Orientation by Taste in Fish of the Genus Ictalurus

Abstract. *Fish of the genus* Ictalurus *can find distant chemical clues by means of taste alone, and they exhibit true gradient searching in the absence of a current. Neither unilateral nor bilateral deprivation of the sense of smell impaired their searching ability, but unilateral deprivation of taste receptors which are spread over body and barbels of the animals caused pronounced circling toward the intact side. The relation of swimming paths of the fish to the chemical in the water suggested that comparisons of concentrations were made in time and space.*

Olfaction has long been recognized as a primary sensory modality which aids animals to locate distant clues. Taste, in fish as in other vertebrates, has been considered as a closeup sense, used in testing the palatability of food (*1*). Temporal and spatial patterns of taste stimuli have been considered relatively unimportant, because of the belief that an animal can locate a food source only by direct contact (see *2*).

Some fish, however, have an extremely well-developed taste sense, with branches of cranial nerves distributed on the head, on the flanks even to the tail, and on the fins or barbels, or both (*3*). *Ictalurus nebulosus* and *I. natalis*, the brown and yellow bullheads belonging to this group, have thousands of external taste buds on the body, with especially dense concentrations on the barbels (*4*). Our experiments and observations have established that taste alone can guide these fish to sources of chemical stimuli at least 25 fish lengths away, the limits of our tank. Also, the fish need no current to locate such a source; that is, they perform a true gradient search by means of taste.

Bullheads of the two species between 19 and 27 cm in total length (mean 22.6 cm), trapped from local lakes, were blinded with phemerol (*5*). Some also had their olfactory tracts severed or their nares cauterized, others had some or all of their barbels amputated, and still others had portions of their seventh cranial nerves severed just outside the cranium. Each fish was kept singly in a 26.6-liter aquarium; some were fed liver, others dry pellets. Among the latter, a positive feeding response to cysteine hydrochloride was established; electrophysiological tests had shown that bullheads both smell and taste this substance (*6*). Moreover, untrained bullheads placed in our tanks approached a nozzle from which a solution of this substance emanated.

Searches for chemical stimuli were recorded in a large, flat tank (2 by 3 m) containing 600 liters of water. The water was 10 cm deep, and it could be made to flow at speeds up to 12 liters per minute. Fluorescent compounds helped to ascertain the constancy of flow patterns, which were similar from trial to trial at a given current velocity. On the ceiling above the tank were four ultraviolet fluorescent lights (GE No. 40BLB, 40 watts each). Also on the ceiling above the tank a remotely controlled Pentax HIA 35-mm camera was centered with a 28-mm lentar lens and a Kodak wratten gelatin filter 25A, loaded with Tri X Kodak film. The stimulus solution—either droppings from thawed slices of 1 part pork liver diluted in 10 parts water—or cysteine hydrochloride—was released, anywhere in the tank, through a suspended, remotely operated 50-ml syringe with a long glass nozzle. In some tests the solution was made visible by releasing fluorescein, rhodamine B, or vegetable dyes with it.

A red plastic disk about 1 cm in diameter, sprayed with a commercial fluorescent paint, was sewn onto the skin on the head of each fish, approximately at eye level. Each fish was used only once or twice, except for those we subjected to progressive sensory deprivation by removing successive sets of barbels. In their case the point of stimulus release in the tank was varied from test to test, and the tests were spaced several weeks apart.

Most tests were done in the evening when there was little noise in the building and when bullheads are active. The fish was placed in the tank 6 to 8 hours before a test. When it had been quiet for at least 10 minutes, we released the stimulus; liver juice was used somewhat more often than cysteine hydrochloride. The photographed searching behavior was the same in either case, as was the behavior of the two species within the size ranges used. Stopwatch timing with one watch was begun at the release of the stimulus, while a second stopwatch measured the interval between arousal and the completion of the search. We began exposing the film when the animal showed that it had perceived the stimulus, and we continued the exposure until it found the source. The light trace made by the swimming fish (Fig. 1) appeared on a positive photographic copy as a white line. Its intensity was in inverse proportion to the swimming speed and could be made very clear by adjusting the photographic printing period.

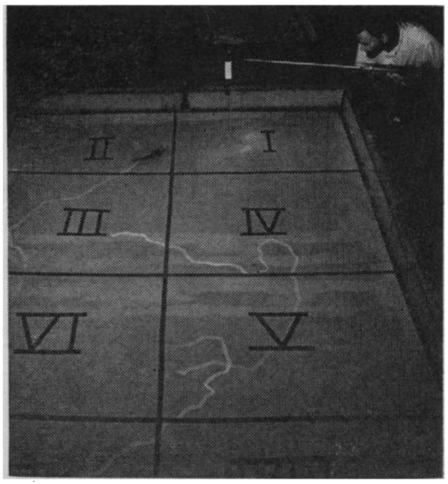

Fig. 1. Bullhead bearing a fluorescent tag approaching the release point of dilute liver extract mixed with fluorescein. [Time exposure, with final flash by P. Davis]

Dye was used only in a few photographed trials because it masked the trace of the fish. Details of swimming behavior, when dyes were used with the stimulus, were therefore observed rather than recorded photographically. When a mixture of the dye and stimulus first reached the previously resting fish, it began its search. Fluorescein alone elicited barbel movements or yawning and sometimes swimming, but never search. Vegetable dyes, which did not permit photography in ultraviolet light but had distribution patterns like

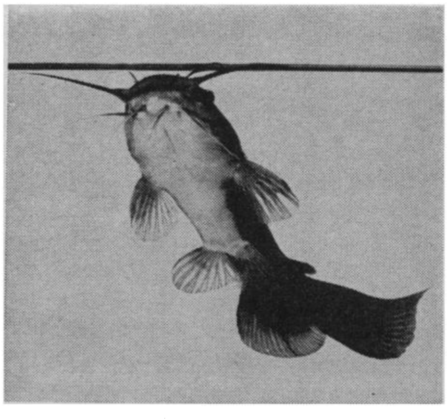

Fig. 2. Bullhead seeking barbel contact with a chemical in the surface film. [Flash photo by P. Davis]

those of fluorescent ones, were disregarded by the animals.

Typically, a blinded bullhead would show that it had perceived a chemical by what is best described as a startled response: the barbels stiffened, the body became rigid for a moment, the head began a slow to-and-fro movement, and the fish almost immediately began swimming.

This pattern of head movement was recorded in 90 out of 122 photographed tests of blinded but otherwise intact animals. In the remaining tests the fish just began to search. When the fish began their to-and-fro movements they often sought contact with the surface film by means of their nasal and maxillary barbels (Fig. 2). At this moment, one or the other of the maxillary barbels was raised and lowered, covering an angle of almost 90°. The lateral movements, combined with the raising and lowering of the barbels, suggest that the fish often compared the chemical concentrations to the right and left of it, either simultaneously or in close succession. A typical trace of a blinded but otherwise intact animal in a current shows this initial scanning (Fig. 3a, sections III and VI).

When the fish reached the vicinity of the release point of the stimulus, its momentum carried it beyond the scent cloud (Fig. 3b), but it immediately swung around and reentered the cloud. Repeated maneuvers of this kind resulted in the typical figure-eight search, early reported for many fishes (*7*). Going in and out of a scent cloud in this manner implies that consecutive reactions of different receptors were compared to govern the animal's muscular response. When the bullhead finally mouthed the nozzle, at the release point, we considered that it had completed the search and stopped the camera. The stimulus diffused more slowly in still water than in a current; consequently, search was begun after a longer time interval without current, up to 18 minutes in some instances, than in flowing water where search began from between 1 to 10 minutes after the stimulus was released; the latency depended on the speed of flow and where the fish was at rest in the tank.

Without a current, some fish found the release point of a diffused chemical with less circling and figure-eight movement (Fig. 3c). Others, swimming slowly, approached the nozzle in an almost straight line (Fig. 3d), a feat their experimental running mates never attained in any of the more than a hundred tests with a current. In still water a chemical gradient persists relatively undisturbed, but in flowing water eddies change the relative concentration continuously, especially at the edges of the field occupied by the chemical. Our tests suggest that, in still water, gradient search by means of taste (Figs. 3, c and d; 4, a and b) might depend on the fish's ability to compare taste bud responses from the barbels with those from the flanks and the caudal peduncle; such neural processes would explain the almost straight approach under optimum conditions (Fig. 4a).

We do not yet know whether eliminating the olfactory sense impairs searching behavior. With liver juice or 0.01*M* cysteine hydrochloride released at a rate of 5 ml per minute into 600 liters of water, bullheads tested with or without a current but without sense of

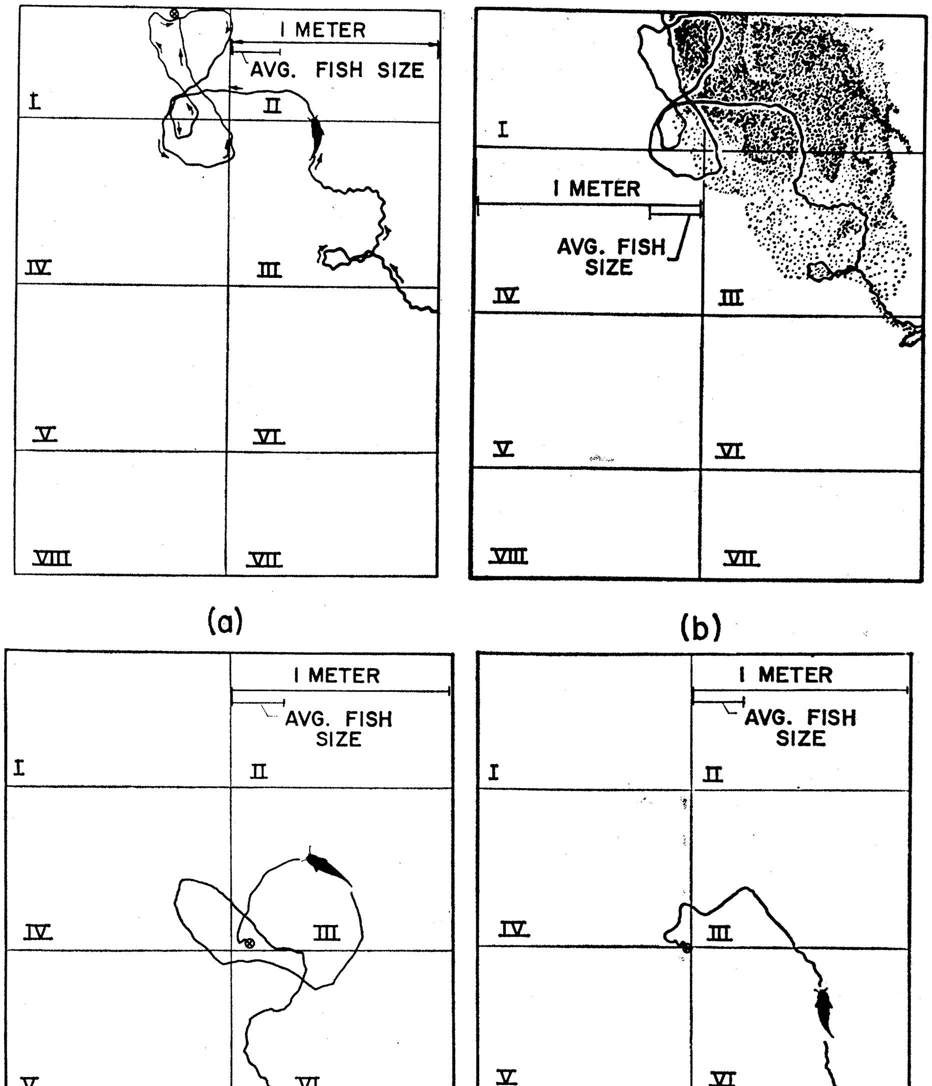

Fig. 3. Traces of fish under various experimental conditions. (a) Trace of a bullhead that started to search for the release point of 0.01*M* cysteine hydrochloride into slowly flowing water 3 minutes after the release of the chemical. (b) Diagram (from a photograph) of a distribution of fluorescein, 3 minutes after the dye was released from the same point as in part (a), with photographic trace of bullhead superimposed. (c) and (d) Traces of blind bullheads locating the source of diluted liver extract in water without a current, illustrating the reduction of circling in still as compared to flowing water.

smell had neither a longer mean searching period nor a greater range of searching times than did the other fish that had all chemical sensors intact.

The gustatory acuity of bullheads may approach the olfactory acuity of many other fish (*8*). Indeed, at the stimulus concentrations we used, the progressive removal of pairs of barbels in fish with their head and body taste buds still intact, either olfactorily capable or not, did not affect the time intervals between the alert to the stimulus and the completion of the search.

Yet the role of olfaction in orientation by bullheads remains puzzling, especially since initial head movements at slow swimming speed by fish with cauterized nares only occurred twice in 20 trials, that is, 10 percent of the times, as opposed to 74 percent in the much larger sample of fish with intact chemical senses. What is more, a fish in still water, without functional nares and barbels but with head, oral, flank, and tail taste buds intact, once alerted, could swim in 24 seconds almost directly to the release point of the stimulus while following a chemical gradient (Fig. 4a).

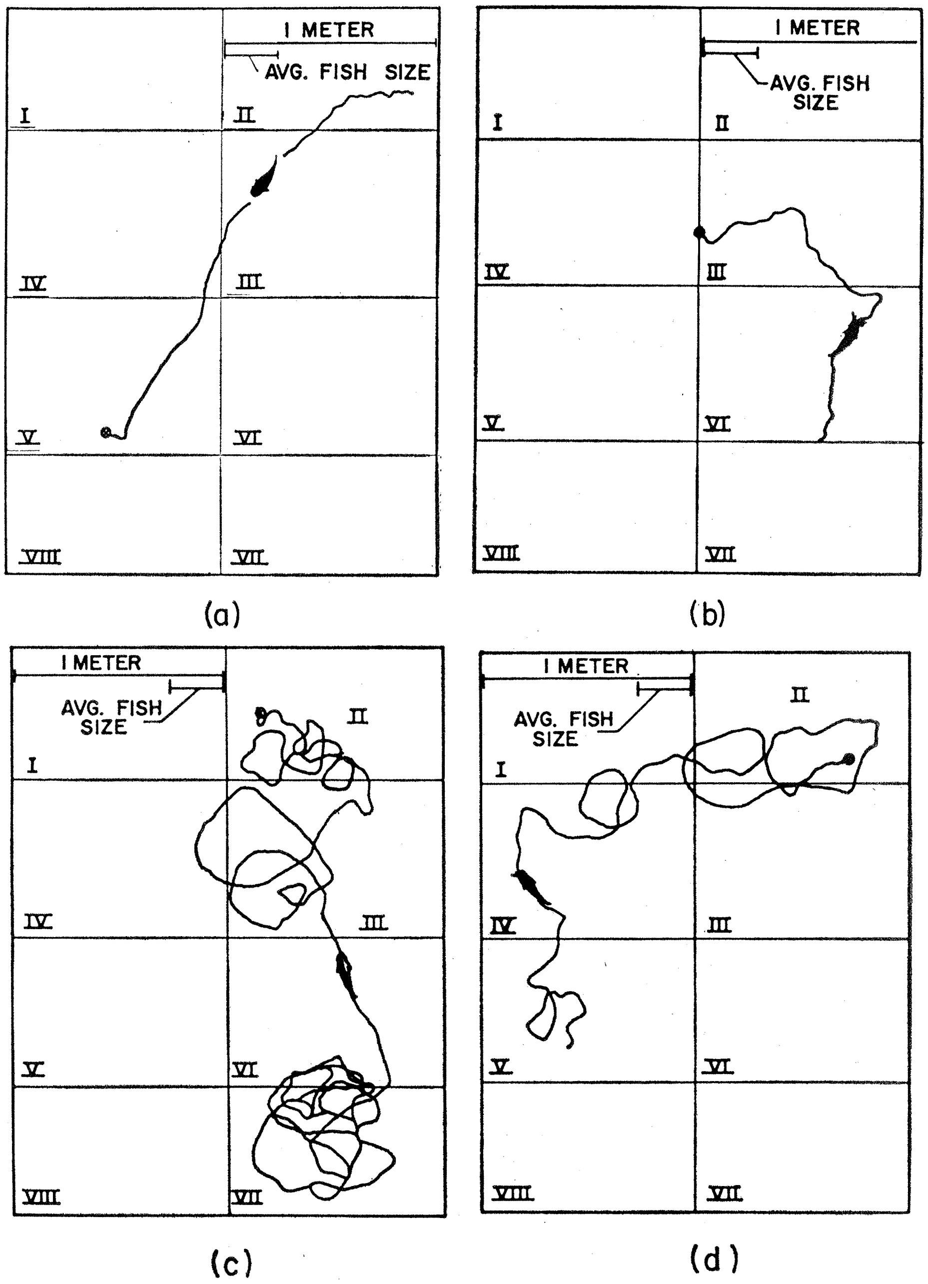

Fig. 4. Traces of blinded bullheads. (a) With cauterized nares and without nasal, maxillary and mental barbels, locating the source of dilute liver extract in still water. (b) With left naris cauterized searching, in still water, for the source of dilute liver extract. There is a high efficiency of finding the source and the left turns in spite of one-sided nasal cautery. (c) With all barbels removed and innervation to taste buds on right flank severed, circling towards the side of greater sensory input while locating the release point of dilute liver extract in a current. (d) With all right barbels removed, locating the source of dilute liver extract in still water, apparently with less circling toward the intact side than in the current (part c).

In contrast to Parker's classic observations of lopsided search after one naris of a shark had been similarly treated (*9*)—an observation not corroborated by later work (*10*)—one-sided elimination of smell in bullheads did not affect their searching ability (Fig. 4b). But when all barbels, or barbels and also flank taste buds, were made inoperative on one side only, creating an imbalance in taste input, the nine fish used in 27 trials always circled pronouncedly toward the intact side. The one-sided looping occurs both in a current (Fig. 4c) and in still water (Fig. 4d).

It has not yet been possible to completely eliminate the gustatory faculty of bullheads surgically in order to study the olfactory component alone, since the taste fibers are distributed at least in the widely branched seventh, ninth, and tenth cranial nerves (*11*), and extend to taste buds in the mouth, the pharynx, the gill cavity, and all over the head and body. This spread of taste sensors enables fish of this genus, and probably others with body taste buds, to compare the concentrations of chemical stimuli which they can then locate by taste alone over distances greater than hitherto suspected.

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