The Importance of the Lateral Line System for the Perception of Surface Waves in the Claw Toad, *Xenopus laevis* Daudin

Claw toads react to concentric surface waves with a movement towards the wave-centre[1]. It was found that among various surface fishes which behave in a similar way the waves are perceived by means of the lateral line system[2–6]. The fact that this system in *Xenopus* is highly sensitive to water currents[7–9] suggested that it might be the receptor organ responsible for the toad's reaction[10]. However, experiments on *Xenopus*' ability to localize a wave-centre gave a surprising result.

Blinded toads (*Xenopus laevis* Daudin) were kept singly in plastic containers (ca. 26 × 35 cm). Before an experiment the water level was adjusted so that there was at least 5 mm of water above a submerged animal. In the experiment, a metal or glass rod (0.5–3 mm in diameter) was dipped into the water at a point near the extremities of the toad or about 10 mm away from its body. For each experiment at least 3 toads were used and at least 280 trials were conducted for each toad.

Untreated control toads turned towards the dipped rod in 50–80% of trials (Figure 1). These percentages indicate mean positive reactions of individual toads to stimuli from all sources (A–H), whereas the columns in Figures 1 and 2 denote mean positive reactions of all (n) toads to stimuli from the individual sources.) In 3 toads the lateral line system was completely destroyed with a thermocauter: nevertheless the animals still reacted to the stimulus (54% of trials, Figure 1), indicating that there must be another receptor responsible for the perception of surface waves besides the lateral line system. Since the waves are accompanied by pressure changes, involvement of the labyrinth was suspected. After unilateral extirpation of the labyrinth in toads whose lateral line system had been destroyed, the animals reacted only occasionally (23% of cases) to the dipped rod, depending on which side of the toad the rod was dipped (Figure 2). When dipped on the side with the intact labyrinth, the toad, if it reacted at all (34% of cases), turned towards the stimulus. When the stimulus was on the other side it turned in the wrong direction as often (10.1% of trials) as in the correct one (10.6% of trials).

However, the lateral line system is not without significance for the localization of the stimulus: 1. Toads with an intact lateral line system but with 1 labyrinth destroyed turned in the correct direction in nearly all trials regardless of which side the stimulus occurred (0.3% incorrect to 43% correct responses); 2. Electrophysiological experiments on isolated toads' skins showed that the sensitivity of the lateral line system can be markedly reduced by drying the neuromasts with a stream of air, thereby making the cupula and sense hairs adhere to the skin. Immediately after this treatment, the organ does not show any alteration of the spontaneous activity on stimulation with a water current, and only after about 2 h do weak reactions begin to indicate recovery. Behavioural experiments demonstrate a similar effect: toads were anaesthetized and their lateral line system dried. When the animals came round 2 h later they still reacted to the stimulus but less frequently than did untreated animals (55% in treated, 69% in untreated animals: $P < 0.001$). Sensitivity was completely restored 2 to 6 days after the

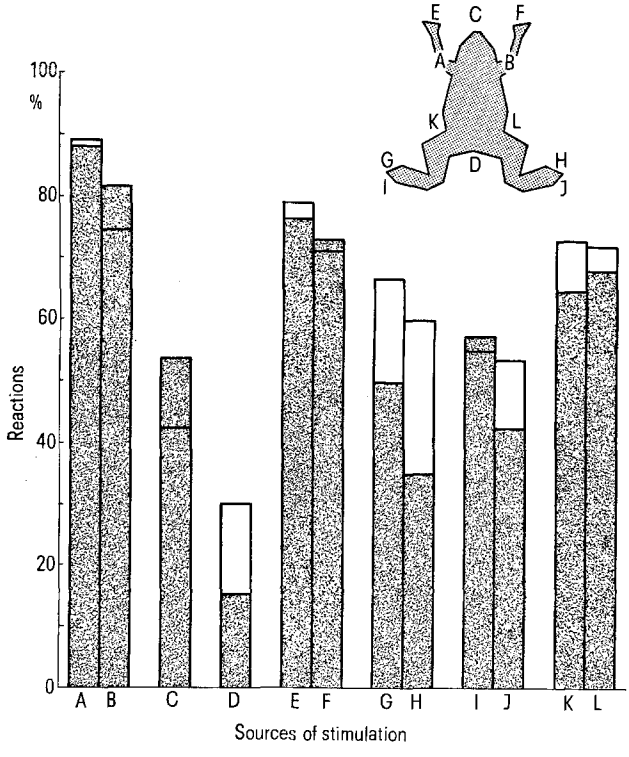

Fig. 1. White columns or the horizontal line in the grey columns, reactions of 17 blinded toads to a dipped metal or glass rod. 10831 trials. Grey columns, reactions of 3 blinded toads after destroying all neuromasts. 851 trials. Letters indicate sources of stimulation (see insert).

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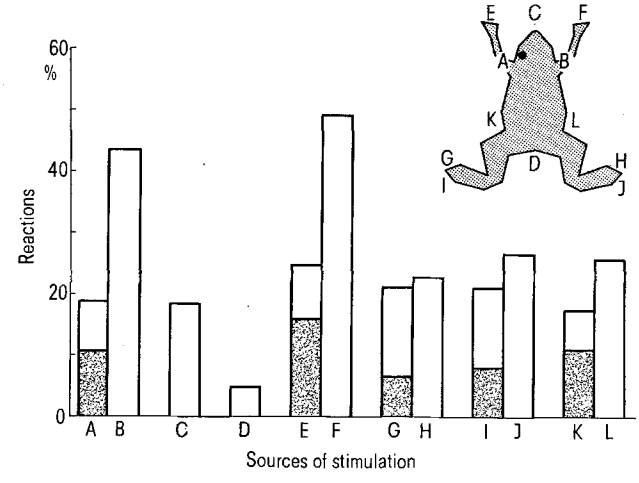

Fig. 2. Reactions of 3 blinded toads after destroying all neuromasts and after extirpating the left labyrinth. The black part of a column indicates reactions to a side opposite to the stimulus. 2993 trials.

drying treatment. Drying of the skin next to the lateral line system did not affect the reaction ($P = 0.8$).

These experiments show that both the lateral line system and very probably the labyrinth are essential for the perception of surface waves.

The part of the labyrinth where the stimulus is perceived seems to be the organ of hearing. After removal of both columellae, the animals reacted in only 52% of trials compared with 68% before the operation ($P < 0.001$). It is not yet clear whether it is the sound of the surface waves which is heard or the noise made by dipping the rod. Our previous experiments (made partly in collaboration with P. MOLLER) support the former possibility: the time before the animal's reaction increases significantly with increased distance of the stimulus, and, as film studies show, the reaction does not take place before the maximum of the wave train has reached the toad. However, since the noise intensity caused by dipping the rod would decrease with increasing distance from the toad and might thus cause greater latency of reaction, we still cannot exclude the possibility that it is the actual dipping of the rod which is perceived rather than the surface waves caused by the rod. The experiments continue[11].

Zusammenfassung. Blinde Krallenfrösche reagieren auch dann auf konzentrische Oberflächenwellen, wenn das gesamte Seitenliniensystem zerstört wird. Weitere Ausschaltversuche zeigen, dass der Reiz (Eintauchen eines Stabes) sehr wahrscheinlich über das Labyrinth perzipiert wird. Ob die Oberflächenwelle selbst oder (und) das Geräusch beim Eintauchen des Stabes wahrgenommen wird, ist noch nicht sicher entschieden.

P. GÖRNER[11]

II. Zoologisches Institut der Freien Universität, Grunewaldstrasse 34, 1 Berlin 41 (Germany),
19 October 1972.

[11] My thanks are due to Dr. M. L. MITTELSTAEDT for critical help and to Miss A. MIDDELMANN for valuable technical assistance. This work was partly supported by a grant from the DFG.

Neurohumoral Regulation of Motility and Blood Flow in the Colon

The extrinsic nervous control of colonic motility and blood flow has recently been studied[1]. Electrical stimulation and reflex activation of the pelvic nerves produce an intense flushing of the mucosa in the distal two thirds of the colon. Corresponding in time with this mucosal flush there is a marked but transient increase of venous outflow and concomitantly with the vasodilatation a mucoid secretion. Intravenous administration of atropine (1 mg/kg) did not significantly interfere with the vasodilation and the motility response indicating that both might be brought about by a non-cholinergic mechanism largely secondary to an augmented secretion. The release of kinin-like substances similar to those involved in the atropine-resistant vasodilatation in the salivary glands and the pancreas[2,3] is suggested.

In the present study the effects of bradykinin and pelvic nerve stimulation on colon motility and blood flow were compared in an attempt to obtain evidence for bradykinin as a possible mediator in the pelvic nerve response.

Methods. By recording tissue volume and total venous effluent simultaneously, the resistance, the capacitance and the precapillary sphincter segments of the circulation of the cat colon were studied. This pletysmographic method was described in detail in a previous work[1]. In some experiments colonic motility and blood flow were recorded simultaneously. Motility was recorded by a volumetric method keeping intra-colonic pressure constant at about 10 cm H_2O. The pelvic nerves to the colon were cut centrally and mounted on ringformed electrodes for subsequent graded electrical stimulation. Synthetic bradykinin was administered close-intra-arterially.

Results. As is shown in Figure 1, close intraarterial infusion of bradykinin in a large dose (1 µg/ml) produced a marked and shortlasting blood flow increase and con-

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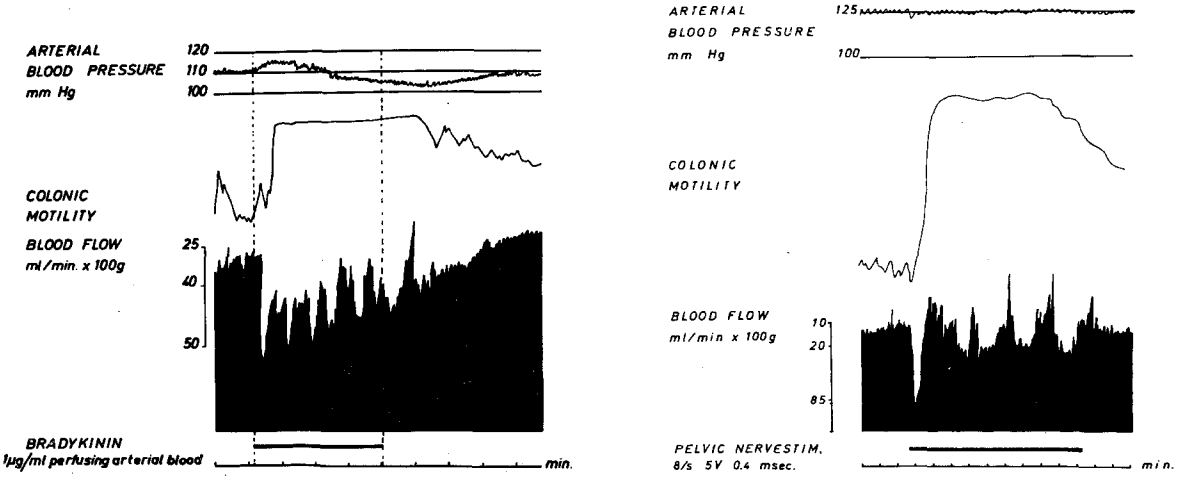

Fig. 1. The effect of supramaximal, intraarterial doses of bradykinin (left panel) and supramaximal pelvic nerve stimulation (right panel). Note the almost identical responses.