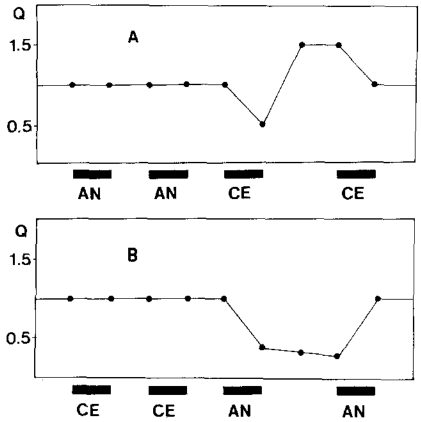

Fig. 2. Reaction spectra of the neuron from Fig. 1. A) Cercal stimuli after antennal stimuli. B) Antennal stimuli after cercal stimuli. *Q* quotient of actual action potential frequency and mean spontaneous frequency. Shown is the frequency at the onset and offset of the stimuli. Stimulus duration 1 s. *AN* mechanical stimulus to ipsilateral antennae, *CE* mechanical stimulus to ipsilateral cercus

an antennal stimulus, a cercal stimulus is given, an inhibitory response is exhibited with a long-lasting excitatory after-effect (Fig. 2A). The reverse situation, an antennal stimulus after a cercal also causes an inhibition which will be terminated if a new antennal stimulus is presented (Fig. 2B). These effects could only be elicited by this stimulus configuration and only if the delay between the different stimuli did not exceed 5 s. The spontaneous activity and the sensitivity of this neuron depend on the combination and succession of the stimuli.

Possible explanations for this neuronal plasticity could follow from the hypothesis of reverberating circuits [10]. Applied to the mushroom-body system, the following is proposed. The spatial separation of the in- and outputs leads to uni-directional flow of excitation (or inhibition) in the mushroom-bodies themselves. The physiological and anatomical features of some of the extrinsic elements lead us to propose circular information flow in the whole mushroom-body system, comprised of extrinsic and intrinsic elements. Depending on environmental influences, such an extrinsic neuron comes into a specific condition and stays there, because of the feedback loop via the mushroom-bodies, until a new stimulus resets the neuron to the former situation. In this way these neurons could contribute to complex integrative processes, such as those causing memory formation or the release and control of specific behavior or behavioral sequences.

I thank Prof. F.W. Schürmann and Dr. R. Cassada for useful comments on the manuscript. The work was supported by a grant from the DFG.

Received September 23, 1981

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Surface Wave Sensitivity of the Lateral Line Organs of the Topminnow *Aplocheilus lineatus*

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The surface-feeding fish *Aplocheilus lineatus* (Pisces, Cyprinodontidae) mainly feeds on flying insects trapped on the water surface. It detects and localizes the surface waves generated by the struggling of the prey with lateral line receptors located on its flattened head and dorsal body surface. While the sensitivity of *A. lineatus* and other surface-feeding fish to surface waves has already been investigated in behavioral experiments [1, 6, 7], the threshold values of the sense organs involved are determined electrophysiologically for the first time in the present study. The lateral line system on the head of *A. lineatus* consists of 3 groups of 3 single neuromasts located dorsolaterally on each side (Fig. 1A). For technical reasons recordings were made only from organ II/2 (long axis diverging 5.8° from long axis of body; for numbering see [6]).

For the experiments the fish were anesthetized by immersion in tricaine methanesulfonate (MS 222, Sandoz) or cold water (8–10 °C), paralysed by subcutaneous Flaxedil injection and placed in an experimental tank filled with Ringer solution [10]. The head was fixed by means of a clamp inserted into the mouth so that the head of the fish contacted the water surface in the same way as in animals hovering for prey.

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Series of sinusoidal wave trains (duration 1 s, rise- and fall times 200 ms) with frequencies in the biologically significant range between 10 and 250 Hz were used for stimulation. Wave amplitudes were measured using a He-Ne-laser beam reflected from the water surface (Fig. 1A). The displacement of the laser beam was monitored with a position-sensitive photodiode and calibrated as described in [9].

Multiunit activity was recorded from a branch of the truncus supraorbitalis (ramus ophthalmicus superficialis) (method see [8]), which innervates only organ II/2. Only those preparations where a clear answer to a drop falling on the water was given (12 out of 18 animals) were used. For each frequency tested the wave amplitude was increased until a distinct answer could be heard on the spike audio monitor and/or recognized in the PSTH after 32 sweeps. This displacement amplitude was defined as vibration threshold and is given as pp-value. In most cases the PSTH showed a strong twice stimulation frequency component.

The organ II/2 of the head lateral line system of *A. lineatus* is very sensitive to water surface waves (Fig. 1B). The threshold curve decreases sharply from 3.4 μm ± 3.1 (mean and S.D.) at 10 Hz to 0.04 μm ± 0.01 at 100 Hz and remains at this low level with values slowly increasing up to 0.09 μm ± 0.03 at 180 Hz and 1.2 μm ± 1.0 at 250 Hz. Thresholds at frequencies greater than 250 Hz were not determined for technical reasons. The threshold values measured for the sense organ are higher

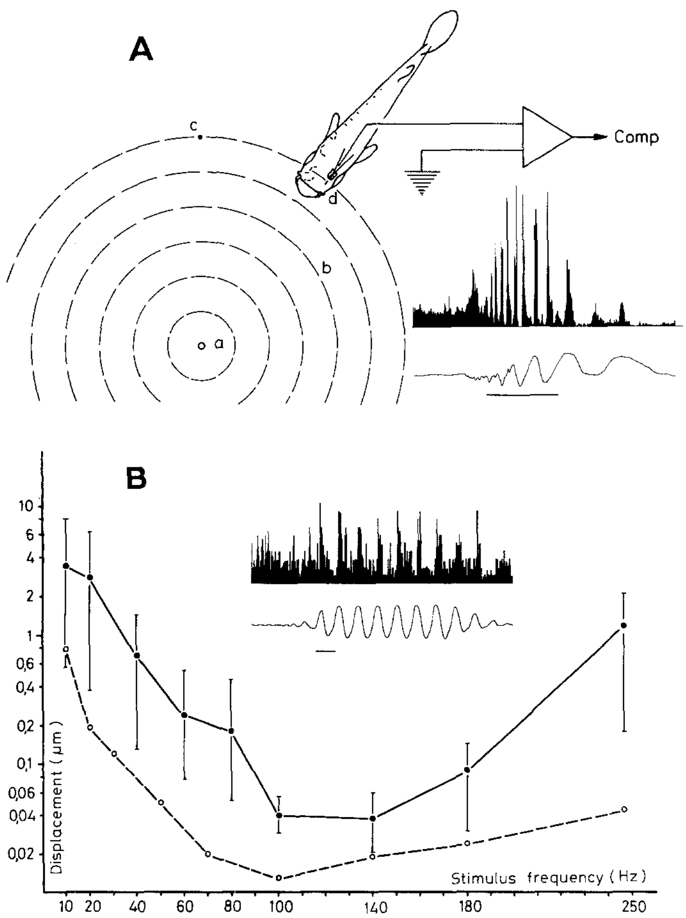

Fig. 1. A) Experimental arrangement: A vibrator (*a*) generates sinusoidal surface waves (*b*) whose amplitudes are measured (*c*) at a distance to the wave source equal to that of the lateral line organ recorded from (*d*). In all cases the fish was oriented so that the waves travelled along the long axis of organ II/2 (=direction of max. sensitivity). All lateral line organs involved in surface wave perception are shown on the right hand side of the fish; on the left hand side only II/2 is shown. After removing 3 scales caudally to organ II/2 the surface of the skull was thinned with a dental burr and cut away with scissors to expose the nerve. The nerve was hooked onto a 30 µm silver wire, cut distally before entering the skull and lifted clear of the surface of the Ringer solution. Inset: PSTH (bin-width 1 ms, 100 sweeps) to a click of 20 µm max. displacement. In this case the wave signal was recorded at organ II/2 itself by measuring the electrical resistance between a submersed Ag-AgCl emitter electrode and a receiver electrode (method see [4, 7]). *Comp* computer. B) Mean threshold amplitude (●) and deviation of impulse initiation by sine wave stimulation. Behavioral thresholds (○) [1] are shown for comparison. Inset: PSTH (2 ms bins, 32 sweeps) evoked by a 10-Hz signal (3 µm displacement). Time bars 100 ms

than behavioral thresholds by a factor 3 to 5 (Fig. 1B). Since our electrophysiological recordings were made from single organs we assume that this difference is due to the ability of the intact animal to integrate information from up to 18 or more neuromasts.

In three fish the response to click signals (heterofrequency) were also measured (inset Fig. 1A). The lateral line organ is more sensitive to the fast propagating high-frequency part at the beginning of a click than to the more slowly propagating low-frequency components. The threshold for the first water ripples contained in a click (frequency, depending on the max. amplitude, from 140–170 Hz) varies between 0.01 and 0.05 µm whereas it is between 1.65 and 3.5 µm for the last waves (10–15 Hz). For *A. lineatus* in the most sensitive frequency range both the behavioral [1] and electrophysiologically determined thresholds are 5 to 10 times lower than those previously published for other fishes and amphibians (e.g. [3]).

For technical reasons, these experiments were performed in Ringer solution. The surface wave orientation reaction of *A. lineatus* kept for 14 days in Ringer solution showed no significant difference to those of control animals in water. In addition recording of microphonic potentials from II/2 in water obtained similar threshold values [9] to those reported here (e.g. 0.06 µm at 25 Hz) and we therefore conclude that the ionic milieu [5] did not significantly affect our data.

Abiotic waves caused by wind or falling leaves and branches have an energy maximum in the 8–14 Hz region and do not contain frequencies beyond 50 Hz. Prey-generated waves, on the other hand, contain frequencies as high as 70–140 Hz and their displacement maxima are in the 12–45 Hz range [4]. Since the lateral line system of *A. lineatus* is particularly sensitive to these higher frequencies the fish should be able to separate prey-elicited waves from such abiotic waves at a reasonable distance (about 15–20 cm), despite the strong damping of high-frequency waves at the water/air interface (e.g. 8.6 dB/cm at 140 Hz [4]). It has been demonstrated recently that *A. lineatus* can discriminate surface waves of different frequencies [2].

Supported by the Deutsche Forschungsgemeinschaft (grant to E. Schwartz Schw. 21/5). We thank Prof. E. Schwartz for his support in this work and Prof. F.G. Barth for critically reading the manuscript. Our thanks are further due to D.M. Caird for translating the manuscript and B. Kahnert for technical advice.

Received October 14, 1981

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