

## SPECIFIC NERVE IMPULSES FROM GUSTATORY AND TACTILE RECEPTORS IN CATFISH

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Investigations in recent years have indicated a certain degree of quantitative specificity of impulses in afferent nerve fibers related to structural properties of the fibers (Erlanger, Bishop, and Gasser, 1926; Erlanger, 1927; Erlanger and Gasser, 1930). This specificity of impulses appears to be correlated, in part, with specific sense modalities (Matthews, 1929; Adrian, 1930, 1931; Adrian, Cattell, and Hoagland, 1931; Hoagland, 1932).

In a recent investigation, for example (Hoagland, 1932), action potentials from single nerve fibers supplying individual receptors in the skin of the frog were examined. Of forty-five receptive endings, thirty-two were found to respond only to light touch and not at all to 20 per cent acetic acid or to crushing, while thirteen responded only to these latter stimuli but not to light touch. The "touch" endings were not destroyed by the acid since they responded to light contact, giving characteristic action potentials in their supplying fibers during the time that the acid was on the skin. Ten other endings responded to both forms of stimulation. The action potentials initiated by stimulating the touch receptors as recorded by a Matthew's amplifier and oscillograph in conjunction with a camera, a loud speaker, and a standing wave screen, were typically of large amplitude and high speed in 75 per cent of the cases,—the *A*-type impulses of Erlanger and Gasser. Impulses initiated by stimuli which in man would be called painful travelled at a slower speed and were only from 5 to 50 per cent of the amplitude of those from fibers supplying tactile organs—the *B*- or *C*-type impulses of Erlanger and Gasser. In about a quarter of the cases this classification did not seem to hold. It was suggested that the specificity, probably correlated with diameter of

nerve fiber, might be a basis for epicritic and protopathic sensibility in the frog.

W. J. Crozier recently pointed out to me that catfish are known to be very sensitive to chemical stimulation and that an investigation of impulses set up by stimulating taste-buds located in the barbels might be of interest. The barbels of *Ameiurus*, as well as the lips, mouth, and skin of the flank possess numerous typical taste-buds (Herrick, 1901, 1903; Olmsted, 1920; May, 1925) and experiments involving responses to gustatory stimuli indicate clearly that these organs are extremely sensitive to sapid substances in the water (Herrick, 1903; Parker and Van Heusen, 1917).

#### *Responses to Mechanical Stimulation*

The facial nerve complex of *Ameiurus nebulosus* Les., described in detail by Herrick in his paper of 1901, was bared by removing the eye in freshly decapitated catfish. The nerve leaves the skull sub-orbitally and sends a number of branches forward to the upper and lower lips and to the barbels. By clearing away connective tissue the myelinated branches of the nerve, some 5 to 8 mm. in length, may be separated from each other and their electrical responses tested by stimulating the skin supplied by them. Facial nerves in some twenty catfish were examined by drawing branches of the nerves across silver, silver-chloride electrodes connected through two amplifiers containing in all eight valves, resistance-capacity coupled, to a Matthews' iron armature oscillograph (Matthews, 1928). The impulses were recorded by means of a standing wave screen, a loud speaker connected to the output amplifier through an auxilliary amplifier, and a camera using moving bromide paper.

After drawing a branch of the nerve to be tested across the electrodes, a map of the cutaneous area of sensitivity supplied by it was determined by touching the barbels and lips and listening to the bursts of impulses on the loud speaker. In this way the sensitive areas for each branch of the nerve were clearly determined. The nerve and incision were kept bathed with Ringer's solution and the lips and barbels were stimulated while immersed in water. They were found to be extremely sensitive to mechanical stimuli—bursts of rapid impulses of large amplitude being set up in response to slight disturbances in

the water. In time relations the impulses were typical of the *A*-type impulses of Erlanger and Gasser (1930) produced in the cutaneous nerves of frogs in response to mechanical stimulation of the skin (Adrian, 1931; Hoagland, 1932).

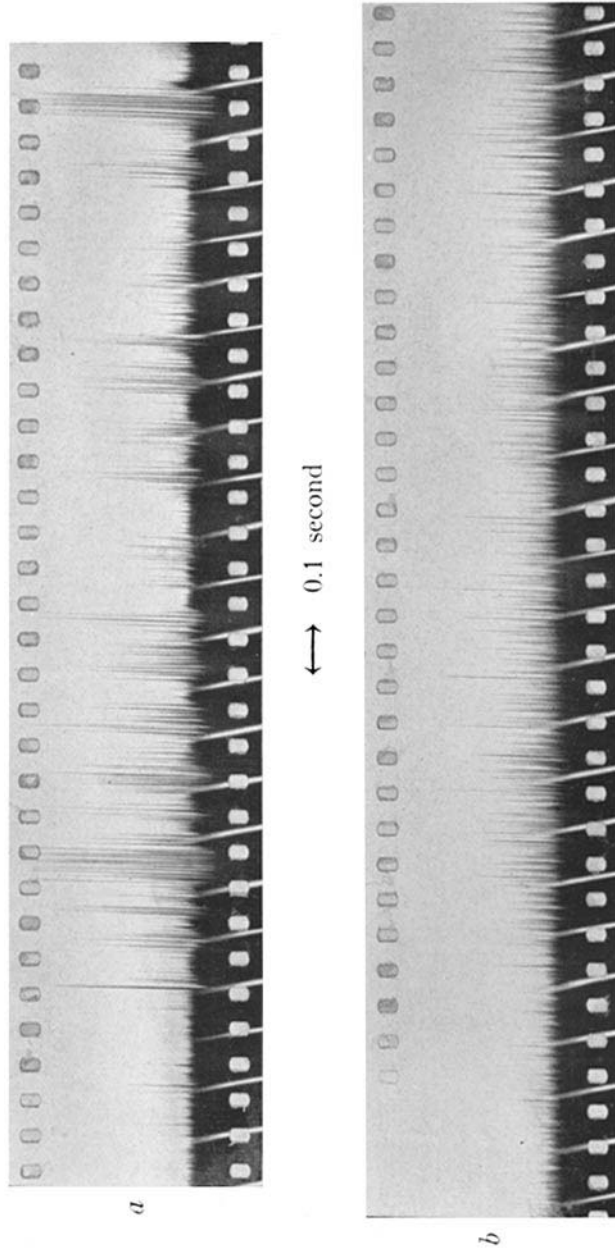
Fig. 1 shows typical records of action currents in response to (*a*) touching the barbels, (*b*) to the impact of a gentle stream of water from a pipette discharged beneath the water, a centimeter from the preparation towards a barbel at a rate of 5–10 cm. per second, and (*c*) to ripples in the water. In some preparations reflex bendings of the barbels occurred spontaneously. These movements were accompanied by bursts of impulses, an example of which is shown in Fig. 1 *d*. It is impossible to say whether impulses such as those of 1 *d* were produced exclusively from pressure receptors stimulated by the movement of the barbel through the water or by muscle spindles in the barbel. Both types of receptors may have been involved. Owing to the sensitivity of the barbel to relative motion of the water it seems certain that tactile receptors were stimulated.

No responses were elicited from the cutaneous receptors of the barbels or lips by tuning forks pressed against the outside of the dish or thrust into the water bathing the preparation. Forks of 100, 200, and 250 double vibrations were tried.

#### *Rheotropism*

Groups of *Ameiurus* (at least two fishes), when in an aquarium with which they were familiar, were found to orient and swim treadmill fashion against a stream of water entering at one end of the tank and passing out at the other. This phenomenon is manifest when care is taken to eliminate influences of light since *Ameiurus* appears to be negatively phototropic. 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. The forward parts of the large maxillary barbels especially at the middle third of their length were found to be extremely sensitive to mechanical stimuli, as judged from the volume of impulses initiated by currents of water and by stroking the skin.

This symmetry of sensitivity furnishes a basis for rheotropic orientation according to Loeb's well known mechanism of bilateral equaliza-



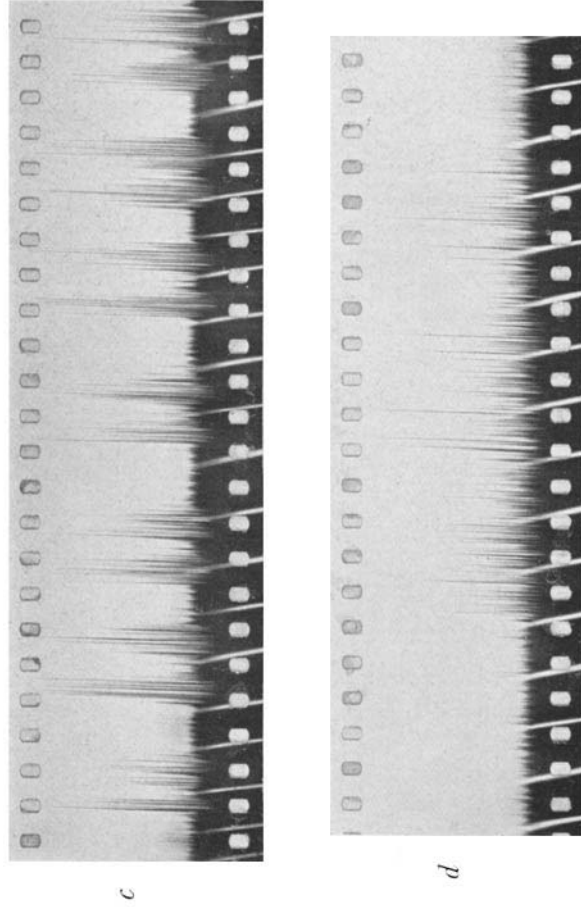


FIG. 1. Typical impulses from an immersed barbel of *Ameiurus* in response to mechanical stimulation. The lips and barbels all give similar responses and are about equally sensitive.

- (a) Bursts initiated by touching the skin with a feather. The response is the same for immersed barbels as for those in the air.  
 (b) Effect of a current of water (5–10 cm./second) from a pipette. A similar effect is produced by pressing against a barbel.  
 (c) Bursts set up by rippling the water.  
 (d) Impulses due to reflex movement of the barbel in the water.

tion of central excitatory states. The findings are consistent with the experiments of Jordan (1917) on the rheotropism of the grouper fish *Epinephelus*, which he found to depend upon integumentary sensitivity, especially the sensitivity of the lips.<sup>1</sup> Maxwell (1921 *a*, 1921 *b*) has shown that contact stimuli applied to the skin of the snout and head produce systematic orienting movements of the swimming appendages of the skate and dogfish. The effects are also produced by streams of water from a pipette. The importance of rheotropic orientation in large scale movements of fishes such as the upstream spawning migrations of salmon (*e.g.*, Ward, 1927, 1928) makes this mode of orientation one of especial interest.

#### *Responses to Chemical Stimuli*

Experiments with gustatory stimuli yielded surprising results since with the amplification ordinarily used dissolved substances in the water were found, apparently, to initiate no nerve impulses from the barbels and lips. Acetic acid solutions ranging in concentrations from 1.0 per cent to 20 per cent, a 10 per cent solution of NaCl, and a saturated solution of sugar 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. By adjusting the potentiometer controlling the sensitivity of the output amplifier to yield maximum sensitivity, very indistinct impulses were visible on the screen in response to chemical stimulation against the background of a very ragged base line. Photographs of these impulses, however, were not very convincing since the camera speed was slow compared to that of the standing wave screen and the impulses were largely ob-

<sup>1</sup>Loeb (1918) did not apply the notion of bilateral tactile stimulation as a basis for rheotropism. He preferred to explain the upstream orientation of fishes in terms of movements of retinal images in the opposite direction to that of progression—a sort of nystagmus phenomenon. In cases of “treadmill” rheotropism in which swimming takes place without forward progression, no movements of retinal images occur. While the movement of retinal images undoubtedly explains certain cases of apparent rheotropism (Lyon, 1904, 1905, 1909) it is certainly only a partial explanation.

literated by the fluctuation of the base line. The fact that impulses of extremely low potential were being initiated was best indicated by the loud speaker since characteristic sounds were produced lasting sometimes as much as several minutes after exposure of the receptors to all of the above solutions with the exception of the sugar solution. The sounds were not produced by tap water or by Ringer's solution—they were renewed by reexposure to the stimulus, except in cases of exposures to very strong acid (concentrations > 5 per cent). This treatment evidently anesthetized or destroyed the taste-buds after about a minute's exposure.

The striking thing about these results is that they indicate a high degree of quantitative specificity of impulses for taste in *Ameiurus nebulosus* Les. The amplitude of the impulses for taste are at the very threshold of sensitivity for present recording systems; they are of the order of 5 microvolts. They show roughly less than 10 per cent of the amplitude of the impulses initiated in different fibers of the same nerve in response to mechanical stimulation.

Since, in general, small action potentials are produced by small fibers and large action potentials by large fibers, one is led to suspect that fiber size may be the basis of the impulse specificity in this case. Herrick (1901) pointed out that the mandibular and maxillary branches of the trigeminus both receive general cutaneous and communis fibers in approximately equal proportions and furnish all of the barbels with fibers from these two systems. In *Ameiurus*, as indeed in siluroids and cyprinoids in general, the taste-buds are primarily innervated by the communis components of the 7th cranial nerve and to a lesser extent by components of the 9th and 10th cranial nerves. The communis fibers to the taste-buds take origin from the geniculate ganglion. The tactile endings in *Ameiurus* are of the free-ending type and are supplied by fibers from the Gasserian ganglion. To quote from Herrick (1901, p. 183): The cells of "the geniculate ganglion are all small, so that the general relations of the two ganglia can be determined despite their intimate fusion." This difference in size of the cells of origin which send axons to the taste-buds and to tactile endings respectively may therefore serve as a basis for the specificity in magnitude of potential of the impulses for the two sense modalities.

## SUMMARY

1. Receptors in the lips and barbels of the catfish *Ameiurus nebulosus* Les. are very sensitive to mechanical stimuli, giving large rapid (A-type) impulses in fibers of the facial nerve in response to touching the receptive surfaces and to movements of the water in which the preparation is immersed.

2. The great sensitivity of the barbels and lips to currents of water and the bilateral symmetry of the distribution of sensitivity of the facial nerve may serve as a basis for observed rheotropic orientation in the catfish.

3. Acetic acid, NaCl, and meat juice, dissolved in the water bathing the barbels and lips, set up impulses of very small and barely detectable potential in the fibers of the facial nerve.

4. It is suggested that the specificity of impulses for the two sense modalities may be correlated with the large size of the cells of origin of the axons in the Gasserian ganglion supplying tactile receptors and the small size of the cells of origin in the geniculate ganglion sending axons to taste-buds.

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