skin beneath the surface of the bath.

Maps of the cutaneous areas supplied by the facial nerves on the two sides of the head showed complete bilateral symmetry for the distribution of sensitivity. This symmetry of nerve supply along with the great sensitivity of the lips and barbels to streams of water furnishes a basis for rheotropic orientation according to Loeb's well-known mechanism of bilateral equilibration of central excitatory states (cf. also Jordan³).

The barbels of *Ameiurus* as well as the lips, mouth and skin of the flank possess numerous typical tastebuds^{4.5.6.7} and experiments involving responses to dissolved materials indicate clearly that these organs are extremely sensitive to sapid substances in the water.^{5.8}

Solutions of substances were allowed to diffuse slowly into the water near the skin. Solutions of acetic acid ranging in concentrations from 1 per cent to 20 per cent, a 10 per cent solution of NaCl and a concentrated sugar solution were used as stimuli. In addition, juice pressed from meat which normal catfish devour voraciously was tested. These solutions were allowed to diffuse very slowly against immersed lips and barbels which, before, during and after chemical stimulation were highly responsive to mechanical stimuli. With maximal amplification very indistinct impulses were visible on the screen and were audible from the loud speaker in response to all of the reagents, excepting the sugar solution. These impulses were not produced by tap water or by Ringer solution. Adaptation to the stimulus took place after a few minutes' exposure, but was renewed by reapplication of the solution, except in cases where strong concentrations of acetic acid (75 per cent) had been used initially. This treatment evidently anaesthetized the tastebuds after a minute's exposure.

The marked specificity in magnitudes of potential of the impulses for touch and taste from the same nerve (the "taste" impulses were always less than 10 *per cent* of the amplitude of those set up by touch) may possibly be correlated with the size of the fibres supplying touch and taste receptors.⁹ In *Ameiurus*, according to Herrick,⁶ the tastebuds are primarily innervated by communis components of the 7th cranial nerve. The communis fibres take origin from the geniculate ganglion. The tactile receptors are of the free ending type and are supplied by fibres from the Gasserian ganglion. The cells of the geniculate ganglion are all small, while those of the Gasserian ganglion are, for the most part, large.

Changes of temperature of the water bathing the skin to various levels, between 0° and 28° C., produced no detectable nerve impulses in spinal or facial nerves.

The lateral line system of *Ameiurus* has been described by Herrick⁶ and Brockelbank.¹⁰ (Cf. also Parker^{11, 12}.) The neuromasts or sensory cells lie at intervals along the lateral line canal between the pores which mark exteriorly the course of the canals along the flank. The sensory cells have, at their distal ends, tufts of hair-like processes which project into the lumen of the canal.

Tests of the lateral line nerve showed that the nerve appears to be in a state of continuous spontaneous activity. This was true for 29 out of 32 nerves examined. Since the three inactive nerves failed to respond to any form of stimulation whatever, I have concluded that they were altogether nonfunctional, perhaps as a consequence of the operation. The spontaneous discharge continued unabated, in some preparations, for several hours. The impulses were diphasic but could be rendered monophasic by crushing the nerve under the distal electrode. Anaesthetization of either the nerve or the neuromasts resulted in cessation of the discharge. Lowering the temperature of the nerve in addition, slowed the rate of conduction of the impulses.

The discharge was increased during the direct application of pressure to the skin over the lateral line canal. Ripples in the water caused a corresponding fluctuation of the frequency of discharge. In some preparations slow spinal reflex swimming movements persisted when the trunk was immersed in water. These movements were accompanied by increased frequency of discharge from the lateral line nerves, probably due to pressure on the neuromasts from surrounding tissues.

Parker and Van Heusen¹³ found by means of nerve cutting experiments that the lateral line organs of *Ameiurus* act as mechano-receptors and among other things they respond to low vibration-frequencies of a submerged telephone, up to approximately 350 dvs. per second. To test this effect I pressed activated tuning forks of 100, 200 and 250 dvs. against the outside of the dish containing the preparation. In about 40 *per cent* of the cases no effects were obtained but in the majority of experiments photographs of the responses showed that the randomly discharging neuromasts were apparently synchronized and thrown into a rhythmic beating by the fork. This rhythm varied between 40 to 70 beats per second and never corresponded to the rhythm of the fork, being relatively constant for a given preparation. The synchronization passed with the cessation of the vibrations of the fork, the nerve fibers again discharging at random. Other nerves failed to give this synchronous effect with tuning forks. Cutaneous nerves were made to discharge massively by pressure on the skin. The type of discharge could thus be made temporarily similar to that of the spontaneously firing lateral line nerve. Tuning forks applied to the dish during these discharges never produced synchronization of the response, indicating that the effect was characteristic of the lateral line system and not a rhythmicity set up in the recording system.

The frequency of the spontaneous discharge was found to depend upon temperature between the experimental ranges of 0° to 28°C. By lowering the temperature of the bath in which the preparation was immersed the frequency of discharge was markedly reduced; raising the temperature produced a recovery in the frequency. A quantitative analysis of these records is now in preparation. Since the lateral line system is directly responsive to small temperature changes, and since facial and spinal nerves do not emit impulses in response to mild thermal stimulation, I am led to believe that the neuromasts might act as thermal receptors. According to experiments of Wells¹⁴ normal catfish are very responsive to temperature differences.

The spontaneous activity of the neuromasts is unlike the behavior of any other sensory cells tested, so far as I know. It is possible that the hair-like filaments projecting into the lumen of the canal may actually be cilia which by beating set up a state of continuous excitability in the end-organs of which they are a part. There seems to be no direct evidence concerning this point one way or the other.

¹ Matthews, B. H. C., "A New Electrical Recording System for Physiological Work," J. Physiol., 65, 225-242 (1928).

² Erlanger, J., and Gasser, H. S., "The Action Potential in Fibres of Slow Conduction in Spinal Roots and Somatic Nerves," Am. J. Physiol., 92, 43-82 (1930).

³ Jordan, H., "Rheotropic Responses in Epinephalus striatus Bloch," Am. J. Physiol., 43, 438-454 (1917).

⁴ Herrick, C. J., "Nerves of Siluroid Fishes," J. Comp. Neurol., 11, 177-249 (1901). ⁵ Herrick, C. J., "On the Phylogeny and Morphological Position of the Terminal Buds of Fishes," J. Comp. Neurol., 13, 121-138 (1903).

• Olmstead, J. M. D., "The Results of Cutting the Seventh Cranial Nerve in Ameiurus nebulosus (Les.)," J. Exptl. Zoöl., 31, 368-401 (1920).

⁷ May, R. M., "The Relation of Nerves to Degenerating and Regenerating Taste-Buds," J. Expt. Zoöl., 42, 371-410 (1925).

⁸ Parker, G. H., and Van Heusen, A. P., "The Responses of the Catfish, Ameiurus nebulosus, to Metallic and Non-metallic Rods," Am. J. Physiol., 44, 405-420 (1917).

⁹ Erlanger, J., Bishop, G. H., and Gasser, H. S., "Experimental Analysis of the Simple Action Potential Wave in Nerve by the Cathode Ray Oscillograph," Am. J. Physiol., 78, 537-573 (1926).

¹⁰ Brockelbank, M. C., "Degeneration and Regeneration of the Lateral-line Organs in Ameiurus nebulosus (Les.)," J. Exptl. Zoöl., 42, 293-305 (1925).

¹¹ Parker, G. H., "Hearing and Allied Senses in Fishes," Bull. U. S. Fish Comm., 22, 45-64 (1902).

¹³ Parker, G. H., "The Function of the Lateral-line Organ in Fishes," Bull. Bureau of Fisheries, 24, 183-207 (1904).

¹³ Parker, G. H., and Van Heusen, A. P., "The Reception of Mechanical Stimuli by the Skin, Lateral-line Organs and Ears in Fishes, Especially in *Ameiurus*," *Am. J. Physiol.*, **44**, 463–489 (1917).

¹⁴ Wells, M. M., "Resistance and Reactions of Fishes to Temperature," *Trans. Illinois* Acad. Science, 7, 1–11 (1914).

ACCOMMODATION COEFFICIENT OF GASEOUS IONS AT CATHODES

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The behavior of a cathode in an ionized gas can be studied from three principal points of view: first, electrical relations described by the application of Poisson's equation to the surrounding region; second, thermal relations described by the application of the energy principle to the various processes which develop or absorb heat at the cathode surface; third, pressure reactions which are described by the application of the principle of conservation of momentum at the cathode surface.

The electrical relations were first pointed out by J. J. Thomson¹ and later made more specific and greatly extended by Langmuir and his collaborators.² From these considerations, applied to current-carrying and to exploring electrodes, we have gained a nearly complete picture and interpretation of the phenomena occurring between the electrodes. Of equal importance with this, however, is an understanding of the phenomena occurring at the electrode surfaces, especially at the cathode. For this study we need more information than can be gained from Poisson's equation. We need to know, for example, what fraction of the current at the cathode is carried by electrons emitted from it; what is the mechanism responsible for this emission; if this emission is of thermionic origin, what factors maintain the requisite high temperature, etc. Since there are several unknown quantities, we obviously approach the solution by investigating from several independent points of view, so as to get several independent equations. It is particularly for this reason that studies of energy and pressure relations at a cathode have considerable significance. The most complete analysis of these relations, thus far made, is in a recent paper by the author³ which, while directed particularly at the problem of the mercury arc, is nevertheless generally applicable in principle.

Attempts to investigate cathode phenomena by studying its heat balance