Contributions from the Biological Laboratory of the U. S. Fish Commission
at Woods Hole, Massachusetts.

# THE ORGAN AND SENSE OF TASTE IN FISHES.

By C. JUDSON HERRICK,
*Professor of Zoology in Denison University.*



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## CONTENTS.

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## INTRODUCTION.

The practical problems connected with the fisheries have been attacked (and in large measure successfully solved) by a rough-and-ready application of the method of trial and error, and the scientific investigator has merely to follow after and explain why a given form of trap or method of lure is successful with one species of fish and not with another. But there remain many unsolved problems of great economic importance, and it is the function of scientific research to contribute to the solution of these problems in a more orderly and economical manner, even though it often happens that the investigator best qualified to solve the scientific problem has not the practical knowledge of fishery matters necessary to apply his own results to economic problems, and so his facts have to be worked over from the other point of view before they become practically useful.

We are, in fact, profoundly ignorant of the senses and instincts of the fishes, even those connected with their feeding habits, which are of so direct importance to all commercial fisheries. Nearly all which one finds in the scientific literature bearing on the senses of fishes is merely inference of function based on a study of the structure of the organs—a most precarious pathway for scientific research. My own studies on the nerve components of fishes have led me to certain inferences regarding the functions and the distribution of the organs of taste in fishes, and the present study is an attempt to follow out these inferences by the determination of more exact facts regarding the pathways of gustatory stimuli as anatomically demonstrable, together with sufficient direct physiological experiment to furnish definite information of the function served by this system of sense organs and of their nervous paths in the fishes.

Neurologists have always paid a great deal of attention to the conduction paths within the central nervous system, and in recent years special efforts have been made to isolate the various functional systems of neurones, tracing the exact path of the sensory impulses from the peripheral organ to the primary sensory center, thence to the various secondary centers and return reflex paths. This motive underlies the recent studies on the nerve components and, indeed, much of the best morphological work on the nervous system in all times.

Some years ago I formulated the following definition of such a functional system of neurones, with special reference to the peripheral members of the system:

> The sum of all the nerve fibers in the body which possess certain physiological and morphological characters in common so that they may react in a common mode. Morphologically each system is defined by the terminal relations of its fibers, by the organs to which they are related peripherally, and by the centers in which the fibers arise or terminate. The fibers of a single system may appear in a large number of nerves repeated more or less uniformly in a metameric way (as in the general cutaneous system of the spinal nerves), or they may all be concentrated into a single nerve (as in the optic nerve).

Now, if we add to this the secondary paths related to the primary central end stations referred to above, and the chief reflex arcs directly associated therewith, we shall have a picture of the system in its entirety.

The functional system with which we are especially concerned in the present research is that known to comparative anatomy as the communis system, including (1) unspecialized visceral sensory fibers ending free in the mucous surfaces of various viscera without special sense organs—probably phylogenetically the more primitive elements—and (2) specialized sensory fibers always ending in connection with highly differentiated sense organs in the mouth, pharynx, lips, or outer skin, known as taste buds, terminal buds, or end buds, and in general serving the function of taste. These specialized elements are probably of more recent phylogenetic origin than the first group, and the term "gustatory system" will be used to designate these organs, wherever placed on the body surface, together with their nervous pathways toward and within the brain. In other words, the gustatory system is that portion of the communis system of neurones which serves the sense of taste, as distinguished from those communis neurones which serve less highly specialized visceral sensations.

These two groups of fibers can easily be distinguished peripherally of the brain, but centrally they have not as yet been successfully analyzed. Hence in treating of the central gustatory path we can not be sure that we do not include the unspecialized visceral system also. But since in some fishes the gustatory fibers preponderate many fold over the unspecialized fibers of the communis system, there is no ambiguity arising from this central confusion of the two elements so far as the gustatory system is concerned, since the secondary paths as clearly traceable in these fishes must be made up chiefly of gustatory fibers.

The central gustatory path is not definitely known either in man or in any other vertebrate, so far as shown by the available literature. I have therefore studied with some care the brains of some fishes in which this system is enormously developed, in the hope that they would throw light on this unsolved problem of vertebrate anatomy. And in this I have not been disappointed, though my study of the central paths is not yet sufficiently advanced for publication.

As intimated above, sense organs belonging to the communis system and presumably serving the function of taste are found in the mouths of all fishes ("taste buds"). They are frequently found upon the lips, and in some cases they are found likewise plentifully distributed over extensive areas of the outer skin of the head and trunk. In this latter case they are commonly termed terminal buds or end buds (*Endknospen*, *Becherorgane*, of the Germans). They must in all cases be sharply distinguished from the neuromasts, or organs of the lateral-line system (German, *Nervenhügel*), though these latter occur in the skin of fishes in a great variety of forms, often resembling the terminal buds very closely. The innervation and functions of the two systems of organs are, however, wholly different, and they really have nothing to do with each other. I shall illustrate more fully in a later section of this paper the structure of the terminal buds and the details of their innervation. I here call attention merely to the important fact that both in structure and in nerve supply they resemble most closely the taste buds of the mouth. From this one naturally infers for them a gustatory function. Since, however, inferences are not in order when facts are available, I have undertaken to determine experimentally the function of these cutaneous sense organs of the communis system.

The experiments which I have made are of an exceedingly simple nature, the attempt being to put the fish while under observation in as nearly normal conditions as possible and to utilize the ordinary feeding and other instinctive reactions so far as possible in the accumulation of the data. These are the methods of the old-time observational natural history, it is true, as contrasted with the methods of precision of the modern physiological laboratory. They have, however, proved sufficient for their purpose, which was merely to determine the class of stimuli to which the terminal buds are sensitive, or the sensational modality which they serve, rather than to contribute to the chemical physiology of taste in general.

The chief obstacle to experiments of this sort, and one which many observers seem to have made no serious efforts to overcome, is the natural timidity or shyness of wild creatures when kept in the confined and unnatural quarters necessary for close observation. The rôle played by fear in animal behavior has been vividly brought to our notice by Whitman ('99), and, like this observer, I find that young animals which have been reared in captivity are much more approachable and tractable under experimental conditions than adults which have been reared in their natural freedom. In fact, with several species I quite failed to get the adults to take food at all in captivity, though they were under observation for long periods.

## REVIEW OF LITERATURE.

Surprisingly little attention has been paid to the physiology of taste in fishes, and this literature is very scanty. On the other hand, the anatomical investigation of these sense organs has been extensively followed for nearly a century, though often in a blind and profitless way. The history of opinion upon the significance of these sense organs has been quite fully given by Merkel ('80) in his great monograph published in 1880, and the earlier phases of this history need not be again reviewed further than to mention a few salient features.

In 1827 Weber observed the taste buds on the peculiar palatal organ of the carp and correctly interpreted their function. He also figured the brain of the carp, illustrating the enormous vagal lobes from which these taste buds receive their innervation. Leydig discovered in 1851 the terminal buds of the outer skin of fishes and gave a detailed account of their structure, which subsequent research has shown to be in some respects inaccurate. In 1863 F. E. Schulze gave a more accurate description of the "*becherförmigen Organe*" of fishes, in which he distinguished the specific sensory cells from the supporting cells. He also correctly inferred their function to be similar to that of taste buds within the mouth, viz, the perception of chemical stimuli.

In 1870 the same author (F. E. Schulze, '70) made a further important contribution to the problem of the terminal buds by the demonstration that they differ structurally from all neuromasts, or organs of the lateral-line system. The neuromasts are commonly sunken below the skin in canals, tubes, or pits, but in some cases they are strictly superficial and resemble in external form the terminal buds very closely—a feature which led Leydig ('51, '79, '94) and others to assume that the two classes of organs are mere varieties of a common type. Schulze showed that the neuromasts can in all cases be differentiated from the terminal buds by the fact that their specific sensory cells (pear cells) extend only part way through the sensory epithelium and fail to reach the internal limiting membrane, while in the terminal buds both specific sensory cells and supporting cells pass through from external to internal limiting membrane.

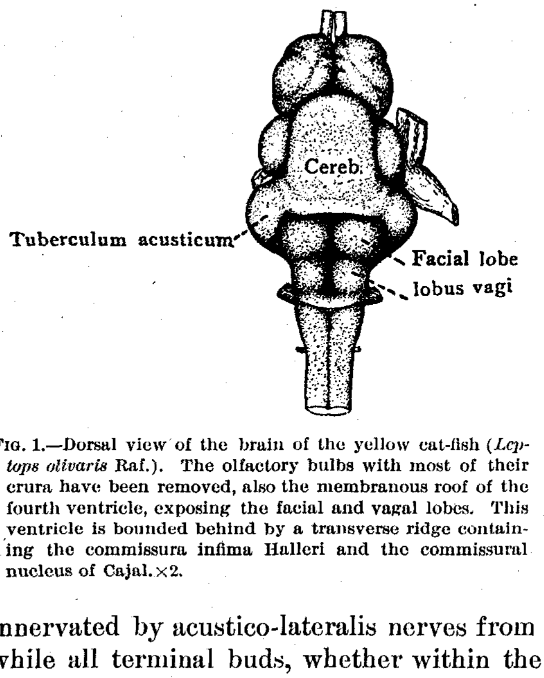


FIG. 1.—Dorsal view of the brain of the yellow cat-fish (*Leptops olivaris* Raf.). The olfactory bulbs with most of their crura have been removed, also the membranous roof of the fourth ventricle, exposing the facial and vagal lobes. This ventricle is bounded behind by a transverse ridge containing the commissura infima Halleri and the commissural nucleus of Cajal. ×2.

This distinction was confirmed by Merkel ('80), who, with curious inconsistency, while recognizing the structural dissimilarity of the two classes of organs, nevertheless, as we shall see below, ascribes to both essentially the same function, touch. This matter was put to the decisive test in my contribution on *Ameiurus* ('01), a type which possesses both terminal buds and neuromasts in great abundance and diversity of forms. Schulze's contention is supported both by the structure of the organs and by their innervation, for I have shown that all neuromasts of whatever form are innervated by acustico-lateralis nerves from the tuberculum acusticum of the brain, while all terminal buds, whether within the mouth or in the outer skin, are innervated by communis nerves related centrally to a single center within the brain. This center is bilobed, the lobus vagi receiving most of the communis fibers from the mouth cavity by way of the vagus and glossopharyngeus and the lobus facialis the communis fibers from the terminal buds of the outer skin by way of the facial nerve (cf. fig. 1).

Similar terminal buds have been found in the outer skin of many species of Teleostomes and in Cyclostomes, but, so far as certainly known, nowhere else among vertebrates (save on the lips of some other classes). Their distribution among the fishes is very irregular, being most abundant among the siluroids, cyprinoids, ganoids, and cyclostomes, in general bottom fishes of sluggish habit, often living in mud and rarely belonging to the predaceous types which find their food chiefly by the sense of sight. The following list of fishes which have been shown to possess terminal buds on the outer skin is by no means complete, but will serve to illustrate the wide range of species which have acquired this peculiarity:

*Fishes possessing terminal buds on the outer skin.*

*Acerina.* On fins and body (Merkel, '80).
*Acipenser sturio*, sturgeon. On barbel (Merkel, '80). Also other sturgeons.
*Agonus cataphractus*, pogge. On the villiform tentacles beneath the head (Bateson, '90).
*Ameiurus melas*, cat-fish, and other North American Siluridæ. On barblets and nearly the whole body surface (Herrick, '01).
*Amia calva*, bowfin. On skin of head and other parts (Allis, '97).
*Anguilla vulgaris*, eel. On the fins, lips, and anterior nostril (Merkel, '80; Bateson, '90).
*Aspius alburnus* (Merkel, '80).
*Barbus fluviatilis.* On barblet (F. E. Schulze, '63).
*Branchiostoma lanceolatum* = *Amphioxus lanceolatus*, lancelet. On the oral cirri (Merkel, '80).
*Carassius auratus*, gold-fish. On the whole body (numerous authors; Herrick).
*Cephalacanthus* = *Cobitis fossilis*, flying gurnard (Merkel, '80).
*Cottus scorpius*, sculpin. On fins (Merkel, '80).
*Cynoscion* = *Corvina* (Merkel, '80).
*Cyprinus carpio*, carp, and other cyprinoids. On whole body (Merkel, '80, and others).
*Dactylopterus* (Merkel, '80).
*Discognathus lamta*, Indian carp. Over the whole body surface (Leydig, '94).
*Enchelyopus* = *Motella*, four-bearded rockling. On barblets and pelvic fins (Bateson, '90).
*Gadus callarias*, cod. On lips, barbel, fins, and body (Merkel, '80; Herrick, '00).
*Gadus luscus*, pouting. On the lips, barblet, and pelvic fins (Bateson, '90).
*Gadus merlangus*, whiting. On lips (Bateson, '90).
*Gadus pollachius*, pollack. On lips (Bateson, '90).
*Gaidropsarus* = *Motella*, three-bearded rockling. On all the barblets and pelvic fins (Zincone, '78; Bateson, '90).
*Gobius*, goby. On fins (Merkel, '80).
*Hippocampus*, sea horse (Merkel, '80).
*Leptocephalus conger*, conger eel. On the outer and inner lips (Bateson, '90).
*Leucaspius delineatus.* On the body generally (Leydig, '94).
*Leuciscus dobula* (Leydig, '57).
*Lota vulgaris*, ling. On barblet (Merkel, '80).
*Mullus barbatus*, mullet. On barblet (Zincone, '78; Merkel, '80).
*Petromyzon fluviatilis*, lamprey. On skin of whole body (Merkel, '80, and others).
*Pygosteus* = *Gasterosteus pungitius*, stickleback (Merkel, 80).
*Rhodeus amarus.* On the body generally (Leydig, '94).
*Scorpæna* (Merkel, '80).
*Silurus glanis*, cat-fish (Merkel, '80).
*Solea vulgaris*, sole. "Contrary to the natural presumption, the villi on the lower (left) side of the head do *not* bear sense organs, though, as Mr. Cunningham informs me, such organs are found between the villi" (Bateson, '90).
*Tinca vulgaris*, tench. On barblet (Merkel, '80).

As already suggested, our knowledge of the functions of all of the sense organs of fishes is very imperfect, since speculation based upon structure has seemed more attractive to most authors than accurate physiological research. The monograph of Merkel ('80), with its great wealth of accurate anatomical data on the structure and distribution of terminal buds in all classes of vertebrates, gives an excellent illustration of the dangers in the path of even so skillful an observer when he goes beyond the bounds of observed fact and enters the field of speculation. This author recognizes the close structural resemblance between these organs and the undoubted organs of taste in the human body. He controverts, however, the clear argument of F. E. Schulze for their gustatory function on merely theoretical grounds. His first objection is based on their innervation. Instead of being supplied by a single gustatory nerve, the glossopharyngeus, they may be supplied, he says, by any other body nerve. This objection has been totally removed by the discovery (compare especially my own *Ameiurus* paper, already referred to, published in October, 1901) that all terminal buds, no matter where located on the body and no matter from what nerve branches their innervation seems to come, are in reality supplied by nerves of a single physiological system, terminating in the brain in a single center—the communis nerves.

Again, he objects to Schulze's theory that the terminal buds serve to localize gustatory stimuli on the various parts of the body, on the ground that an organ of chemical sense stimulated by substances in solution in the environing fluid could not receive a sufficiently circumscribed stimulation. It is unnecessary to follow the argument in detail, for the experiments which I shall describe shortly show conclusively that when the sapid substance is brought into contact with these organs or very near to them the stimulus is accurately and very promptly localized, and in fact some of the fishes studied habitually find their food by this very power, the gustatory stimulus calling forth an immediate reflex movement toward the point stimulated. It is probable that the local sign is not given by the gustatory (communis) nerves, but by the accompanying tactile (general cutaneous) nerves of the corresponding cutaneous area (which general cutaneous nerves Merkel, curiously enough, denies to the fishes altogether, whereas, in fact, they are plentifully supplied to all parts of the skin), though my experiments do not decisively answer this question.[a] Weak stimuli, especially when uniformly diffused through the water, are, it is true, not at all localized; but strong stimuli are unquestionably localized by one method or another.

In fact, Merkel agrees with Jobert that the terminal buds of the outer skin are tactile in function. This is based largely on the erroneous belief, referred to above, that there are no free tactile nerve endings in the skin of fishes, and also on the observed tactile sensibility of the barblets and other parts of the body known to be most plentifully supplied with terminal buds. But I have shown that all of these parts of the body receive, in addition to communis nerves for the specialized sense organs, a most liberal general cutaneous innervation for tactile sensibility; and the experiments which follow go to show practically that these two functions commonly cooperate in setting off the reflex of seizing food, though they may be experimentally isolated.

Merkel now proceeds to carry his argument to its logical conclusion (and likewise to a *reductio ad absurdum*) by denying the gustatory function to all terminal buds, even those within the mouth supplied by the glossopharyngeal nerve, of all vertebrates below the *Mammalia*.

He finally concludes that both the neuromasts of the lateral-line system and the terminal buds are tactile organs, the buds being the more delicate; but if these are deficient, then the neuromasts may be elevated to a more delicate functional value; both of which conclusions, in the light of our present knowledge, illustrate the dangers attending an attempt to determine function on the basis solely of observed structure, without adequate physiological control.

The general works contain numerous references to the subject, but usually chance observations or speculative conclusions. Günther says, under the caption "Organ of taste":

> Some fishes, especially vegetable feeders, or those provided with broad molar-like teeth, masticate their food; and it may be observed in carps and other cyprinoid fish that this process of mastication frequently takes some time. But the majority of fish swallow their food rapidly and without mastication, and therefore we may conclude that the sense of taste can not be acute. The tongue is often entirely absent, and even when it exists in its most distinct state it consists merely of ligamentous or cellular substance, and is never furnished with muscles capable of producing the movements of extension or retraction, as in most higher vertebrates. A peculiar organ on the roof of the palate of cyprinoids is perhaps an organ adapted for perception of this sense; in these fishes the palate between and below the upper pharyngeal bones is cushioned with a thick, soft, contractile substance, richly supplied with nerves from the Nervi vagus and glossopharyngeus.

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[a] On this point, see the further experiments recorded in the Addendum, pp. 270-271.

Regarding the peculiar palatal organ of the cyprinoids, it has been known since Weber's account in 1827 that this is plentifully supplied with taste buds, and Weber himself brought forward strong indirect evidence that its function is gustatory. The following observations (and many similar ones might be cited from the literature of sport) are taken from the section on "The Trouts of America," by William C. Harris, in the American Sportsman's Library.

The angler can not resist the belief that the senses of smell and taste are well developed in trout. They eject the artificial fly, if the hook is not fast in the flesh, at the instant they note its nonedible nature, or when they feel the gritty impact of the hook. They will not eat impure food, and they have the faculty of perceiving odors, and various scents attract or repel them. This has been verified from the earliest days of our art, when ancient rodsmen used diverse and curious pastes and oils, which were seductive to fish; in Walton's day, and long after, this practice was followed and the records tell us of its success. When I was a boy and the Schulkill River was swarming with the small white-bellied cat-fish, than which no more delightful breakfast food ever came out of the water, the only bait used to catch them was made of Limburger cheese, mixed with a patch of cotton batting to hold it firm on the hook. No other lure had the same attraction for them because, no doubt, of the decided odor of the cheese.

The problems connected with the relative significance of the several sense organs of the fishes have been treated both anatomically and experimentally in the excellent paper of Bateson ('90). After anatomical remarks, based largely on his own careful studies, on the eyes, olfactory organs, and gustatory organs, he recounts a series of admirable and well-considered experiments made to test the parts played by these organs in the normal feeding of various kinds of fishes.

These observations are grouped under two chief heads, viz, "Senses of fishes which seek their food by scent" and "The senses of fishes which seek their food by sight." Though the taste buds in the mouth and outer skin are described and correctly interpreted in the anatomical part of the paper, these organs are scarcely considered at all in the physiological part, and this is really the greatest weakness of the paper. Since my own observations in part follow so closely in the footsteps of Bateson (though completed in the main before his paper was accessible to me), and since they are in general confirmatory of his, it will be of interest to review portions of his paper at this time.

He gives the following list of fishes which he has observed "to show consciousness of food which was unseen by them, as, as will hereafter be shown, there is evidence that they habitually seek it without the help of their eyes":

*Protopterus annectens*, mud-fish.
*Scyllium canicula*, rough dog-fish.
*Scyllium catulus*, nurse-hound.
*Raja batis*, skate.
*Conger vulgaris*, conger eel.
*Anguilla vulgaris*, eel.
*Motella tricirrata*, three-bearded rockling.
*Motella mustela*, five-bearded rockling.
*Nemacheilus barbatula*, loach.
? *Lepadogaster gouanii*, sucker.
*Solea vulgaris*, sole.
*Solea minuta*, little sole.
*Acipenser ruthenus*, sterlet.

He says: "To this list may almost certainly be added the remainder of the *Raiidæ*, together with the angel-fish (*Rhina squatina*) and *Torpedo*." Unfortunately, however, Bateson in his list does not distinguish between those fishes in which smell obviously plays the leading part and those in which taste or touch or both are used to compensate for the reduction of vision, and it is this defect which it is hoped that the present contribution may in part correct.

Most of the forms in the list above are more or less nocturnal animals, but they differ much in this regard. The part attributed to the sense of sight and smell in Bateson's studies is so similar to my own conclusions in many respects that it seems fitting to quote the greater part of his description, especially since the species observed by us are in all cases different. He says:

None of these fishes ever start in quest of food when it is first put into the tank, but wait for an interval, doubtless until the scent has been diffused through the water. Having perceived the scent of food, they swim vaguely about and appear to seek it by examining the whole area pervaded by the scent, having seemingly no sense of the direction whence it proceeds. Though some of these animals have undoubtedly some visual perception of objects moving in the water, yet at no time was there the slightest indication of any recognition of any food substance by sight. The process of search is equally indirect and tentative by day and by night, whether the food is exposed or hidden in an opaque vessel, whether a piece of actual food is in the water or the juice only, squeezed through a cloth, and, lastly, whether (as tested in the case of the conger and the rockling) the fish be blind or not. * * * The perceptions, then, by which these animals recognize the presence of food are clearly obtained by means of the olfactory organs and apparently exclusively through them. I was particularly surprised to find no indication of the possession of such a function by the sense organs of the barbels and lips or by those of the lateral line. As has been already described, the pelvic fins and barbels of the rocklings (*Motella*) and the lips, etc., of most fishes bear great numbers of sense organs closely comparable in structure with the taste buds of other vertebrates. No one who has seen the mode of feeding of the rockling or pouting (*Gadus luscus*) can doubt that these organs are employed for the discrimination of food substances; but the fact already mentioned, that the rockling in which the olfactory organs had been extirpated did not take any notice of food that was not put close to it, points to the conclusion that they are of service only in actual contact with the food itself.

Bateson gives also a considerable list of fishes which he has observed to get their food chiefly by the sense of sight, and he is doubtless correct in asserting that the majority of fishes belong to this class. None of these sight-hunting fishes while living in his tanks appeared able to see their food by night, or even in twilight. None of the fishes which he enumerates as belonging to this class showed symptoms of interest when the juice of food substances was put into the water, and other evidence is brought forward to show that the sense of smell plays little or no part in helping them to discover their food.

I have not studied any of the species mentioned by Bateson, but for the forms studied by me, which have an extensive supply of terminal buds on the outer skin, I fully confirm most of the statements quoted above, save that in determining the part played by sight I did not blind any of my fishes and save that the statement that in fishes of his first group "at no time was there the slightest indication of any recognition of any food substance by sight" is strictly true of none of my fishes except *Ameiurus*, though in some of the other cases it is approximately true.

The only important respect in which my observations are not in harmony with those of Bateson is in connection with the part played by the sense of taste in some of these types of fishes. I have studied the gustatory reactions of fishes closely allied to the rockling and having the same arrangement of terminal buds on the barblets and pelvic fins, and am convinced that Bateson's failure to get clear gustatory reactions from these organs was due to the insufficiency of his methods of experiment rather than to the absence of the function. In general, it may be stated that the part played by the gustatory reflex in the case of fishes having an extensive supply of terminal buds on the outer skin is of vastly greater importance than Bateson appears to have recognized.

The only other paper of importance dealing with the sense of taste in the fishes experimentally which has come to my notice is the great monograph on the senses of taste and smell by Nagel ('94). He investigated the sense of taste in the following fishes:

(1) FRESH-WATER TYPES: *Anguilla anguilla* (old and quite young); *Cyprinus carpio; Barbus fluviatilis; Leuciscus cephalus; Gasterosteus aculeatus; Gobius fluviatilis; Silurus glanis* (young specimen); *Cobitis fossilis.*

(2) MARINE TYPES: *Pristiurus; Scyllium catulus* and *S. canicula; Syngnathus acus; Uranoscopus scaber; Lophius piscatorius.*

Nagel tested all the fresh-water fishes mentioned in this list by bringing bitter, sour, sweet, and salty solutions in contact with the skin, without getting any response to the stimulus. Thus, the carp, wels (*Silurus*), and stickleback did not respond to a stimulation of the skin of the body with quinine, though the last-named fish gave an immediate response when the solution touched the lips. He concludes:

In the fresh-water fishes, according to my observations, the power of taste is completely lacking in the outer skin; or, more precisely, in no part except the head is there gustatory sensibility.

For such of these forms as possess no terminal buds on the skin of the body this is doubtless true; but for the other fishes, including, doubtless, *Silurus* and *Cyprinus*, it is certainly a mistake. In gadoid fishes I got a clear reaction against quinine solution when it was applied to the free fin rays, which are known to be supplied with terminal buds, but not from other parts of the skin.

Among the elasmobranch fishes Nagel found *Scyllium catulus* and *S. canicula* to be sensitive to very dilute solutions of vanilla all over the body and fins. Bitters were not perceived thus, nor oil of rosemary, but they are very sensitive to creosote. He controverts Schwalbe's argument that the terminal buds of the outer skin of fishes probably have a gustatory function by reason of the similarity of their structure with that of taste buds in the mouth, and concludes:

A real sense of taste, such as man and many other animals have in the mouth, appears to be absent in the outer skin of all fishes and Amphibia.

It will appear from the following pages that this conclusion is erroneous. I will merely add here that if Nagel had worked with sapid solutions, with which his fishes were presumably already familiar, instead of with substances like sugar and vanilla, toward which no clearly established reflexes had been established in the natural environment of the fishes, his conclusions might have been different.

## TERMINAL BUDS AND THEIR INNERVATION.

The terminal buds of the fishes tabulated above, and doubtless many others which might be mentioned, are of the same type and presumably provided with similar innervation by communis nerves, for cutaneous branches of the communis root of the facial nerve are known to reach the areas provided with the buds in all cases which have been adequately studied. These organs may therefore all be defined morphologically as belonging to the communis system of sense organs, along with the taste buds of the mouth cavity and as distinct from the lateral-line organs and all other types of sense organs. In order to support this position there remains merely the proof that the terminal buds and taste buds have a similar function. This evidence is presented subsequently in this paper.

The terminal buds of fishes have been often described and figured, and I have little to add to the classical descriptions save in the matter of distribution and innervation. Those in the mouth are supplied by branches of the x, ix, and vii pairs of cranial nerves, the first two nerves supplying those in the gill regions and the pretrematic branch of the glossopharyngeus also running forward to supply those on the hyoid arch (tongue). The communis root of the facialis (= portio intermedia of human anatomy) and its geniculate ganglion supply the taste buds on the palate by the r. palatinus facialis (= great superficial petrosal nerve of man), and other buds on the lining of the cheek, on the jaws, and on the lips by other branches, some of which are secondarily associated with branches of the trigeminus and most of which have no homologues in mammalian anatomy, though some one or more of them probably represent the chorda tympani.

In *Ameiurus* I have shown ('01) that terminal buds occur in the skin of practically the whole body surface, most abundantly on the barblets and diminishing in frequency toward the tail. These buds (see fig. 2) rest on a low papilla of the dermis, quite different from that figured by Merkel ('80, plate v, fig. 1) for the terminal buds of *Silurus*. His figure shows a much smaller organ, resting upon a greatly elongated papilla in an epidermis which is apparently thicker than in *Ameiurus*. Merkel states ('80, p. 72) that terminal buds always occur on such a dermal papilla. While this is certainly the general rule, we find occasionally instances where the papilla is absent, as on the filliform fins of the hake, where I find the buds imbedded in the epidermis and extending only part way through it, with a layer of unmodified epidermal cells between the bud and the dermis.

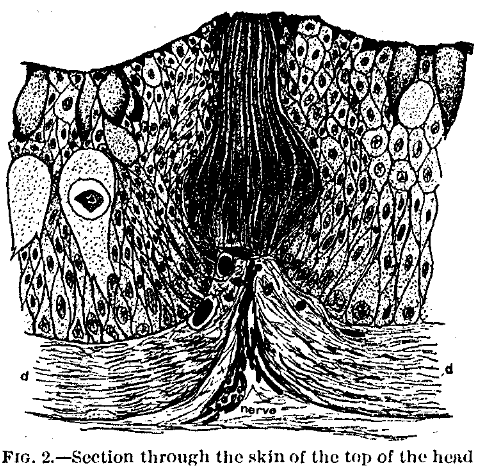

FIG. 2.—Section through the skin of the top of the head of *Ameiurus melas*, showing a terminal bud. × 375. (From the *Journal of Comparative Neurology*, vol. xi, No. 3, Oct., 1901, plate xvii, fig. 11.) At *d* is the dermis, which is raised into a low papilla under the sense organ and whose center is pierced by the nerve for the organ.

All parts of the body of *Ameiurus* which are supplied with terminal buds are reached by branches of the facial nerve from the geniculate ganglion. In other words, the rami from the communis root of the facialis are distributed to nearly the whole outer body surface of this fish. On the distal side of the ganglion these rami usually join themselves to other cutaneous branches which are phylogenetically older, belonging to the general cutaneous and lateral-line systems. Even the great recurrent branch into the trunk, the ramus lateralis accessorius, which passes out of the cranium as a practically pure communis nerve, anastomoses with the spinal nerves at their ganglia and its fibers are ultimately distributed along with the general cutaneous fibers from these spinal ganglia. Fig. 3 illustrates the courses of the chief cutaneous branches of the communis system in *Ameiurus melas*, the nerves of all other systems being omitted from the sketch.

Proximally of the geniculate ganglion the communis root of the facialis pursues an uncomplicated course to the primary gustatory center within the medulla oblongata. In most fishes this root passes back close to the floor of the fourth ventricle as the fasciculus communis (=fasc. solitarius of mammals) to terminate in the vagal lobe of the same side, and receives in its course the communis root of the glossopharyngeus nerve. But in siluroids and cyprinoids, where the very abundant terminal buds of the outer skin are all innervated from the communis root of the facial nerve, the consequent increase in the size of this root has resulted in a great enlargement of the cephalic end of the gustatory center (vagal lobe) which appears on the dorsal surface of the oblongata as the facial lobe. This structure is paired in siluroids and was formerly called the lobus trigemini, an inadmissible term, since it has nothing whatever to do with the trigeminus nerve. In cyprinoids it is unpaired and is referred to in the older literature as the tuberculum impar.

The cyprinoid fishes also have long been known to have terminal buds (*Becherorgane*) widely distributed over the outer body surface; but neither the innervation of these organs nor the exact composition of the cranial nerves has ever been worked out in any cyprinoid fish. A cursory examination of a series of sections prepared

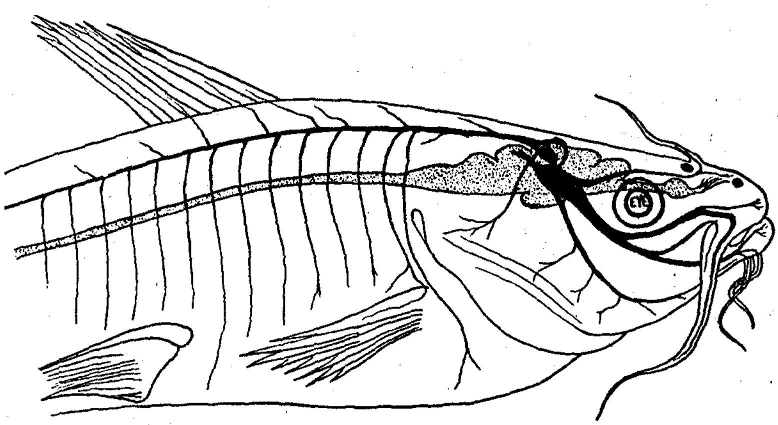

FIG. 3.—A projection of the cutaneous branches of the communis *root of the facial nerve in Ameiurus melas*, as seen from the right side. The outline of the brain is indicated by the stippled area and the positions of the eye and anterior and posterior nostrils are indicated. The projection is reconstructed from serial sections, but is not drawn accurately to scale. More detailed reconstructions of the cranial nerves and lateral-line sense organs of this fish are given in the *Journal of Comparative Neurology*, vol. XI, No. 3, plates XIV and XV (Herrick, '01).

by the Weigert method through the entire head and body of a small gold-fish (*Carassius auratus*) has convinced me that the same conditions in general prevail in the cyprinoids as in the siluroids. That is, the enormous size of the vagal lobes of cyprinoids is explained by the fact that these are the terminal centers for the vast numbers of nerve fibers entering the brain by way of the IX and X nerves from the palatal organ, this remarkable structure being crowded over its entire extent with taste buds and probably serving to filter food particles out of the mud taken into the mouth.

On the other hand, the tuberculum impar, or facial lobe, receives the entire communis root of the facial nerve. This root receives fibers from practically all parts of the outer surface of the body, and we may infer by analogy with other fishes that these fibers connect with the terminal buds in these cutaneous areas, though we have as yet no actual demonstration of this fact. The terminal buds of the skin of the head are supplied mainly, as in *Ameiurus*, by way of the infraorbital trunk. The terminal buds in the skin of the body of the gold-fish are not, however, supplied by a ramus lateralis accessorius, or recurrent facial nerve, as in *Ameiurus* and the gadoid fishes, for this nerve, as has long been known, is absent in the cyprinoids.

There is, however, in these fishes an intracranial anastomosis between the V+VII ganglionic complex and the IX+X complex, the composition of which has thus far remained unknown. This proves to be the recurrent branch of the facialis, carrying communis fibers from the geniculate ganglion into the trunk. The details of the peripheral distribution of these fibers have not been fully worked out, but the main path in the gold-fish is as follows:

The geniculate ganglion of the facialis is clearly separable from all other ganglionic masses of the trigemino-facial complex and is composed of two portions, each of large size. The more dorsal portion corresponds to the greater part of the ganglion in other teleosts and distributes its fibers chiefly by way of the infraorbital trunk. The more ventral portion sends cephalad a very large palatine nerve, and caudad a still larger nerve which represents morphologically, though not topographically, the r. recurrens facialis of the siluroids, etc., or the facial root of the r. lateralis accessorius as found in the cod.

This nerve passes back along the lateral side of the great auditory root and at the level of the superficial origin of the IX nerve it divides into several strands, one of which passes dorsally of the IX root, the others ventrally. These latter, however, pass upward so as to lie, farther back, dorsally of all of the vagus roots except that of the lateralis branch of the vagus. All of these communis fibers now join themselves to the r. lateralis vagi and, passing through the ganglion of the latter nerve, both components enter the body of the fish bound up in a single nerve trunk in which the fine communis fibers are for a time completely surrounded by the coarse lateralis fibers. The communis fibers go off in successive branches along with lateralis fibers. The details of the distribution have not been worked out, though I think it would not be difficult to do so with the material at hand. It is highly probable that the communis fibers are for the terminal buds sparsely distributed over the skin of the body and that the terminal buds of the trunk are all innervated from these communis fibers in the r. lateralis vagi, just as the buds in the skin of the head are innervated by other communis fibers from the geniculate ganglion of the facialis, an arrangement substantially identical in morphological plan with that of the siluroid fishes.

The conditions here, so far as studied, confirm essentially the conjectures to which I was led from a study of the literature (Herrick, '99, p. 400), and accord so completely with the morphological interpretation there proposed that we merely refer the reader to that passage in the Menidia paper.

## FUNCTIONS OF TERMINAL BUDS.

### EXPERIMENTS ON SILUROID FISHES.

The cat-fish (*Ameiurus nebulosus*) upon which this series of experiments was conducted (except a few experiments specifically designated) were hatched in the open at Granville in the spring of 1901. In October of that same year they were taken to the laboratory and kept through the following winter in tanks. Microscopic examination of the skin and barblets shows that their skin and cutaneous sense organs at this age are practically in the adult condition. During the winter they were fed on various kinds of meat chopped fine, sometimes cooked, but usually raw.

In one small aquarium were kept half a dozen cat-fish, several ordinary "shiners" (*Notropis* sp.[a]), and some small "spotted suckers" (*Minytrema melanops* Rafinesque). Casual observations made during the winter while feeding showed that the shiners use the eyes chiefly in capturing their food. A bit of meat dropped into the water will usually be seized instantly and devoured before it has time to sink to the bottom of the tank. After it has fallen to the bottom it is apt to be long overlooked unless the fish happens upon it in its aimless wanderings, or unless its attention is called to it by the movements of other fishes which may be eating it. These fishes, when observed, are usually swimming about in the mid-depths of the tank, not resting near the bottom. I have observed the same behavior in *Menidia* and other large-eyed species.

The behavior of the suckers was totally different. These fishes lie on the bottom most of the time unless disturbed, though if frightened they are very active, swimming powerfully and leaping out of the water. When food is thrown in they never pay the slightest attention, nor are they attracted by the sight of other fishes struggling for the meat. They are exceedingly shy and rarely eat when under observation. They lie quietly much of the time or swim slowly about, dragging the fleshy lips of the highly protrusible mouth over the bottom of the tank. If they thus happen upon a bit of meat this is sucked into the mouth, worked over with the pharyngeal teeth apparently, and then often ejected forcibly from the mouth, to be again taken, perhaps, and the process repeated—a behavior very characteristic of the way they take the bait, I am told by fishermen.

The cat-fish, like the suckers, keep strictly to the bottom of the tank. They are often quiet in the darkest corners or lying under débris, but much of the time are slowly dragging the mental and post-mental barblets along the bottom. The nasal barblets are held projecting well upward, and the maxillary barblets are directed outward and backward, their tips trailing the bottom or waving gently back and forth. They appear never to use their eyes directly for catching food to the slightest degree under the conditions of these experiments. No attention is paid to particles of food thrown into the water, even though they settle down within a few millimeters of the nose or barblet of the fish. The only case observed by me in which the eyes seem to serve in finding food is when a large piece of meat is thrown in and one fish begins to "worry" it. His movements may attract others until as many fish as can reach it are all tugging at it at once. If, however, a shadow is caused to fall upon the water, as by hovering the hand over the aquarium, the fishes are greatly disturbed and dart wildly about. They always seek the darkest corners of the tank and lie under dead leaves resting on the bottom of the tank for the most part, showing that the eyes are not by any means functionless and the fishes are strongly negatively phototactic.

If the cat-fishes in the course of their aimless movements along the floor of the aquarium touch a bit of meat with the lips or barblets, it is instantly seized and swallowed. Food in the immediate neighborhood of the fish is not discovered at once, but after a time appears to affect the fish in some way, probably through the sense of

[a] *Notropis* has very small tuberculum impar and vagal lobes, the latter scarcely larger than in the cod, *Menidia*, and physoclistous fishes generally. From this one may safely infer that cutaneous terminal buds are not as highly developed in this form as in the larger cyprinoids.

smell, as the maxillary barblets begin to wave about more actively and finally the fish becomes restless. He does not find the food, however, unless in the course of his movements it actually touches some part of the body.

During May and June, 1902, more systematic experiments were undertaken with these fish, and since these experiments are typical of those subsequently performed on other species of fishes I shall recount them in some detail. At first a few specimens were taken out in a shallow tray and the attempt made to feed them in various ways under close observation. They were, however, so much frightened by the exposure to bright daylight and by the proximity of the observer, in spite of all precautions, that no reactions could be obtained which were at all satisfactory. A bit of fresh meat on a long-handled needle could be thrust slowly toward the fish as he lay quietly on the bottom, rubbed over his body or on the barblets, and even over the lips, without evoking a movement of any kind in response. The same observation was made with the spotted suckers. The fishes in both cases had been without food for several days and were very hungry, but were obviously too much frightened to respond to the food stimulus.

On another occasion the same conditions were prepared, except that a few dead leaves were littered over the bottom of the tray. The fish when placed in the tray immediately sought the shelter of the leaves, and, after a suitable interval to enable them to become accustomed to the place, the feeding experiments were repeated. Selecting a fish which was entirely concealed under a large leaf, save for a projecting barblet, a bit of meat on a slender wire was gently passed down into the water in such a way as to touch the projecting barblet. It was instantly seized and swallowed. This was repeated many times with several of the fishes.

In subsequent experiments the fish were not removed from their own tank, but the water was drawn off so that it was only about six inches deep. Here they would lie under the leaves and the experiment could be continued with a minimum of disturbance to the fishes. The experiment of touching the barblet with meat was repeated hundreds of times with an almost invariable result that the fish instantly turned and snapped up the morsel. If the meat was merely held very close to the barblet it usually produced no response. The reaction was obtained equally well, no matter which barblet was touched.

In a later series of experiments I found that the fish would almost always turn and seize the meat if he were touched at any point on the head or body. If the tail of the fish projected out from under a leaf and the skin near the root of a tail fin were touched with meat the fish would turn and seize the meat. This reaction was not so uniformly made at first as that from the barblets, but after a dozen or so of trials it followed with equal promptness and uniformity, the fish apparently requiring a little practice to learn the movement perfectly.

The experiments last described were repeated the next day and by this time it was found that the fishes had become so tame that they would take the meat if offered to them in the open, without the shelter of the dead leaves, though not so certainly as when under the cover of the leaves, often taking fright from the shadow of the observer's hand or from some other cause.

In none of these cases did the fishes appear to see the bait or to perceive it in any way other than by actual contact with the skin at some point. If the bait were held a moment in front of them and then moved slowly away they would not follow it. If, however, it touched a barblet and then moved rapidly away before the fish had time to seize it, then the fish would sometimes follow it a short distance.

At this point the relations of vision and smell to these reactions should receive some further consideration. These young fishes, like their adults, spend much of their time buried under the débris of the bottom, with perhaps a barblet or a portion of the tail only projecting. Under these circumstances it is easy to apply the stimulus to various parts of the skin with the assurance that the contact is wholly invisible to the fish. Many such experiments show decisively that the reaction takes place in the same way whether the fish is able to see the stimulus applied or not. The visual factor being so conclusively ruled out, I have not thought it necessary to blind the fish for further control.

This conclusion of course must be limited strictly to fish of the species and age under investigation. It by no means follows that they may not subsequently learn to use their eyes in finding food, as well as in escaping from their enemies. Indeed, during the later experiments of this series, after the fishes had been fed for several weeks almost daily with meat on the end of a wire, I saw some slight evidence that they took note of the bait by the sense of sight, but the observations were in no case conclusive. Whether the adult *Ameiurus nebulosus* ever uses the eyes in the capture of food I have no definite information, though from the habit of spending much of the time during the day completely buried in the mud and of feeding chiefly at night it is very improbable that they do so. With the channel cat-fish, *Ictalurus*, the case is certainly different.

Mr. I. A. Field tells me that while fishing for bass in the Black River, Ohio, he has sometimes caught large specimens of *Ictalurus* with live minnows as bait. The current was swift and the minnows were kept off the bottom of the river and in motion all the time. At the meeting of the American Association for the Advancement of Science, at Pittsburg, July 1, 1902, in the course of a brief report upon these experiments, I asked the question whether anyone ever caught a cat-fish on a spoon hook. Dr. L. L. Dyche stated that he has occasionally caught the channel cat (*Ictalurus*) on a spoon in a small lake, but only in bright sunlight. Dr. Eigenmann stated that *Ictalurus* has much better eyes than *Ameiurus*. They are not only larger, but the retinal pattern is more nearly like that of other fishes, while that of *Ameiurus* is decidedly degenerate.

The part played by the sense of smell is much more difficult to determine. As intimated above, I have evidence that the gustatory organs of the skin can function only in contact with the sapid substance. The most highly flavored food can be held within a millimeter or two of the barblet or lips without calling forth the characteristic instantaneous reflex. I will narrate one experience which was many times repeated in a variety of modifications. Three fishes were lying quietly under a small water-soaked leaf. A bit of rather stale beefsteak, with a strong odor, was held on the tip of a fine wire over the edge of the leaf under which they were lying and separated by a centimeter or two from the nostrils of the fishes. The leaf was considerably corroded by decay, and doubtless the odor could freely permeate it, though it was nearly or quite opaque. After some ten seconds the fishes began to move restlessly about in circles under the leaf, which was soon swept away by their movements.

As a rule the fishes swam in narrow circles close to the bottom and for a long time failed to find the meat, though they seemed to be aware of its general position for they never circled far away. If the meat were very slowly moved across the aquarium the fish could be drawn in this way after it for a considerable distance, though the meat was never found unless in the course of their apparently aimless movements one of the fishes came in contact with it, when it was instantly snapped up.

This aimless circling movement may be termed provisionally the *seeking reaction*, since it is so different from the characteristic movement made when the stimulus is in contact with the body—a sharp turn of the body and instantaneous seizing of the bait—which I shall term the *gustatory reaction*. Unfortunately, I have not had opportunity as yet to carry out extirpation experiments on *Ameiurus* to determine decisively the part played by the olfactory organ in this reaction. (Compare the experiments on the tomcod narrated below.)

The fishes upon which these experiments were performed have unfortunately been lost. At the present time I have a fresh lot of *Ameiurus* fry under observation, and have already verified many of the conclusions reached with the first lot. But this second collection of fishes has not, at the time when this report is submitted, been in captivity long enough to become sufficiently accustomed to their new surroundings to feed freely and fearlessly. After some months of further preliminary observation, I hope to carry on experiments which may shed some light on the sense of smell in these fishes. But this must be reserved for a later report. A few subsequent observations are noted on pages 270–271.

We must content ourselves at the present time, then, with the inference that the sense of smell plays at least a small part in these reactions, for the animals became slightly restless in the proximity of the stimulus, though they were not in contact with it; this, however, appears never to provoke a definite reaction of seizing the food, but merely a vague reaction in search of food. On the other hand, physical contact with the irritating substance causes a definite and precise reaction which is practically constant. This points either to touch or to taste.

To test the relative part played by stimulation of these two sets of sense organs, the following series of experiments was performed. A half dozen fish in an aquarium were tested a score of times with fresh meat on the tip of a wire, as in the previous cases. The reaction was obtained uniformly, no matter what part of the body or head was touched. Half an hour after the close of these experiments a bit of cotton wool was wound around the tip of a wire and the fishes were tested with this exactly as they had been with the meat. For the first six trials the barblets only were touched. The fish in each case turned and seized the cotton as promptly as the meat had been taken. The cotton would be immediately dropped. After a few more trials the fishes would generally turn when touched, but would check their movement before the cotton was actually taken into the mouth. Several specimens were now tested on the trunk with the cotton. One or two turned completely around and took the cotton, but generally there was a slight movement only toward the cotton, which was checked before the cotton was reached. After a few further tests, the fishes would usually pay no attention to a contact with the cotton on the skin of the body and the reaction by the barblets became uncertain, until finally the cotton could be freely rubbed over the barblets or lips of some of the individuals without producing any response.

These experiments were many times repeated, sometimes using white cotton, sometimes red cotton, and sometimes fresh meat. The reaction was uniformly obtained with the meat. If at the close of a few experiments with the meat a minute pledget of cotton was substituted for the meat, there was feeble or no response from rubbing the body with the cotton, though upon touching the barblets the fish would usually turn and often would seize the cotton and drop it again at once. After several repetitions, the fish became wholly indifferent to the cotton, no matter how it was applied, or they would if touched upon a barblet turn toward it without biting it. They were now again tested with bits of meat. This they took as eagerly and as precisely as before, showing that they were still hungry.

After the interval of a day or two the fishes would still appear to remember the cotton, and I rarely, after the first trials, got a prompt "gustatory" reflex with the cotton. If they noticed it at all, they would turn slowly and touch it with the lips or a barblet in a tentative or inquiring manner, only to turn away again without taking it into the mouth. This deliberate movement may be designated, for reasons to appear immediately, as the *tactile reflex*, as distinguished from the instant seizing of food, the "gustatory reflex."

These experiments seem to show that in the reactions to the meat, both from the barblet and from the skin of the body, the senses of taste and touch both participate. This is in accord with the known innervation of the skin and barblets, for all parts of the body surface receive general cutaneous (tactile) nerves, and all parts are plentifully provided with terminal buds (taste buds) which are innervated by communis (gustatory) nerves. The experiments further suggest that these two sensory factors can be experimentally isolated by training.

The fishes having become accustomed by brief training to make the simple reflex of seizing the food under the stimulus applied to any part of the barblets or skin, and doubtless utilizing both gustatory and tactile sensations, the gustatory factor is eliminated by the substitution of cotton wool for the meat. The tactile sensation alone proves to be sufficient to set off the reflex after the training previously given. The stimulus is, however, never followed by satisfaction and is soon given up, the fishes after further practice not reacting to the tactile stimulus alone. If, however, the gustatory sensation is added, by the substitution of meat for the cotton, the original reflex is given as promptly as before. This would seem to indicate that, while the tactile sensation alone is not sufficient to maintain the reflex, the addition of the gustatory element is sufficient, and therefore that the gustatory element is the essential element in setting off the reflex. This hypothesis was tested by an extensive series of experiments similar in plan to those last described.

In general there was no noticeable difference between the reaction to the white cotton and that to the red, though in some cases, especially toward the end of the series of experiments, after the fishes had learned to pay no attention to white cotton when touched at any point by it, they would sometimes turn and touch the red cotton with the lips or a barblet, immediately to turn away again without biting the cotton as they did at first. The reaction is not the quick turn and instant seizing of the bait, which I have termed the "gustatory reaction," but a more deliberate movement similar to what I termed above the "tactile reaction." This occurred only when the cotton was in plain view at the time of the contact and is probably in this case partly a visual response, called forth by the similar appearance of the red cotton and bits of beefsteak on which they were habitually fed. It was not by any means constant, for, in general, after the first few days, contact with neither color of cotton called forth any response whatever.

After this result was reached, I dipped the pledgets of white cotton in the filtered juice of fresh beef and touched the body surfaces and barblets with them in the same way as before. In all cases I got a typical "gustatory" reaction exactly the same as with the meat, and this reaction persisted after many trials with no diminution. The cotton was taken instantly into the mouth and tugged vigorously. No amount of training served to eradicate or to weaken this reflex.

I next prepared a small bulb syringe, with the delivery tube drawn out to a very fine point. This was filled with the water in which the fishes were and a fine jet directed against their bodies. They either paid no attention or were disturbed and swam away. I now substituted for the water in the syringe the juice of raw beef pressed out and strained. When a jet of this fluid was directed against the side of the body, the fish always instantly turned and tried to take the end of the syringe. The reaction was identical with that produced when a corresponding part of the body is touched with raw meat. I invariably got the reaction, both from the sides of the body as far back as the root of the tail fin and from the skin of the head and barblets.

I also tested the fishes with bits of red brick held in forceps. The forceps seemed to frighten the fishes. They either paid no attention to the contact with the brick (when touched in such a way that they could not see the point of contact), or else the harsh contact seemed to frighten them. I then touched them on various parts of the body and the barblets with bits of brick which had been soaked in raw meat juice. In most cases they would turn and touch the brick with the lips or take it into the mouth, but often they seemed frightened and would swim away. I then gave them a few bits of meat with the forceps and found that they took it eagerly, being very hungry, but it had to be given more cautiously than with the wire, as they were afraid of the forceps if they saw them clearly.

Next I dropped bits of brick which had been soaked in meat juice in front of the fishes as they lay under leaves with the barblets projecting beyond the edges of the leaves. In all such cases, upon touching the brick with a barblet, they seized the brick and bit at it viciously. Often they would return to it a second or third time and try to bite it. I dropped similar bits of brick which had not been soaked in meat juice in front of them in the same way, but they paid no attention to them, or in a few cases they would touch them with the barblets and then swim away again ("tactile" reaction). They never attempted to bite them. Clearly they taste the meat juice in the bricks when they are touched by a barblet, and the experiment when the body was touched by a similar brick held in forceps shows that they taste the juice by the body also.

On one occasion I tested the fishes with pieces of cooked meat that had been long boiled so that nearly all of the extractives were drawn out. The experiments were conducted just like those with the raw meat, but the fishes gave by no means so clear reactions to it. Upon touching the sides of the body, the fishes usually paid no attention to the stimulus, treating it just as they did cotton. I then touched the barblets a few times, and to this they would generally react by turning and taking the meat, but not always nor so promptly as with fresh meat. Upon testing the sides of the body again after this experience I got a reaction. The fishes would turn and touch the meat with the barblet or lips before taking it, rarely giving the quick reaction characteristic of fresh meat. Evidently the cooked meat has less taste to the fishes than fresh meat and this interferes with the reaction. They eat the cooked meat when they are sure that it is edible.

These experiments, all of which were many times repeated and controlled, I think show conclusively that practically the whole cutaneous surface of *Ameiurus* is sensitive to both tactile and gustatory stimuli, and that the latter call forth characteristic reflexes which are of the greatest value to the fish in procuring food. The fish normally reacts to contacts on the body by both types of stimuli—to the mere tactile stimulus (if at all) by a tentative movement calculated to bring the doubtful substance into contact with the more highly sensitive barblets or lips, but to the tactile stimulus accompanied by the gustatory by an immediate, rapid, and precise movement calculated to seize the food. This latter reflex is unvarying and is very persistent under a great variety of forms of stimulation. The former ("tactile") reflex is less stable, and may be readily eliminated by a simple course of training. Clearly the gustatory element of the sensation complex resulting from a contact with a sapid substance is more important than the tactile element.

It is clear that in order to call forth the characteristic "gustatory" reflex the stimulus must be quite strong and rather sharply localized. For when there is only a small amount of meat juice diffused through the water, as by the presence of a piece of fresh meat near the fish, he is not able to localize it accurately, but exhibits only the "seeking reaction." I have not as yet been able to convince myself whether the fish could accurately localize a strong and sharply localized gustatory stimulus with no tactile element. In all the experiments in which meat juice was directed against the body with a pipette or syringe there was doubtless some tactile effect produced by the impact of the jet. We know from the experiments that pure tactile stimuli can be accurately localized on the skin, and there can be no doubt that under normal conditions these assist in the localization of the food object. Compare the further discussion in the Addendum, pages 270–271.

## EXPERIMENTS ON GADOID FISHES.

The preceding experiments were all carried on in the zoological laboratory of Denison University; the experiments on marine fishes which follow were made during the summer of 1902 at the U. S. Fish Commission laboratory at Woods Hole. The feeding reactions of three types of gadoids were studied, viz, young pollock (*Pollachius virens*), about 10 cm. long; hake (*Urophycis tenuis*), about 20 cm. long, and young adult tomcod (*Microgadus tomcod*).

As is well known, the hake and tomcod have a mental barblet which is known to be abundantly set with terminal buds and which receives both communis and general cutaneous innervation. In all three types the lips are freely supplied with terminal buds and there is a recurrent branch of the facial nerve, the ramus lateralis accessorius, which carries communis fibers into the trunk to supply terminal buds found on the fins, especially the free rays of the ventral or pelvic fins. These fins are far forward under the throat. In the pollock they are but little modified; in the tomcod two rays are about twice as long as the others and for about half their length they project freely below the rest of the fin. In the hake all of the rays of this fin are suppressed save these modified free rays, so that the fin is filliform, branched at the end. Microscopic examination shows that the terminal buds are more abundant on the more highly modified fins. The hake also has a free filament on the dorsal fin produced by the extension of the third and fourth rays beyond the others. I have not examined this free filament microscopically, but know that it receives communis fibers from the r. lateralis accessorius, and have no doubt that it also has numerous terminal buds, as the experiments show it to be very sensitive to gustatory stimuli. The pollock have very large eyes and are excellent visualizers. When food is thrown into the water, they dart for it and in general they take their food by the visual reflex. So keen is the vision that it would be difficult to carry on any experiments, such as I have done with the other two species, without first blinding the fish. Nor do they habitually drag the bottom with the free ventral fin rays as the others do. I have, therefore, not devoted much attention to this species, preferring to study more carefully those species in which the gustatory reflex plays the greater part in the life of the fish.

*The hake* (*Urophycis tenuis*).—These fishes, like the tomcods, readily adapt themselves to life in captivity, and are easily experimented upon in small tanks. They are excellent visualizers, though not so much so as the pollock. When bits of meat are thrown into the water they usually catch them before they fall to the bottom, and their keen vision makes difficult such experiments as I carried on with the cat-fishes. They do not seem to recognize by sight food lying on the bottom, but only when it is in motion. But bits of meat, fish, or clam lying on the bottom are usually found by the aid of the free ventral fins. These fishes spend much of their time in slowly swimming in an apparently aimless manner close to the bottom of their tank. During these movements the filamentous pelvic fins are so held that their tips drag the bottom. These fin rays are quite long, and they are usually directed obliquely forward, outward, and downward, with the two branches of each fin widely divaricated, so that the four tips touch the ground in a line transverse to the body axis at about the level of the mental barblet. In this way the bottom under the fish and for a short distance on either side is thoroughly explored as the fish swims over it, and all food particles with which the barblet or free fin rays come in contact are taken by a quick and precise movement similar to that set off in the siluroids by contact with their barblets. Bits of meat or clam on the end of a slender wire could be laid on the bottom of the tank and then slowly moved up under or behind the fish and the reflex from the ventral fins tested in this way. Such experiments, however, had to be made with great caution and many times repeated to rule out possible visual sensations which likewise call forth an immediate reflex.

Bateson ('90, *a*) records similar reactions with the rockling (*Motella*), a gadoid fish with the same general structure and distribution of terminal buds as the hake, but with better developed barblets. (On the structure of the pelvic fins of *Motella* compare Bateson's account on p. 214 with that on p. 234 of the same volume.) Bateson, moreover, got the same reflex with fishes which had been blinded, and I have not thought it necessary to repeat this experiment, for my fishes give sufficiently clear evidence that this reflex from the fins is wholly independent of vision. We have, however, to investigate the parts played by tactile, gustatory, and olfactory sensations.

Bateson's remarks ('90, *a*, p. 214) in this connection on the rockling may be quoted here. The three-bearded and the five-bearded rockling are nocturnal and lie still all day.

> Generally, both the animals take no notice of food until it has lain in the water some minutes, when they start off in search of it. The rockling searches by setting its filamentous pelvic fins at right angles to the body, and then swimming about feeling with them. If the fins touch a piece of fish or other soft body, the rockling turns its head round and snaps it up with great quickness. It will even turn round and examine uneatable substances, as glass, etc., which come in contact with its fins, and which presumably seem to it to require an explanation. The rocklings have great powers of scent, and will set off in search of meat hidden in a bottle sunk in the water. Moreover, a blind rockling will hunt for its food and find it as easily as an uninjured one.

The above, taken in connection with other passages, shows that this author considers that the food is found largely by scent, and that the fin reaction is essentially tactile, though he has seen the sense organs on the pelvic fins and recognized their resemblance to taste buds.

Examination of stomach contents shows that the normal food of these hake is largely crustaceans, particularly shrimps. I fitted up a tank with some seaweed and put into it a large number of prawns (*Palæmonetes*), mostly living, but some dead. Upon putting the hake into this tank, they immediately ate some of the dead prawns from the bottom and afterwards caught the live ones, but very slowly and with many failures. The response seems to be wholly visual. The fishes would repeatedly pass directly over living prawns, touching them with the fins or being brushed by their antennæ, but so long as the crustaceans were quiet they seemed not to notice them. If, however, a prawn was killed and crushed and thrown back into the water, it was immediately found. Upon another occasion I put a live clam into the tank with the hake, where it remained for several days, with siphons greatly extended. The fishes repeatedly brushed over this siphon with their free fins, but never paid any attention to it, though if a similar siphon were cut off from a live clam, so as to allow some of the juices to escape, it would be immediately taken and eaten. Evidently live food is not clearly located by the gustatory organs of the fins.

Besides observing as fully as possible the normal feeding habits of the hake, I experimented upon the reactions to stimuli applied to both the pelvic and the filamentous dorsal fins. As mentioned by Bateson, the pelvic fins are freely used to explore all manner of substances which may attract the notice of the fish, whether edible or not. After these fishes have become accustomed to being fed small bits of meat or clam or mussel (*Modiola*) in their tank, they immediately swim toward any small unfamiliar body with the pelvic fins thrust forward to touch it before the mouth reaches it. Sometimes the tips of these fins close over it with a movement strongly suggestive of grasping, though of course this they can not do.

Upon testing by contact with meat or other bait, the free dorsal filament is found to be quite as sensitive to gustatory stimuli as the filamentous ventrals. The reflex in this case is very characteristic and constant—the fish upon touching a savory morsel checks its forward movement and immediately "backs water" so as to reverse the movement of the body until the object is directly above the mouth, when it is taken at once. This reflex usually (though not so invariably) follows a contact of meat upon any part of the dorsal fin, as well as the free filament. The reflex rarely fails when any one of the filamentous fins is touched by freshly cut meat. After meat has been in the water for fifteen minutes or more it seems to lose its savor and the fins may be repeatedly dragged over it without calling forth a response, and the same is true of the barblet and lips.

I tested the filamentous fins with a wisp of cotton wool on a fine wire, as I did the cat-fishes. It was rarely noticed at all by the pelvic fins, but at the first contact with the filamentous dorsal the fish reacted just as he did to meat with which he had been tested immediately before. Upon repetition, the response was soon discontinued. For a few tests the fish would pause, and perhaps back up slowly so as to smell the suspicious object or touch it with the barblet, but it was not taken into the mouth. After from two to ten tests no further attention was paid to the cotton, or the fish would pause a moment without backing up. This experiment was many times repeated in the course of the first day of its trial and daily thereafter for some time. If three or four hours intervened between two series of about twenty tests, the first one or two tests of the second series might be followed by an incomplete reaction, but after that usually no notice was taken of the cotton. The fishes apparently remembered the preceding tests. But if more than twenty-four hours intervened between tests, the process of training usually had to be gone over again.

The fact that the hake does not appear to remember the difference between the pure tactile stimulus and the tactile plus the gustatory for so long a time as the cat-fish does is probably to be explained by the fact that the number of taste buds on the filamentous fins of the hake is much less than that on the barblets of the cat-fish, and therefore the gustatory element in the sensation complex is doubtless much less in the hake. The whole course of the experiments indicates that the response is in fact much more strongly tactile in the hake.

During the course of these experiments I often alternated bits of meat with the cotton wool, and at other times substituted cotton that had been soaked in clam juice. In these cases I always got the characteristic gustatory reaction by all of the filamentous fins, no difference being observable between the reaction to meat of clams or fish and that to cotton soaked in filtered clam juice.

I also tested the hake with gelatin which had been soaked up in cold water. Shreds of the well-softened gelatin were fastened to the end of a wire and brought into contact with the body surface. The reactions were identical with those obtained with white cotton. The gelatin shreds are very nearly colorless and absolutely tasteless to my tongue. But to the sense of touch they are almost exactly the same as the bits of fresh clam meat with which most of these experiments have been conducted. The hake at first would take the bait when the filamentous dorsal was touched, but if the gelatin was taken into the mouth it would be immediately rejected, and after a few trials the fish would no longer respond to the stimulus. He acted in the same way when the pelvic fins were stimulated. Shreds of the softened gelatin falling through the water were sometimes noticed, but rarely taken into the mouth, and if so, were immediately rejected. Similar shreds lying on the bottom were neglected, even though the barblet and filamentous fins dragged over them repeatedly.

I next took small clam shells that had been lying long in the tanks containing the fish and were thoroughly cleaned of fleshy matter and which the fishes had not paid any attention to for days. These I dried and warmed and then filled with melted gelatin which had been previously softened up in cold water. Upon cooling there results a mass, colorless, tasteless, and odorless, which feels almost exactly like the flesh of the clam, which has often been fed to the fishes in this way. Upon dropping these shells into the water, the fishes eagerly snatch them up, feel of them with the lips or barblet, and then bite into the gelatin. They immediately reject the gelatin and they never repeat the process. Even if they draw the fins or barblets repeatedly over the shells and the contained gelatin, they never again pay any attention to them.

I also repeated with the hake the experiments which I had previously carried out upon the cat-fish, using a fine-pointed pipette and sapid solutions. The fishes were in all cases first tested with sea water taken from the tank in which they were swimming. On one occasion (the first test made) a jet of water directed against the filamentous dorsal was followed by the characteristic backward movement of the fish, so that he finally received the jet in the face. He turned and tried to take the point of the pipette in his mouth—a purely tactile reflex apparently. This response I never got again with this or any other fish, though occasionally the fish would stop, hesitate a moment, and then swim on, paying no further attention to the stimulus. If the jet of water is directed against the pelvic fin while it is extended and searching the bottom for food, the fin is usually quickly withdrawn and pressed against the side of the body.

The pipette was then filled with the freshly prepared and strained juice of the mussel (*Modiola*), and this was directed against the fish in the same way. The fishes responded instantly, just as when stimulated by meat, whether the jet was directed against the filamentous dorsal, or the dorsal fin at any part, or the side of the body, or the free pelvic fin. The reflex is immediate and unmistakable, more sharply defined than I usually get by contact with the meat of the same mussel. The experiment was many times repeated, always with the result that the jet of water was ignored or avoided, while the jet of mussel or clam or crab juice was eagerly sought, the fish usually snapping at the end of the pipette.

I have carried out no systematic chemical experiments to determine the gustatory preferences of the fishes, having shaped my experiments so far as possible along the lines of the normal feeding habits of the species studied. Nagel and some other previous students of these problems have relied chiefly on reactions to unpleasant stimuli, and the reader is referred to their works, though I consider this a less satisfactory line of inquiry than the study of normal reactions to food substances. The few fragmentary observations which I have made with chemical stimulants I shall, however, record in their appropriate places.

Specimens of hake were tested with a 0.2 per cent solution of hydrochloric acid made up in distilled water, the acid being directed against the body by means of a fine pipette. The dorsal and ventral fins, the sides of the body, and the lips were tested. When first tested on the fins one hake turned and tried to take the pipette, much as he did with the clam juice. Afterwards this fish, as well as all the others from the first, seemed rather to dislike the acid and would swim slowly away. There is no constant reaction, however, and in fact the fishes act very much as they do when a jet of simple sea water is directed against them. They do not appear to dislike the acid intensely. Later I tested these fishes with a 1 per cent solution of hydrochloric acid in sea water. This is decidedly unpleasant and is uniformly avoided.

The experiments recorded seem to show clearly that the hake receives both tactile and gustatory stimuli by means of the free fin rays and to some extent doubtless by other parts of the outer body surface. What rôle may be played by the sense of smell remains obscure. To test the powers of locating concealed food the following experiments were tried:

In a tank containing two hake which were very hungry I placed a piece of fresh clam meat concealed between two small, old, and thoroughly clean clam shells which had been lying for some time in the bottom of the tank. The fishes did not seem to smell the meat at a distance and so be attracted to the spot where the shells were, but if in the course of their aimless movements along the bottom of the tank they passed over the shells, they generally stopped a moment, smelled around, and then passed on, first feeling over the whole area of the shell with their free fins. As time passed, this reaction became less clear until after some fifteen minutes they generally passed over the shells without paying any attention. They never found the meat. This experiment was many times repeated with the same result. The sense of smell can play no strong part in the locating of their food. It may play some small part, though I incline to believe that the interest which the fishes show in the concealed bait is excited by a vague stimulus to the terminal buds on the fins. Compare the experiments made after extirpation of the olfactory organs in the tomcod described below

*The tomcod* (*Microgadus tomcod*).—These fishes are much less active than the hake, spending most of the time lying quietly on the bottom of their tank. They have not so keen sight as the hake and pollock, but still obtain much of their food by this sense, catching food thrown in before it reaches the bottom. They do not catch live prawns in captivity so well as the hake do, yet prawns and other active crustaceans are found in the stomachs of specimens taken with the seine. The dorsal fin lacks the free filamentous rays and is not especially sensitive to gustatory stimuli. The ventral fins are, however, very efficient in locating sapid substances lying on the bottom. They are shorter than those of the hake and are not thrust forward, but incline slightly backward. Like the hake, the tomcods spend much time in slowly exploring the bottom, though they assume a very different position, with the head directed downward at an angle of some 30° to 45° with the bottom, so that the tips of the barblet and ventral fins just drag the bottom. When food particles are located they are snapped up by a quick lateral movement similar to that of the cat-fishes. Sometimes, however, stimulus of the ventral fins is followed by a reversed swimming movement, the fish backing up to take the bait. At other times the fish when exploring the bottom swims slowly backward, so that no change of direction is necessary when food is located.

I made a series of tests with cotton wool and cotton dipped in clam juice similar to those described for the hake, and with the same results. I also repeated the tests made with sea water and with strained clam juice by the aid of a pipette, with identically the same results as with the hake. After a few tests the fishes ignore sea water and plain cotton, but invariably respond to cotton soaked in clam juice and to the juice itself as they do to meat. The tomcod reacts to bits of clear gelatin soaked up in water essentially as the hake does.

I also tested the tomcod with hydrochloric acid, 0.2 per cent in distilled water and 1 per cent in sea water. Both are obviously avoided. I filled a fine pipette with a solution of quinine sulphate in sea water, about 0.1 per cent—a very bitter solution. The tomcod swims away immediately if applied either to the lips or to the pelvic fins, but appears not to notice it if applied to other parts of the body.

Within two old clam shells, which had been lying in the tank with the tomcods for several days and had remained unnoticed, was placed a piece of fresh clam. They were then closed together and laid on the bottom of the aquarium containing a tomcod. Shortly the fish passed near it, appeared to perceive it, turned from his course, and passed and repassed the spot until the shell was located, apparently by smell, by a method of "trial and error." Then he rooted at the shell vigorously until the two halves were separated and he could get the meat. I repeated this with a piece of squid within the shells with the same result. I tried two empty shells in the same way. He saw me put them into the water, came up to investigate, smelled (?) of the shells and went away without so much as touching them, and never came back to them again.

These experiments were repeated in many forms many times. In most of these cases the efficient organ in discovering the presence of the food was almost certainly the pelvic fin. At least, this alone located it, for the fish swam about (possibly feebly smelling something good), but did not make a definite movement toward the bait until the fins were dragged over the crack between the two shells containing it, from which the juices were doubtless being diffused out into the surrounding water. Then he backed up in the typical way. If the bait was not found within a very few minutes it was left unnoticed, even though subsequently uncovered.

These fishes almost invariably find a concealed bait, though the hake rarely does so. The hake seems to perceive the odor or savor of the food, for he lingers about the spot where it is concealed, but never makes a movement to uncover it. The tomcod, on the other hand, actively pushes things about with his snout until the bait is discovered. But, unlike the gadoid fishes which Bateson describes, these fishes do not get the scent of the food at any considerable distance and then search for it. They do not notice the bait until within a few centimeters of it, and there is no evidence that the sense of smell assists at all in the localization.

To test this point the olfactory organ was extirpated in several tomcods which had given the reaction last described clearly. Several ways of performing this operation were tried. The most successful method was to etherize the fish sufficiently to keep him quiet and then operate in a shallow tray with the mouth kept under water, cutting off the olfactory nerves or crura with a sharp scalpel. The wound suppurated badly, but appeared to give the fish no serious trouble, as they feed normally from the second day onward. Without going into the details of the observations, I may say that after the third or fourth day the fishes took their food in all respects like uninjured fishes, so far as could be observed. They gave all of the characteristic reflexes that have been mentioned above, including the discrimination between cotton wool and cotton dipped in clam juice and between sea water and clam juice applied with a pipette, etc. The operated fish would locate a concealed bait by means of the pelvic fins exactly as the normal fish does, and he would similarly root it out and eat it. In short, the gustatory reflexes, so far as I have observed them, were absolutely unmodified by the operation. That the olfactory apparatus was totally destroyed was verified by autopsy dissections made after the close of the observations.

### OTHER FISHES.

*The sea-robin* (*Prionotus carolinus*).—The three finger-like rays of the pectoral fins of the gurnards have long attracted the attention of zoologists, and the American species of *Prionotus* have been made the subject of a careful research by Morrill ('95). He finds that, as in the closely related European *Trigla*, the free rays are totally devoid of terminal buds or other specialized sense organs and that the sensory nerves with which these free rays are so abundantly supplied end free, like tactile nerves in general.

He also made some interesting physiological experiments. The normal food of these species, so far as known, is small fish, young clams, shrimps, amphipods and other small crustacea, squid, lamellibranch mollusks, annelids, and seaweeds. (Linton, 1901, p. 470.) They are constantly feeling about the sand, turning over stones and feeling under them, etc., with these free rays, and undoubtedly find their food largely in this way, especially the annelids, mollusks, and crustacea; but in captivity the eyes are used chiefly in securing the food. Morrill writes further:

> In order to test the use of the free rays independently of sight the crystalline lens and cornea were removed from some fish, and in other cases the cornea was covered with varnish, balsam, or tar. The repeated experiments were negative in their result, as the fish paid no attention to the food, even when it was placed in contact with the free rays.

Morrill concludes "that the free rays have been modified for tactile purposes, and that they are mainly, if not altogether, used in searching for food."

Morrill's dissections leave it uncertain whether the free rays of the pectoral fins receive communis nerves, as they should do, of course, if these organs had given evidence of gustatory powers. The only source of communis fibers for this fin would be through the ramus lateralis accessorius (r. recurrens facialis). Stannius (1849, p. 49) did not find this nerve in *Trigla gurnardus* and *T. hirundo*. I dissected a specimen of *Prionotus carolinus* and found the same to be true here, so that it can be taken as assured that no communis nerves reach the pectoral fin in this species.

After an examination of the feeding habits of the adult sea-robin and of young specimens about 10 cm. long I quite agree with Morrill that the reaction to food particles by the free fin rays is tactile only, with no gustatory element. When adults are fed with fresh clams or mussels, the shells split open to expose the meat, they turn and bite out the meat as soon as a free ray touches the soft flesh. Young fishes did not give this reaction so invariably, and evidently relied much more on sight. Clean clam shells filled with melted gelatin were reacted to like the fresh clams once or twice by each fish, but usually were thereafter ignored.

The free rays constantly stir up the sand and gravel of the bottom. If soft edible particles are touched the head may be turned to snap them up, especially with old fishes. With younger ones this usually does not happen unless the particle is seen while in motion. In fact, with these younger fishes the purpose of the activity of the free rays seems to be in the main the agitation of particles on the bottom to bring them into the range of vision. Almost any unfamiliar object, such as a bit of coal or a brightly colored pebble or any soft particle, if seen while in motion, will be apt to be taken into the mouth. The analysis is done here—not by the peripheral cutaneous organs. All small objects thrown into the water are taken into the mouth as they fall; bits of filter paper, gelatin, etc., will be taken and immediately rejected. The same bit of paper or excrement may be taken and rejected a half dozen times in rapid succession, the reflex following in a perfectly automatic way as soon as the moving object is seen. Small worms when thrown into the water would be captured before they had time to reach the bottom, but if placed on the bottom they would seek shelter under pebbles and remain unnoticed until they were stirred up and sent floating off, when they would be seen and taken at once. The free fin ray was observed to touch the worm when concealed without evoking a response. A moment later the worm was set in motion and taken at once.

I got no evidence that the fishes smell or otherwise detect the presence of food at a distance or concealed from sight and touch. Meat inclosed between clam shells, which a tomcod would have secured within a minute or two, remained unnoticed, though the outsides of the shells were repeatedly fingered over by the free rays and similar bits of meat were taken at once if in motion near the fish.

The young sea-robins eat crab meat well. I made a strong extract of crab meat and filtered it. Now with a fine pipette a jet of clean sea water was directed against the free pectoral-fin rays. There was no response, or if the jet was strong the fin was folded against the body. The extract of crab applied in the same way with the pipette gave the same result. Even when the jet is directed against the lips the fish usually pays no attention or is disturbed and swims away. This would seem to indicate that the sense of taste is absent or very feeble on all of the exposed parts of the body. Thus the absence of special gustatory sense organs, of communis nerves, and of gustatory reactions from the free rays of the pectoral fins serve as mutual controls.

*The king-fish* (*Menticirrhus saxatilis*).—These fishes have a short, thick mental barblet, and they were studied to compare their reactions with those of the siluroid and gadoid fishes. Most of the types of experiment made previously on the latter fishes were repeated on the king-fish. Without going into details, the experiments seemed to show in general that the king-fish is not a pure visualizer, though vision is somewhat used in finding food. This seems to be in the main a tactile reaction, as most of the food taken was by contact and nonnutritious substances were generally taken if they felt like food. For instance, colorless gelatin is taken at the first contact and repeatedly thereafter for an indefinite number of times, though in each case it is at once rejected as soon as it enters the mouth. The sense of taste seems to be limited to the mouth, and I found no evidence of a gustatory reaction by the barblet, though the experiments were not sufficiently numerous or varied to be conclusive. They do not find a concealed bait.

*The toad-fish* (*Opsanus tau*).—These fishes were experimented upon at the same time as the hake and tomcod, and by the same methods. The toad-fish never found a concealed bait and never seemed to get food by any other reflex path than the visual or tactile. The fleshy, cutaneous appendages of the skin were especially tested to bring out possible gustatory reactions, but with negative results save for those bordering on the lips, where it was impossible to exclude the participation of taste buds on the lips. This agrees with the anatomical findings of Miss Clapp (1899), whose careful study of the skin of this fish failed to reveal any terminal buds on these appendages or elsewhere away from the buccal cavity. A jet of sea water directed against these appendages or the body surface in general usually disturbs or frightens the animal merely, if it is noticed at all. A jet of clam juice similarly applied calls for the same reaction unless it is so directed as to reach the lips, in which case the fish reacts to it just as the hake and tomcod do, attempting to take the tip of the pipette in the mouth. The following solutions were applied in the same way by a fine pipette to various parts of the body surface: 0.2 per cent hydrochloric and 1 per cent hydrochloric acid in sea water, and 0.1 per cent quinine sulphate in sea water. In all cases the fishes paid no attention to the stimulus unless the substance was so applied as to come into contact with the lips. The experiments lead me to conclude that the toadfish can taste only within the mouth and on the lips, and that if the cutaneous appendages have any sensory function it is tactile only.

## CONCLUSION.

The morphological and physiological significance of the terminal buds of fishes is a problem which has exercised some of the ablest morphologists for over half a century. The methods of the older anatomy have signally failed to yield concordant results. Not until the innervation of the cutaneous sense organs was worked out from the standpoint of nerve components was this confusion relieved. The older morphologists (Schulze, Merkel, and others) discovered a morphological criterion, the "hair cells," by which the terminal buds could be distinguished from cutaneous sense organs belonging to the lateral-line system. But this fact attained its significance only when it was discovered that the organs of the lateral-line system, or neuromasts, which possess the "hair cells," are always innervated by lateralis nerves related centrally to the tuberculum acusticum, while terminal buds, which lack the "hair cells," are always innervated by communis nerves which are related centrally to the primary gustatory centers of the vagal and facial lobes.

Presumably, then, lateral-line organs and terminal buds have different functions; and, further, the function is probably not tactile in either case, since all parts of the skin receive general cutaneous nerves in addition to the special sensory components, and these general cutaneous nerves are related proximally to different centers from either of the others. The lateral-line organs are known to be used in the maintenance of bodily equilibrium and the perception of mass motion of the water. (Compare the recent works of Lee and Parker.) On the other hand, the terminal buds are related in structure and innervation to undoubted taste buds of the mouth, and hence the inference that their function is taste. This inference is abundantly confirmed by the experiments here recorded, and the function and morphological rank of the terminal buds are at last definitely fixed.

It may be regarded as established that fishes which possess terminal buds in the outer skin taste by means of these organs and habitually find their food by their means, while fishes which lack these organs in the skin have the sense of taste confined to the mouth. The delicacy of the sense of taste in the skin is directly proportional to the number of terminal buds in the areas in question.

Numerous unrelated types of bony fishes from the siluroids to the gadoids which possess terminal buds have developed specially modified organs to carry the buds and increase their efficiency. These organs may take the form of barblets or of free filiform fin rays. The free rays of the pelvic and dorsal fins of gadoid fishes are thus explained, and indeed this is possibly the motive for the migration into the jugular position of the pelvic fins of the gadoids.

In all cases where terminal buds are found on barblets or filiform fin rays gustatory nerves belonging to the communis system are distributed to them. These barblets and free fin rays likewise receive a very rich innervation of tactile or general cutaneous nerves, so that they merit their popular designation—"feelers." Both sets of end organs undoubtedly cooperate in the discrimination of food, and the animal has the power of very accurate localization of the stimulus. Whether the gustatory stimulus alone can be localized apart from its tactile accompaniment can not at present be stated. A purely tactile stimulus with no gustatory element can be localized precisely, and I have as yet no conclusive evidence that a pure gustatory stimulus, even when strong, can be located by the fish. It is certain that feeble and widely diffused gustatory stimuli can not be accurately located by the fishes which I have experimented with, either by the terminal buds or by any other organs.

The fishes in which the cutaneous terminal buds are most highly developed are in general bottom feeders of rather sluggish habit, and in some cases they are nocturnal feeders. The high development of this sense is compensated for in some fishes by the reduction of others. The visual power of the fishes is especially apt to suffer degradation. This degradation may be organic, a positive degeneration of the visual apparatus, as in *Ameiurus*, or it may be merely functional. In the latter case, though the organs of vision are not necessarily modified, these organs are not actually used in procuring food, the fish being unable to effect visual reflexes toward food substances or to correlate visual stimuli with the movements necessary to react toward food substances. The fish may be perfectly able to effect other visual reflexes, but is apparently unable to understand the significance of food when perceived by the sense of sight only. This particular central reflex path has never been developed, or has atrophied from disuse. Nature has here effected for the species something similar to what is accomplished in individual men occasionally by disease, in the production of certain aphasias.

The number of reflex activities habitual to an animal with a nervous system as simply organized as the bony fish is probably far smaller than is commonly supposed, and these activities are in general characterized by but little complexity of organization. It is probably quite within the range of possibility to determine by observation and experiment for any given species of fish, to a high degree of accuracy, what these habitual activities are and to work out by histological methods the reflex arc within the nervous system for each of them; and since the human nervous system is built up on the same general plan as the piscine nervous system it follows that such a thorough and systematic correlation of function with structure would be profitable from many points of view.

Terminal buds do not occur in the outer skin of all fishes; in fact, they are probably lacking here in the greater number of species. But whenever they do occur they tend to be arranged according to one general plan. This is particularly true of their nerve supply, for, though the details of the peripheral nerves of fishes are exceedingly diverse, yet the main communis branches for terminal buds, when such occur, are substantially similar from the *Siluridæ* to the *Gadidæ*. There are, however, striking resemblances in detail between the siluroids and the cyprinoids, which are much more significant of close relationship. Both groups are characterized by an extreme development of the system, reaching generally over the whole body surface; in both cases the peripheral communis nerves correspond to the general teleostean type, though with a remarkable modification of the recurrent branch of the facialis in the case of the cyprinoids, and finally the communis centers in the medulla oblongata differ from those of all other teleosts in that there is developed a facial lobe as well as a vagal lobe in the primary central gustatory center. The facial lobe (the so-called lobus trigemini of siluroids and the "tuberculum impar" of cyprinoids) in both cases receives by way of the communis root of the facialis the nerve fibers from all of the terminal buds of the outer skin, while the vagal lobe is reserved for those from the mouth and viscera. This emphasizes from a new point of view the close relationship between these two gronps of fishes as recognized by the systematists generally.

Though the *Ostariophysi* may have had a different origin from that of the other teleostean orders, yet the resemblances in general plan of the terminal bud system of sense organs in this group and in the other orders make it improbable that this system of organs has arisen independently and followed a paralleled development in the two groups of fishes. Its phylogenetic origin must therefore be sought among the ganoids, and until we have much more exact information concerning the nerve components and sense organs of these fishes further speculation in this direction is idle.

This study has been directed primarily toward the solution of a simple physiological problem; but in a purely incidental way some points of interest to comparative psychology have come up. We have seen that in the cat-fish, hake, and tomcod the reflex of seizing food is normally set off by a combined stimulus of tactile and gustatory end organs. At first the fish will react similarly to a pure tactile stimulus and to the tactile plus the gustatory. After brief training, however, he acquires the ability to discriminate between the former, which is never followed by satisfaction, and the latter, which is followed by the pleasure of feeding. Clearly the fish learns by experience. We find also some differences between the different species of fishes in this respect, depending on the relative importance of the tactile and gustatory elements of the sensation complex in the normal reflex life of the fish.

It would be interesting to inquire the part played by memory in these reactions. In the case of *Ameiurus*, where the tactile and gustatory elements of the reflex of seizing food can be experimentally isolated by training, it would doubtless be possible to measure quantitatively the duration of the persistence of this acquired discrimination. I have made no accurate observations on this point, but can say in general that the memory of these fishes seems to be fairly good. (By the term memory I do not mean to prejudice the question of the part played by consciousness here.

The original reaction may be largely or wholly an unconscious or automatic response and the "memory" may be an organic memory more closely allied to habit.) At the beginning of the tests with cotton the cat-fishes generally seized the cotton just as they did the meat. At the close of the first day's experiments they had learned to ignore the cotton as a rule, and a half an hour after the close of this series of tests they still would pay small attention to the cotton; but by the day following, if tested first with meat, they would take the cotton for a few times or would react to it slightly during the first few tests, but would learn to let it alone sooner than on the first day. But toward the close of the experiments, after several weeks of practice, I rarely got any reaction at all with the cotton under any circumstances, even if the fishes had not been tested for several days. With the gadoids the number of experiments was much smaller and they were continued for a shorter time, but I never got so good evidence of memory of the discrimination. On successive days the tests were much alike. The inability of the tomcod to remember to ignore a tactile contact which is not followed by satisfaction so long as the cat-fish remembers a similar discrimination I take to be an indication that the tactile element plays a much larger part in the reflex complex in the gadoids. The known distribution of the taste buds favors this view also, for while they are very abundant on the barblets and body of the cat-fish they are rather sparse on the free fins of the gadoids and the general cutaneous nerve supply on the fins of these fishes is greatly in excess of the communis nerve supply.

I noticed also that all of the fishes that ate freely in captivity soon accustomed themselves to novel methods of feeding, and in the case of the cat-fishes, and the hake especially, as soon as I approached their tanks after the experiments had been in progress some time, the fishes would rise to the top of the tank and eagerly await the expected food. This restlessness became so great with the cat-fish that the experiments became increasingly more difficult, and, as before mentioned, there was evidence that vision and possibly smell assumed greater importance after this expectation of food had made its appearance.

DENISON UNIVERSITY, *December 15, 1902.*

## ADDENDUM.

During the winter and spring of 1903 some further observations have been made with the purpose of answering (among others) the question raised above, whether fishes can localize a sensation received by the terminal buds alone with no tactile accompaniment; or, in other words, whether gustatory sensations may be provided with a local sign as tactile sensations are. (This question, of course, does not necessarily involve the more general one as to the essential nature of the local sign, whether it is due to a "specific energy" of the peripheral nerve or sense organ or to central differentiation in the terminal nucleus.)

Some recent clinical observations suggest that in human beings such a localization of gustatory sensations is possible. Cushing (Johns Hopkins Hospital Bulletin, vol. XIV, No. 144, 1903, p. 77) reports after destruction of the Gasserian ganglion and total paralysis of general sensation on the anterior part of the tongue, that the gustatory sensibility remains unimpaired, and that in this case the gustatory sensations can be localized. It is not, however, absolutely certain that it is the gustatory fibers which effect the localization, for the chorda tympani, which was uninjured, may carry also a certain number of fibers for general sensation from the facialis root in addition to gustatory fibers, as Cushing assumes is the case with the chorda from some of his results and from those of Köster.

My own observations were made on the young of *Ameiurus* from 5 to 8 cm. long, received from the State fish hatchery, at London, Ohio, in October, 1902, and kept under observation in tanks during the following winter. These fishes prove to be more shy and less teachable than the smaller *Ameiurus* fry (about 3 cm. long) hatched by wild parents, upon which the experiments reported in the preceding pages were made.

I have verified on these fishes most of the observations made on the smaller fishes last year. The most noticeable difference in their behavior is the evidently greater visual power in these fishes. As soon as they began to feed freely in the presence of the observer (which required several months of training) they began to show evidence of visual recognition of a moving bait, if very near them, and provided they had just previously been fed with the same food in the same way. They never under any circumstances notice visually a still bait, and their recognition of a moving bait is at best very imperfect and only an occasional occurrence.

Upon putting a concealed bait in a tank with the fishes I found no evidence that they are able to locate it by the sense of smell or otherwise from a distance, provided the water is still. If, however, they swim near enough to the capsule containing the bait (beef liver, cheese, etc.) to pass the barblets into the strong diffusion currents emanating directly from the bait, it is located instantly. The reactions here are essentially like those by which the tomcod localizes a concealed bait, though I have not completed the experiment by extirpation of the nose to determine what part, if any, is played by the sense of smell. So far as my experiments have gone these fishes will not locate a concealed bait in still water unless they pass within 5 cm. of it.

In running water, however, the case is quite different. I constructed a long, narrow tank, so arranged that a slow stream of water can pass through it from end to end. By covering the lower end of the tank and illuminating moderately the upper end, it can be so arranged that the negative phototaxis will counteract any positive rheotaxis and the fishes will remain in the lower end of the tank. If now liver or other strong bait is placed above them, the fishes will promptly swim up the current and locate the meat.

The experiments seem to indicate that concealed food can not be located by these fishes from a distance in quiet water (cf. Nagel, 1894), but that if the fish passes within a few centimeters of it the diffused juices are recognized and the food located promptly. In running water, however, the fishes will follow the diffused juices up the stream for considerable distances and so find the food—a fact well known to every fisherman. Tactile sensations are clearly not involved; it lies between the senses of smell and taste, and I have not as yet gone far enough with this series of experiments to decide finally the part played by the sense of smell.

I have, however, tested the sensitiveness of the barblets to diffused savors more fully. Raw meat or beef liver was minced, extracted in a little water, and strained. A wisp of cotton was wound on the end of a slender wire, dipped in the meat juice, and gently lowered so as to lie a few millimeters from the tip of a barblet of a cat-fish which was otherwise entirely concealed under a large leaf. The fish was unable to see the cotton and actual contact with the barblet was carefully avoided. Within a few seconds the fish became conscious of the savor and turned *toward the cotton.* Again, I filled a glass tube, of about 3-mm. bore, with the meat juice, closed the upper end with the finger, and carefully lowered the open end down over a projecting barblet, as in the previous case. The specific gravity of the meat juice is slightly greater than that of the water, and from the lower end of the tube (the upper end being kept closed) the juice slowly diffused downward enveloping the tip of the barblet, without, however, any noticeable current being produced in the water. The fish locates the stimulus and turns toward the source of it. In other cases I colored the juice with a little blood, so that the course of the diffusion currents could be observed, and it is evident that the reaction follows the stimulus of the *barblet* only, and not the organ of smell, for the movement is made before the diffusion currents have had time to reach the nostril.

These reactions are not as prompt or precise as those given after a *contact* with a sapid substance where a tactile sensation accompanies the gustatory, and in a large percentage of the cases there is no definite reaction toward the point stimulated, but merely the more vague "seeking reaction" to which reference has been made above. Nevertheless they indicate on the whole that pure gustatory stimuli, if very strong and applied to a small area of the percipient organ, *can be localized in space, or have a "local sign."*

*May 30, 1903.*

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