males are larger and more powerful than the males, and therefore the attempts are likely to be unsuccessful. (ii) Females may alternately oviposit and hunt over several days and, during this time, mate with two or more males. Mimicry could permit a male to locate a hunting female with marginal valence for hunting and change her to a mating condition (seduction-mimicry) [but see (*14*)]. On five occasions when mimicking males landed near flashes on the ground (all noted) they immediately began emitting the pulsing (treetop, nonmimic) pattern. (iii) Males that emit the prey-species pattern in the appropriate activity space and at the proper time may be demonstrating a trait that females favor. (iv) Males may indicate to females, by the patterns they use, the extent or nature of nutritional investment in progeny they are prepared to make. Thus, old males with low probability for survival to the next evening's mating flight might feasibly advertise their candidacy for cannibalism by a mate, this being the ultimate in nuptial feeding (*15*). Energetic and nutritive contributions are also possible through ejaculate (*15*), and the mimicked patterns could indicate the nature of the material the male has acquired from predatory activities.

In choosing among the above hypotheses I favor (ii) (for VR) because it is the simplest, appears stable evolutionarily, and pertinent observations seem to support it; however, a combination of (i) and (iv), a "kamikaze-copulation" as described for mantids (*16*), is also possible. More than one explanation may be involved.

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5. Additional data and details are in preparation.
6. Several unnamed *Photuris* spp. in my revisionary work are designated by letter.
7. VR's pulsing pattern is emitted up to 17 m with only 24 percent below 3 m, whereas 90 percent of its flickers and glows are emitted below 3 m, the space of the *Pyractomena* ($N = 607$).
8. Sustained glows, as in *angustata* and VR, are exceptional ("unknown") for species whose congeners flash, and are usually restricted to genera regarded as behaviorally primitive—for example, *Robopus* spp. in Jamaica and *Phausis* spp. in the eastern United States.
9. J. E. Lloyd, *Coleopt. Bull.* **27**, 19 (1973); unpublished data.
10. *Photuris cinctipennis* flicker (25°C), $\overline{X} = 14.35$, standard deviation = 0.88, $N = 25$ flickers from 11 males. The single recording I have of *angulata* at a comparable temperature shows a rate of 12.5 Hz. Extrapolation of *angulata*'s rate-temperature regression indicates that the *cinctipennis* flickers were similar but not identical to those predicted for *angulata*.
11. Mark-release-recapture studies have not been made, but other evidence (such as transitional patterns at decoys) indicates that a single species emits the three patterns in Florida. It is possible that Maryland *cinctipennis* is a separate and sibling species. Regardless, these points are not critical to the phenomenon under consideration.
12. J. E. Lloyd, *Entomol. News* **80**, 169 (1969); E. G. Farnworth, thesis, University of Florida (1973).
13. If *Photuris* spp. were present in southeast Asia, they would end aggregative, sedentary mating systems of *Lucola* and *Pteroptyx* because males (and luminescing females) of these species are "sitting ducks." Similar behavior probably occurred in Western Hemisphere species before the evolution of *Photuris* predation. *Photinus pallens* of Jamaica does form sedentary aggregations, but it is larger than the resident *Photuris*.
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Nonolfactory Sensory Pathway to the Telencephalon in a Teleost Fish

Abstract. *Pathways conveying lateral-line sensory information within the brain of a bullhead catfish terminate in a localized zone within the telencephalon. Thus, the telencephalon in teleosts, as in amniote species, contains regions that receive specific sensory input. Therefore, this lemniscal organization is not restricted to mammalian or amniote species but is a feature common to most, if not all, vertebrates.*

One concept of the evolution of the vertebrate central nervous system (CNS) is that in the "primitive vertebrate condition," the telencephalon was associated only with the olfactory apparatus. The evolution to the mammalian brain is viewed as a process of "encephalization" in which nonolfactory functions invade and finally dominate the telencephalon (*1*).

The brain of mammals and other amniote vertebrates contains a number of lemniscal channels, separate sensory pathways ascending from specific sensory nuclei in the brainstem to an ultimate telencephalic target (*2*). In mammals these telencephalic sensory target zones lie within the pallium, that portion of the telencephalon covering the lateral ventricle. The telencephalon of teleost fishes, however, lacks a neural pallium. Perhaps for this reason, a number of investigators have concluded that the telencephalon in teleost fish contains no specific sensory areas and acts instead as an "olfactory correlation" or "general arousal area" (*3*). However, recent evidence indicates that, at least for some elasmobranch fishes, information from nonolfactory sensory systems has access to the telencephalon (*4*). I undertook this study to determine whether one major nonolfactory sensory modality, the lateral line system, ultimately projects to a restricted area within the telencephalon of a teleost.

The primary sensory area for the lateral line system in fish lies within the rostral medulla (*5*). A prominent fiber bundle, the lateral lemniscus, leaves the primary lateral line sensory area, decussates, and ascends within the brainstem to terminate in the torus semicircularis of the mesencephalon (*5*). Until recently, higher order connections of the lateral line sense were largely a matter of conjecture on the basis of normal anatomical material. Many investigators have reported that the torus semicircularis provides a substantial input to the optic tectum (*6*). The tectum, then, was envisioned as a coordinating center for the various sensory modalities (*6*). Recent studies, however, indicate that the optic tectum is not the major target for the fibers arising in the torus semicircularis (*7*).

The bullhead catfish (*Ictalurus nebulosus*) was chosen for this study because it has a well-developed lateral line system comprising both mechanoreceptive and electroreceptive modalities. These modalities maintain separate CNS representations at both the medullary and mesencephalic levels (*5*). I dealt primarily with the connection of the mechanoreceptive component of the lateral line system.

Efferents of the torus semicircularis were determined by means of anterograde tracer techniques. A small quantity (20 to 30 nl) of tracer was injected under pressure through an oil-filled glass pipette system or applied on the tip of an insect pin (*8*). Horseradish peroxidase (HRP) is an efficient anterograde (as well as retrograde) tracer in fish (*9*); thus an injection into a given zone will label axons which arise from neurons lying within the injected zone. The mechanoreceptive torus as described by Knudsen (*5*) of three fish was injected with HRP (Sigma type VI or Boehringer Mannheim) by means of the insect pin method. In one other animal, the same region of torus was injected by means of the glass pipette in order to minimize contamination of the overlying optic tectum. For these and following HRP cases, the animals survived 2 to 6 days postoperatively, after which they were reanesthetized and perfused with 4 percent glutaraldehyde in 0.1*M* phosphate buffer. The brains were then sectioned and processed for peroxidase (*10*). Tritiated proline (10 mCi/mmole) was injected by means of a glass pipette into the mechanoreceptive torus of yet another animal. After 2 days, the animal was perfused through the heart with 10 percent Formalin and processed for autoradiography (*11*).

For purposes of comparison, the electroreceptive torus rather than the mechanoreceptive portion was injected with HRP in two additional animals. To control for spread of the tracer substances into the optic tectum, four tectal injections were carried out, three with HRP and one with tritiated proline. Injections of tracer into either optic tectum or electroreceptive torus did not label fibers terminating in the thalamic zone, which receives input from the mechanoreceptive torus.

Injection of an anterograde tracer into the mechanoreceptive torus semicircularis revealed a major efferent bundle which emerges from the ventrolateral aspect of the torus semicircularis and turns anteriorly toward the diencephalon (Fig. 1). Most fibers terminated ipsilaterally within a complex of nuclei lying within a ventral region of the thalamus and extending rostrally nearly to the level of the ansulate commissure. These nuclei, herein termed the mechanoreceptive thalamic zone, lie medial to the lateral recess of the third ventricle but do not extend to the medial wall of the diencephalon. Some of the toral efferent fibers cross the midline in the ansulate commissure. A fraction of these terminate in the contralateral mechanoreceptive thalamic zone, but the bulk of the crossed fibers turn caudally to end in the contralateral torus semicircularis. A minor thalamic target of the toral efferent system lies between the medioventral thalamic nucleus and dorsal pretectal nucleus. Toral efferents were also traced to the optic tectum and midbrain tegmentum.

Since HRP is taken up by axon terminals and transported in a retrograde direction to label the cell bodies sending axons into the injection site, different areas of the telencephalon were injected with HRP in 12 fish to test for an ultimate telencephalic target for the lateral line system. The animals were processed for HRP as described above, and the brains were examined for the presence of retrogradely labeled neuronal somata. Retrograde labeling in the mechanoreceptive thalamic zone would indicate that the axons of those cells terminate in the telencephalon.

Cells within the mechanoreceptive thalamic zone were retrogradely labeled after some but not all injections of HRP into the telencephalon. Optimal retrograde labeling occurred only when the injection site included the area dorsalis centralis (DC) underlying the posterior area dorsalis medialis (DM) of the telencephalon. Injections confined to DM labeled very few of the mechanoreceptive thalamic zone (MTZ) neurons. Furthermore, HRP injections located more anterior, lateral, or medial to the indicated site fail to retrogradely label the MTZ neurons. Thus, the telencephalon seems to contain a limited target zone for ascending mechanoreceptive lateral line information.

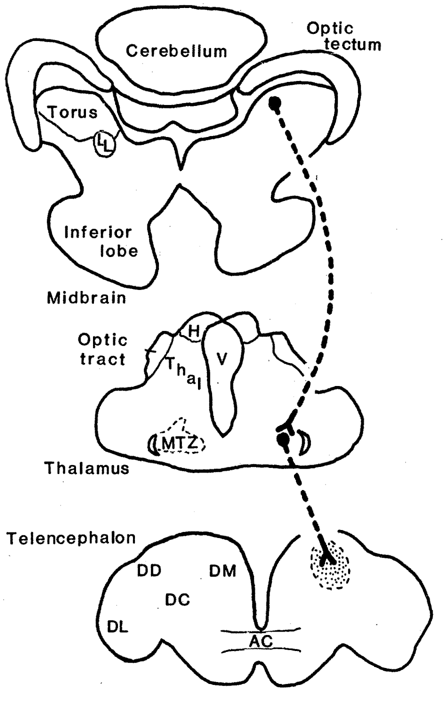

Fig. 1. Schematic indication of the lateral line pathway to the telencephalon in the catfish. Neurons in the torus semicircularis project to the mechanoreceptive thalamic zone (*MTZ*), which relays the information to a specific area in the dorsal part of the telencephalon (stipple). Abbreviations: *AC*, anterior commissure; *DC*, area dorsalis centralis; *DD*, area dorsalis dorsalis; *DL*, area dorsalis lateralis; *DM*, area dorsalis medialis; *H*, habenula; *LL*, lateral lemniscus; *Thal*, dorsal thalamus; *Torus*, torus semicircularis; *V*, third ventricle.

The results indicate that the lateral line sensory system maintains a distinct lemniscal pathway within the CNS up to the telencephalic level. Contrary to earlier reports, lateral line information does not predominantly end in the optic tectum after reaching the torus semicircularis. Rather, the torus semicircularis projects massively to a zone within the ventral half of the thalamus, which then projects to a restricted area in the dorsal telencephalon.

The central organization of the mechanoreceptive lateral line system resembles the central auditory pathway in amniotes (*2, 12*) in terms of the general location and number of sensory nuclei and the point of decussation of the pathway. The mechanoreceptive lateral line system, like the auditory lemniscus, proceeds from a primary sensory area in the rostral medulla, across the midline to a midbrain relay nucleus (inferior colliculus or MLD), then to a thalamic nucleus (medial geniculate or nucleus ovoidalis), and finally to a specific telencephalic target area. In catfish, acoustic inputs reach at least a limited portion of the MTZ (*13*). Whether or not acoustic information reaches the telencephalon in catfish remains to be determined.

The similarity in the central organization of the auditory and lateral line systems might be ascribed to their both being hair-cell sensory systems. However, the electroreceptive lateral line modality, also a hair-cell sensory system, does not share the thalamic relay nucleus with the mechanoreceptor and auditory systems (*13*). The central organization of the electroreceptive lateral line system rostral to the midbrain remains unknown.

In light of recent data on limited distribution of the olfactory tracts (*14*) and the presence of lateral line input to the telencephalon, the concept of the fish telencephalon as a purely olfactory structure should be abandoned. The presence of a restricted lateral line target area in the telencephalon lends credence to the hypothesis that lemniscal pathways are not limited to mammals or amniotes but are a general feature of the organization of the vertebrate nervous system (*2*).

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Attentional Factors in the Inhibition of a Reflex by a Visual Stimulus

Abstract. *A brief stimulus presented to various regions of the visual field inhibited the eyeblink elicited by a subsequent tap to the skin between the eyebrows. Subjects were able to switch their attention toward or away from the target area without moving their eyes. In doing so they changed the amount of inhibition.*

More than a century ago, Helmholtz noted the "curious fact" that by mere conscious effort one can focus attention on any portion of the visual field and that the process "is entirely independent of the position and accommodation of the eyes" (*1*). According to Helmholtz, an observer might be gazing at a fixation point while at the same time concentrating on some other part of the visual field. If, at this moment, a stimulus is presented briefly, the observer's impression of its features in the attended region will be markedly enhanced.

We wondered whether a reflex-modification procedure could be used to study the attentional phenomenon that Helmholtz described. Reflex-modification describes the finding that almost any sensory event presented prior to a reflex-eliciting signal can, given an appropriate lead interval, inhibit the reflex so that it either fails to occur or occurs with reduced amplitude (*2, 3*). We asked if the amount of reflex inhibition engendered by a brief visual stimulus would vary as a function of its location in the visual field and if this amount would change when subjects were told where the stimulus would appear.

In these experiments, the target response was the reflexive eyeblink elicited by a brisk tap to the glabella (the flattened region between the eyebrows), and the reflex-modifying stimulus was a brief (50-msec) spot of light presented 150 msec before the tap. The spot of light subtended a visual angle of 2° and had a brightness of 5.38 μL, a value that was near but clearly above the threshold for its detection.

The devices for eliciting and measuring the eyeblink have been described elsewhere (*3*). Briefly, they consisted of a miniature solenoid and a d'Arsonval meter, the pointer of which was connected to a length of polyethylene tubing fastened to the left eyelid with a small piece of micropore tape. Both units were attached to a lightweight headband and were positioned so that activation of the solenoid (15 V d-c for 30 msec) caused a silicone rubber ball (5 mm in diameter) to strike the glabella. The resulting eyeblink caused the meter coil to move through a magnetic field, generating a voltage that was amplified and displayed on a storage oscilloscope. Visual stimuli were produced by briefly illuminating a grain-of-wheat bulb mounted behind a neutral density filter fastened to the cursor of a standard perimeter. The track on which the cursor rode girded a black, fiberboard half cylinder (radius, 28 cm) having a series of 1-cm (diameter) holes along the horizontal meridian at 0° (the foveal location) and 20°, 40°, 60°, and 80° in both the nasal and temporal fields. Translucent plastic covered each hole so that the subject could not tell where the cursor was and hence where the flash might appear. Just above 0° were two additional holes; behind one was an infrared light source and behind the other was the telescopic lens of an infrared television camera used to monitor the subject's direction of gaze (*4*).

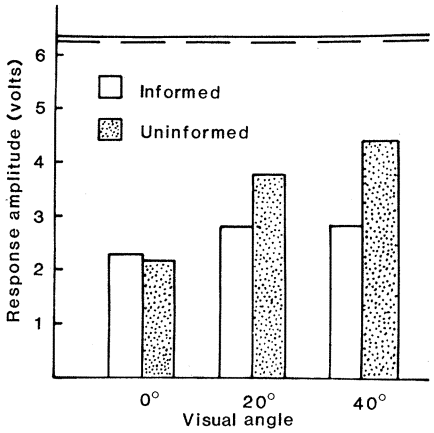

Fig. 1. Mean amplitude of tap-elicited eyeblinks when taps were preceded by a reflex-inhibiting light flash at various visual angles. Subjects were either informed or uninformed of where the flash might appear. Also indicated are the mean amplitudes of tap-elicited eyeblinks on control trials when subjects were informed (solid line) or uninformed (dashed line) of where a flash might appear, but the flash was withheld.

Testing was conducted in a dimly illuminated room. After a subject had been fitted with the headband and experienced a few taps, she was told that a series of such taps would be delivered and that on some trials the tap would be preceded by a flash of light in one or another of the holes. Subjects were told that they need pay no attention to the taps but that they should report when and where each flash appeared. At the start of a trial, the subject placed her chin in the chin rest and fixated her right eye on a small (visual angle, 4 minutes) point of dim light 2 cm above the 0° location.

Twenty subjects (*5*) each received 36 trials at intervals of approximately 15 seconds. Each trial ended with a tap. On half of the trials the subject was informed of where the light flash might appear. This instruction had the following form: "If there is to be a visual stimulus on this trial it will appear at location *X*." Of the 18 informed trials, 12 contained a tap preceded by a reflex-modifying light flash at either the foveal location (0°) or at the 20° or 40° locations on the temporal side. This stimulus was presented at each of these three locations four times. On the remaining six informed trials (two per location) the tap was presented but the visual stimulus was withheld. On the 18 uninformed trials, subjects received no instructions regarding the location of

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