

## The role of ventral lateral line organs in water wave localization in the clawed toad (*Xenopus laevis*)

Andreas Elepfandt

Universität Konstanz, Fakultät für Biologie, Postfach 5560, D-7750 Konstanz, Federal Republic of Germany

Accepted March 23, 1984

**Summary.** 1. The role of the ventral lateral line organs in water surface wave localization in the clawed toad, *Xenopus laevis* Daudin, was tested in blinded animals with various lesions of lateral line organs.

2. After destruction of all its dorsal lateral line organs, but with all its ventral organs intact, *Xenopus* shows normal responsiveness and full response accuracy to waves from any direction (Fig. 2).

3. Additional partial destruction of ventral organs seriously impairs wave localization (Fig. 2). Determination of the stimulus side, however, is mostly not affected by these lesions (Table 1). Thus, information about the side to which to turn, and the angle through which to turn are obtained differently from lateral line input.

4. *Xenopus* with only one side's dorsal receptors intact responds to waves as accurately as animals with intact dorsal and ventral receptors on that side (Fig. 2). Thus, ventral input does not improve accuracy of localization in the horizontal plane beyond that provided already by the dorsal receptors alone.

5. *Xenopus* with only its ventral receptors intact shows a significant increase in turning down, which is specific for this type of lesion (Table 2). Thus, comparison between dorsal and ventral inputs is involved in vertical localization.

6. In *Xenopus* with only its ventral receptors on one head side intact, turn angles to given stimulus angles vary more than in specimens with total lateral line destruction. This suggests a hierarchy in *Xenopus*' reliance on its sense organs for wave localization in that even indistinct lateral line input is taken as more relevant than the information from the frog's other wave localizing organ(s).

### Introduction

The clawed toad *Xenopus*, a purely aquatic frog, can determine the direction of water surface waves impinging on its body and responds to them with a turn into the direction of the waves' origin (Kramer 1933; Dijkgraaf 1963). Detailed analysis substantiated previous assumptions (Kramer 1933; Dijkgraaf 1947, 1963; Görner 1973) that the underlying localization is done by means of the animal's lateral line system and demonstrated that the frog can localize waves from any direction with full accuracy even if only small subgroups of the lateral line organs (stitches) are left intact (Elepfandt 1982; Görner et al. 1984).

No attention, however, had been paid in these investigations to the role of the ventral stitches, which in *Xenopus* comprise approximately 30% of the whole system's sensory inputs. Water surface waves are not limited to the surface but extend also into the depth (Sommerfeld 1970). *Xenopus*' ability to localize waves also when it is sitting on the bottom of a shallow water reflects this fact. But the strength of the wave decreases exponentially with depth, so that under normal circumstances input to the dorsal organs is stronger and thus ventral input conceivably could be disregarded for wave localization by the animal. Such partial neglect of lateral line input for wave localization is found in surface feeding fish, where destruction of only the lateral line organs on the head completely abolishes normal orienting responses to water waves (Schwartz 1965). (Recently Müller and Schwartz (1982) induced water wave taxis after total lateral line ablation in the fish *Aplocheilichthys lineatus*. But for this reaction a specific pretraining is necessary, and the time course of the responses

differs from that of lateral line taxis, so these responses are not relevant to lateral line system organization).

The present study shows that *Xenopus* can still determine wave directions with full accuracy after destruction of its dorsal lateral line organs, and further analyzes the organization and role of the ventral organs for localization.

## Materials and methods

Adult male and female *Xenopus laevis* Daudin were taken from the laboratory colony. Since large specimens are unwilling to make large turns (Elepfandt 1982) smaller specimens of only 30–50 g body weight (6–8 cm snout to anus length) were chosen. To eliminate visual responses, animals were blinded by enucleation. Lesions of the lateral line system were made by electrocoagulation of the appropriate stitches. The snout was taken as the rostral border between dorsal and ventral sides (Fig. 1), so that the term ventral lateral line organs indicates the mandibular, hyomandibular, anterior lower, posterior lower, median ventral, and anal lateral lines, whereas the maxillary lateral line, which fringes the snout rostrally, is taken as part of the dorsal lateral line organs (nomenclature after Shelton (1970)). Experiments started three days after lesioning and lasted 2–4 weeks, dependent on the difficulty of eliciting responses from the animal after the lesion. After each test series inspection under the dissection microscope verified that destroyed stitches had not regenerated.

For testing, the blinded and lesioned frog was placed individually in a large circular water basin of 90 cm diameter and 7 cm water depth and was given few days for adaptation. It remained in the basin for the entire test period. During the test *Xenopus* was stimulated in open loop by dipping a small rod into the water at fixed angles relative to its longitudinal axis (0° indicates frontal direction). Stimulus intensity was 100–400  $\mu\text{m}$  p-p (cf. Elepfandt 1982). Stimuli were given only when the animal was at rest. The frog responded to frontal stimulation by swimming forward, and by turning to stimuli from the side or behind. Response angles were measured via a video system suspended overhead and compared to the re-

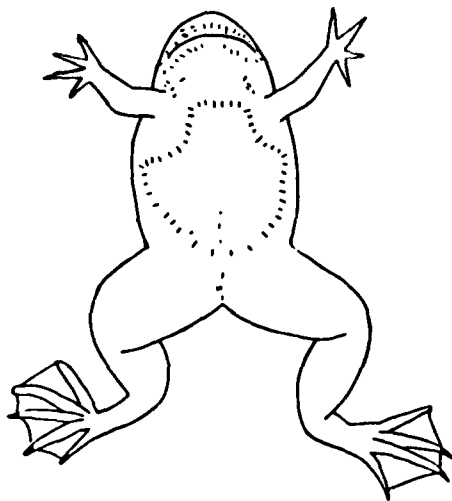


Fig. 1. Location of the ventral lateral line organs and the maxillary lateral line organs in *Xenopus laevis* (after Murray 1955)

sponses of specimens with intact lateral line system and of specimens with all stitches destroyed. Stimulation during a test was continued, until the animal had responded ten times to each stimulus angle. Sample size for comparison was ten tests from at least three animals. In *Xenopus* without organs or with only one side's ventral head stitches left intact the appropriate number of responses had to be gathered from a higher number of tests, because these specimens were quite unresponsive. Response angles were compared for differences in their mean and their variance to any given stimulus angle using H- or U-tests. Rates of contralateral turns were compared using the Fisher-test. For further details see Elepfandt (1982).

In addition, during testing the vertical position ('up' and 'down', for detailed description see Results) of the animal was noted at the beginning and end of each response. The effect of lesions on vertical positioning was tested with the Fisher-test.

## Results

*Xenopus'* ventral lateral line organs (Fig. 1) are localized mainly at the animal's snout – which is generally raised slightly when *Xenopus* is sitting on the bottom – or ventrolaterally along the trunk. Thus, even when *Xenopus* is sitting on the bottom, most ventral stitches are accessible for waves. However, the wave pattern in this situation is certainly rather distorted by reflexions from the bottom and the frog itself, so that the ventral input in a sitting *Xenopus* might be quite different from the input in cases when the wave can pass freely underneath the floating frog.

Response data of *Xenopus* with intact lateral line system and of *Xenopus* without lateral line organs agree with previous results (Elepfandt 1982). After complete lateral line elimination *Xenopus* still can localize wave directions to some degree, but its response accuracy is significantly worse than with intact system and, except for 90°, the difference was highly significant (Fig. 2, rows 1, 2).

*Xenopus* with all dorsal stitches destroyed but all ventral ones intact show normal responsiveness to waves from any direction. Response accuracy, too, is practically as good as with intact system (Fig. 2, row 3). Thus, ventral lateral line input is sufficient to localize accurately all wave directions and to elicit normal orienting behavior. The variance of responses to anterior stimulus angles is slightly increased (significantly at 0°). This does not necessarily indicate less accuracy of the ventral receptors, however, but might reflect worse physical conditions for orientation, since after dorsal destruction animals sit more on the bottom of the basin (see below) where the stimulus waves are weaker and more distorted by the substrate (Sommerfeld 1970).

Additional destruction of ventral organs affects both responsiveness and accuracy. If only the ventral stitches on one side are left intact, response

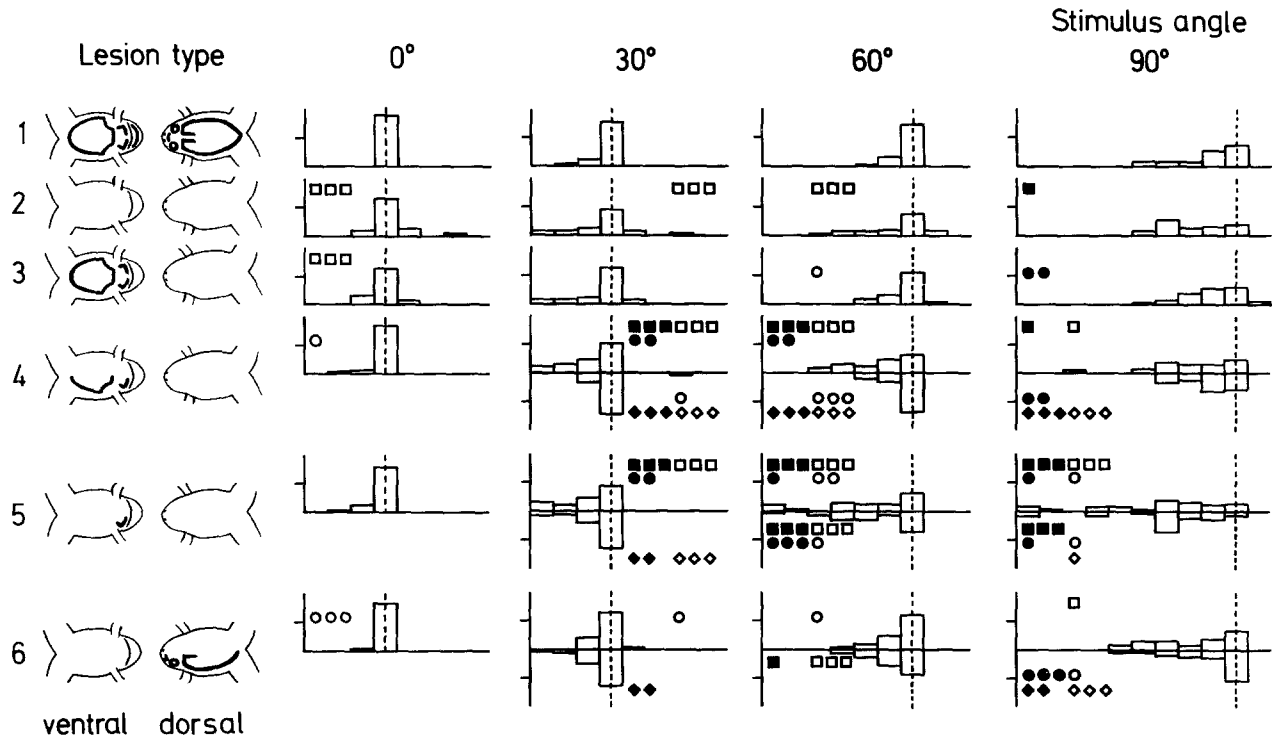
accuracy to stimulation from the more intact side is still normal, but responses to stimulation from the other side are more difficult to elicit and less accurate (Fig. 2, row 4). The effect is particularly strong at stimulation from anterior angles, where response accuracy is worse than without lateral lines. If finally only one side's ventral head stitches are left intact (i.e. one side's mandibular and hyomandibular lines), responsiveness is very low, and response accuracy to any wave direction is less than in specimens without lateral line organs (Fig. 2, row 5). In part this is due to a high percentage of responses in which the animal merely swims forward, which might be no localization response, but rather a search for a place where wave information would be clearer. But, even if these no-turn responses are eliminated from consideration, turn accuracy is still less than in animals without lateral lines, and the lower accuracy is not only expressed by a difference in the average turn angle, but also by highly significantly greater variances. This indicates that the animal still gains some directional information from its remaining stitches – otherwise response accuracy should correspond to that without lateral line input –, but that this information is so indistinct that the uncertainty about wave directions is higher than without it. In contrast to this poor angular information, the rate of contralateral turns is not raised after this lesion except for 150°-stimulation and significantly lower than in specimens without lateral lines (Table 1). That means that side information is not affected by these lesions.

Previous investigations had shown that *Xenopus* after unilateral lesion, i.e. all stitches destroyed on one side and all intact on the other, can localize all wave directions with nearly full accuracy (Elepfandt 1982). In specimens with only one side's ventral receptors intact however, accurate wave localization is confined to the receptor side (Fig. 2, row 4). This raises the question, whether the better performance of *Xenopus* with unilateral lesion is due to a better localization capacity of its dorsal receptors or whether it depends on compound dorsal and ventral inputs. Therefore animals were tested in which only their dorsal stitches on one side were left intact. These animals responded as accurately as animals with unilateral lesion, showing only minor differences from animals with intact lateral line system (Fig. 2, row 6). Thus, dorsal input alone is sufficient to account for turn accuracy of *Xenopus* with unilateral lesion, and joint dorsal and ventral inputs are neither necessary for localization nor does their combination improve response accuracy.

Evaluation of combined dorsal and ventral inputs was discovered, however, in another respect, namely vertical localization. Wave localization in *Xenopus* is not limited to the horizontal plane – though it is the most obvious part of the taxis response – but includes vertical localization. This localization is possible without vision, as can be seen in the blinded frog's ability to catch midwater swimming prey like guppy fish. Occasionally one also can observe how a blind *Xenopus* which had been floating at the water surface suddenly rushes backward down and immediately pushes forward at that height at which a fish just had swum through underneath the frog. Fish prey capture therefore does not depend on accidental encounters but involves active three dimensional orientation.

The involvement of the lateral line system and the comparison of dorsal and ventral lateral line inputs for this vertical localization could be demonstrated in the following way. In the experiments *Xenopus* between trials generally takes one of two resting positions, up (floating at the water surface, with its snout protruding slightly and its body hanging perpendicularly down) or down (sitting on the bottom of the basin), and this vertical position may be altered between trials as well as in the course of a response. By noting the vertical position of the frog at the beginning and at the end of a response one of the four alternatives 'up' (=start up, stay up), 'down' (start down, stay down), 'rise' (start down, end up), and 'dive' (start up, end down) can be attributed to each response. The proportion of these positions can vary between animals and in the same animal between experiments. Previous lesions with dorso-ventrally equal eliminations (Elepfandt 1982) had either not affected the frogs' vertical orientation or had led to a slight increase in up positions, which could be interpreted as a behavior to increase input intensity (waves are stronger at the surface). Animals with only ventral stitches intact, however, show an increased tendency to go down.

Table 2 presents the data of vertical positioning in seven frogs which were tested first with intact system, then after total dorsal lesion, and finally after destruction of all organs. To avoid bias the experimenter who recorded the vertical positions did not know the purpose of these measurements. With intact lateral line system, the specimens showed a wide range of vertical positioning, from nearly all up in one animal to nearly all down in another. This shows that the animals do not always come up to the surface, where the stimuli are presented. Avoidance of the water surface,



**Fig. 2.** Effects of various lesions of the lateral line system on response accuracy to water waves in *Xenopus laevis*. Each histogram shows the turn response angles to a stimulus delivered at the indicated angle. *Top*: stimulus angles; *left column*: lesion types, numbered and described by the location of the remaining intact receptors (black lines in inset figures): 1 all lateral line receptors; 2 none of them; 3 ventral; 4 ventral left side; 5 ventral left side on head; 6 dorsal left side. Histograms show the distribution of turns in 10° bins as a percentage of the total number of responses; the *tick marks* on the y-axes indicate 50%. Except for 0°- and 180°-stimulation only ipsilateral rotations are plotted; the *broken line* indicates the stimulus angle with values to the left of it indicating smaller response angles (at 0°-stimulation turns to the left). For asymmetrical lesions responses to stimuli from the more lesioned side are displayed upwards, to those from the other side downwards. Symbols indicate significant differences; *squares* indicate differences from intact animals; *circles* differences from totally lesioned animals, and *diamonds* designate differences between responses to right and left side stimuli; *filled symbols* indicate differences in average response angle; *open symbols* differences in variance. *Number of symbols* indicates the level of significance: one symbol 5%, two 1%, and three 0.1%

**Table 1.** Frequency of rotations to the contralateral side in response to lateral stimulation and of left and right turns to 180°-stimulation in *Xenopus laevis* after lesions of the lateral line system. Lesion types as in Fig. 2. Numbers before and after the slash indicate numbers of contra- and ipsilateral rotations respectively; at 180° they indicate turns to the left (or more intact) and right side. For asymmetrical lesions the first line indicates responses to stimuli from the more lesioned side, the second line responses to stimuli from the more intact side. Symbols after the numbers indicate significant differences: asterisks differences from animals with an intact lateral line system, crosses differences between right- and left-hand turns. Single symbols indicate 5% significance, doubled symbols 1%

Lesion type	Stimulus angle					
	30°	60°	90°	120°	150°	180°
1	0/96	1/98	3/92	3/95	2/98	48/48
2	7/90**	10/86**	8/89*	17/80**	30/66**	51/45
3	0/99	2/96	0/98	0/97	5/92	51/49
4	0/99	0/98	5/92	10/87*	12/82**	49/48
	0/97	2/98	5/91	5/92	10/88*	
5	1/96	1/97	3/96	7/91	10/82*	46/25 +
	2/97	3/97	2/94	5/95	9/79*	
6	0/94	0/100	0/100	3/95	14/79**	40/56
	0/99	0/98	0/99	4/93	1/96 + +	

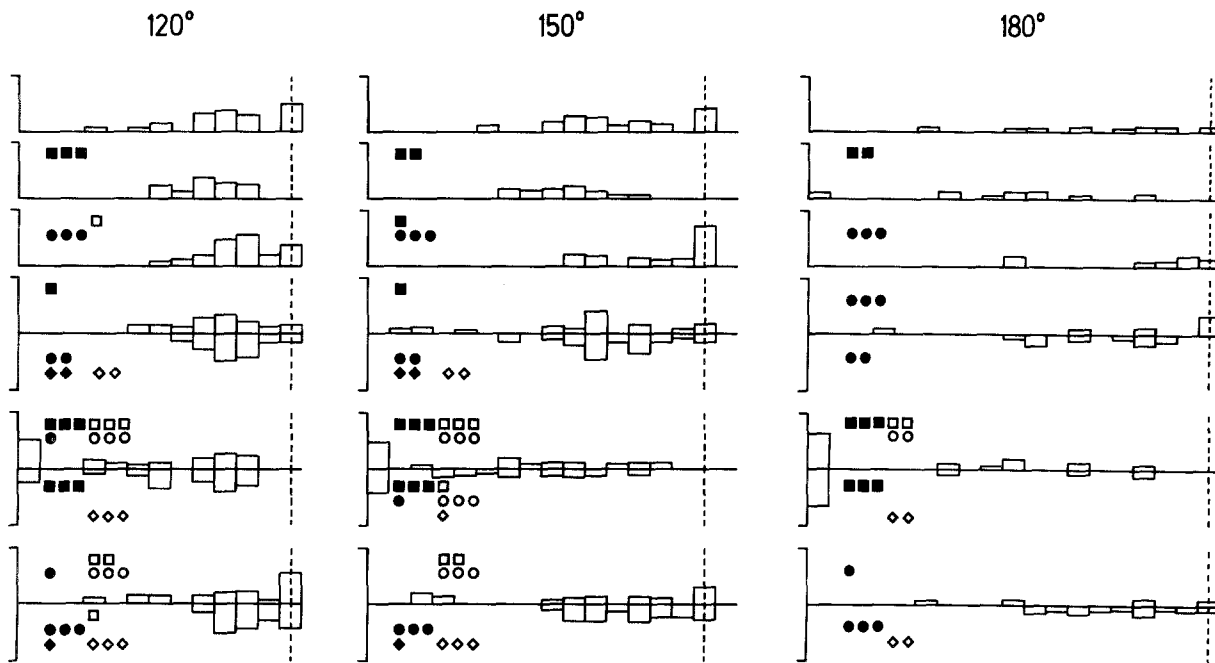


Fig. 2 (continued)

where the animals are easily visible from outside, can often be observed in nature as well as under test conditions. In addition, the sample is slightly biased to animals which are more down with intact system to make sure that random changes in vertical positioning after the lesion should lead on the average to an increase in up positions, i.e. go into the opposite directions as expected from the lesion. Irrespective, however, of the frogs' initial orientation, all of them except for one showed a down shift after dorsal lateral line elimination. This can be seen in a higher rate of down responses and of diving, and a reduction of the rising rate. For the rate of down responses the effect is highly significant even for the individual animals. Significances are somewhat lower for the individual changes in diving and rising rates, because the absolute numbers of diving and rising responses mostly are small anyway, so that even large relative changes sometimes do not come out as significant ones in the contingency tables. But when the data of the seven specimens are added, the changes in rising and diving are highly significant.

The specificity of this lesion effect was controlled in two ways. First, vertical orientation was tested again in the same specimens after their ventral stitches had also been destroyed. Two of the frogs ceased to respond to water waves at all, as is often found in *Xenopus* after total lateral line

elimination. The other five, however, showed a massive and highly significant reversal of the previous down effect, being now mostly up (Table 2). As a second control two animals were tested first with intact lateral line system and then after elimination of all their receptors on one side, i.e. after a lesion which destroyed an equivalent number of stitches as dorsal elimination. The effect of this lesion was an increase in being up (Table 2).

Lesions leaving only some of the ventral lateral line organs intact also led to a higher rate of down responses. Thus the increase in turning down is a specific effect of lesions which eliminate all dorsal inputs but leave ventral inputs intact. With intact lateral line system ventral stitches are stimulated more than dorsal ones only if waves come from below, and the increase in turning down after dorsal elimination indicates that after this lesion the animals at least sometimes erroneously localize the surface wave as coming from below because their ventral input is stronger than their dorsal input. Thus, vertical localization involves comparison of input intensities between dorsal and ventral lateral line organs.

## Discussion

The data demonstrate that *Xenopus* deprived of its dorsal lateral line input but with all ventral lat-

**Table 2.** Effect of various lesions on vertical positioning in *Xenopus laevis*. In the test group seven animals were tested each subsequently with *all*, only *ventral*, and *no* lateral line organs intact (two of them ceased to respond to waves after total elimination). For each of these tests the rates of down end positions among all turns, of diving after start up positions, and of rising from start down positions was determined ('down' is sitting on the bottom, 'up' floating at the water surface). With few exceptions, the animals are more on the bottom, dive more, and rise less after dorsal lesion than with intact lateral line system or after total lateral line lesion. Symbols behind the percentages with intact system or after total lesion indicate significance and direction of the difference from the corresponding values with only ventral stitches; number of symbols indicates the significance level (one symbol 5%, two 1%, and three 0.1%). – In the control group two animals were examined in the same way with intact lateral line system first and then after unilateral line organ destruction, i.e. after elimination of approximately the same amount of lateral line organs as in dorsal lesion. After this lesion animals do not go down, but rather come up. Further see text

Test		Total		Start up		Start down	
		N	down %	N	dive %	N	rise %
1	All	302	95.0 ---	15	33.3	287	1.7 +
	Ventral	362	99.4	3	66.7	359	0.3
	None	293	4.1 ---	284	1.4 ---	9	11.1 +
2	All	507	89.3 ---	63	36.5	444	3.2 +++
	Ventral	368	98.6	11	54.5	357	0.0
	None	370	51.9 ---	190	11.1 ---	180	5.0 +++
3	All	641	71.6 ---	186	15.1	455	5.3 +
	Ventral	364	82.1	67	13.4	297	2.4
	None	556	11.9 ---	489	1.6 ---	67	13.4 +++
4	All	414	71.0 +++	114	6.1	300	4.3
	Ventral	454	58.8	193	5.7	261	1.9
	None	326	12.9 ---	291	3.4	35	8.6
5	All	1078	54.3 ---	464	1.3	614	5.7 +++
	Ventral	600	100.0	0		600	0.0
	None				no response		
6	All	690	54.2 ---	315	2.9 ---	375	2.7 +
	Ventral	366	98.4	6	50.0	360	0.8
	None	270	15.2 ---	234	2.6 ---	36	2.8
7	All	594	4.5 ---	546	0.4 ---	48	48.0 +++
	Ventral	600	35.0	395	4.8	205	6.8
	None				no response		
Total:	All	4226	58.7 ---	1703	4.7 --	2523	4.9 +++
	Ventral	3114	79.0	675	7.4	2439	1.2
	None	1815	19.4 ---	1488	3.3 ---	327	7.0 +++
<i>Control</i>							
1	All	375	58.4 +++	135	7.4	240	12.9
	Left	461	28.9	311	3.2	150	18.0
2	All	354	11.0 +++	319	2.2	35	8.6 –
	Left	333	2.1	330	1.8	3	66.7
Total:	All	729	49.1 +++	454	3.7	275	12.4
	Left	794	17.6	641	2.5	153	19.0

eral line organs intact can determine all surface wave directions, and its responsiveness to the waves is undiminished. Thus, in contrast to surface feeding fish, where wave localization by means of the lateral line system is based on the evaluation of only dorsal organ input (Schwartz 1965), ventral lateral line organs participate in wave localization in *Xenopus*. In addition, localization with only ventral stitches is – except for a minimal increase in

variance – as good as with intact lateral line system. This is the more remarkable since animals after this lesion tend to go down to the bottom, where the wave is not only weaker, but is reflected and deformed before it reaches the ventral organs. Thus, *Xenopus* is able to determine correctly wave directions from its ventral organs' input irrespective of whether it is floating at the surface or sitting on the bottom.

A difference between dorsal and ventral lateral line organization is found, however, in their functional differentiation for wave localization. Whereas the dorsal lateral line organs comprise several subgroups each having full localization capabilities (Elepfandt 1982), no such subgroups have been found among the ventral lateral lines and instead all ventral stitches together form just one subgroup of the whole system. This difference between dorsal and ventral organization is seen most directly in the experiments after unilateral lesion. With only dorsal stitches of one body side intact *Xenopus* still can determine all wave directions, but with only ventral stitches on one side intact accurate localization is confined to the receptor side. When only ventral head stitches on one side remain intact wave localization practically breaks down, a situation which was never found after any lesion leaving dorsal stitches intact. It should be mentioned that these deteriorations of localization capability were not only found when the animal was sitting on the bottom, i.e. when the wave could not pass below it, but also when the frog was floating at the water surface.

The existence of merely ventral and dorsal localization subgroups shows that horizontal wave localization does not require combined dorsal and ventral inputs. Apparently joint evaluation of dorsal and ventral inputs does not even improve localization accuracy beyond that what is achieved already through the respective dorsal or ventral receptor groups separately, as is seen from the fact that frogs with only unilateral dorsal stitches intact localize wave directions as accurately as frogs with both dorsal and ventral stitches on one side intact.

In contrast to horizontal localization, vertical localization involves compound evaluation of dorsal and ventral inputs. The down shift in vertical orientation after dorsal lateral line ablation is highly significant and demonstrates that comparison of dorsal and ventral lateral line inputs gives *Xenopus* information about the vertical component of an arriving wave. Thus wave localization by means of the lateral line system in *Xenopus* is not limited to the horizontal plane. Further experiments are necessary to investigate whether this vertical localization is an accurate measurement comparable to horizontal localization or whether it is simpler, e.g. a mere discrimination between the two levels high and low. Both models would fit the present data. Another point which has been brought up by these data is that subgroups for horizontal localization are not identical to vertical localization subgroups, otherwise the shift after the lesioning should not have occurred. Thus it might

be interesting to see whether there are vertical localization subgroups at all and if so to examine their relation to the horizontal localization subgroups.

*Xenopus*' capability to localize wave directions in a three-dimensional surround might well explain the difference of its lateral line organisation from that of surface feeding fishes. Surface feeding fishes are highly specialized for catching their prey at the water surface; they respond to waves only when they are directly at the surface or immediately below it, and their localization is apparently limited to the two-dimensional plane of the water surface (Schwartz 1965, 1971). Under such circumstances additional ventral lateral line input hardly can improve localization accuracy and therefore can be neglected for this purpose. Localization in *Xenopus*, however, is not limited to this special situation, the frog can localize waves running over it when it is sitting on the bottom and localizes waves passing below it when it is hanging at the water surface. If one further takes into account that *Xenopus* on the bottom often hides at edges and below stones so that only some of its stitches protrude into free water, the utility of using all lateral line organs in localization and the development of localization subgroups becomes apparent. The need for localization subgroups might be less for the ventral organs, because their input probably is most relevant to localize waves coming from below, i.e. under comparatively free water conditions when the frog is hanging at the water surface.

Previous studies on *Xenopus* (Elepfandt 1982) showed that the capacity to correctly determine the direction of a turn and the magnitude of the turn could be separated experimentally. Several lesions – all of which had left intact at least the same percentage of dorsal stitches as of ventral ones – increased the number of direction errors, but even when the frog turned to the wrong side (i.e. away from the stimulus) the magnitude of the turn showed the correct proportionality to the stimulus angle (ibid.). In the present study, lesions leaving only ventral stitches intact caused the converse error. That is, the direction of the turn was correct, but the magnitude of the turn was incorrectly determined as evidenced by greater variance in turn angles following these lesions. These results collectively demonstrate that the direction and magnitude of a turn are determined independently in the lateral line system, possibly with different degrees of fallibility in different subsets of the stitches. Separation of response direction and magnitude might be useful for the frog, because besides the normal direct yaw it can also reach the correct

position by turning into the wrong direction but turning through more than 180°. Such occasional more-than-180° turns are observed mainly in response to large stimulus angles, and these are the angles at which the rate of erroneous contralateral turns is also highest.

After elimination of all lateral lines except for one side's mandibular and hyomandibular lines turn angles to a given stimulus angle vary more than in specimens in which all lateral line organs had been destroyed, i.e. response accuracy is worse than without lateral line input. This indicates a fixed hierarchy of *Xenopus*' reliance on its sensory systems for water wave localization. As long as directional lateral line input is available, the blinded *Xenopus* will rely on this input more than on the information coming from its other still unknown water localizing system(s), even if the lateral line input is highly obscure. Other sensory systems apparently only take the lateral line system's place when directional lateral line information is completely absent.

Recently Müller and Schwartz (1982) reported the existence of a second wave localizing system besides the lateral lines in the surface feeding fish *Aplocheilus lineatus*. The fact that this system has not been detected previously (Schwartz 1965) and the data presented by the authors demonstrate that the same hierarchy between the lateral line system and the other wave localizing system as described here in *Xenopus* applies to *Aplocheilus* as well or might be even stronger. Total lateral line destruction reduces responsiveness completely in *Aplocheilus* (Schwartz 1965) and heavily in *Xenopus* (Kramer 1933; Elepfandt 1982). If, however, an *Aplocheilus* has been trained for a while with only one or very few lateral line organs left intact, then it responds to water waves even after ablation of these last organs (Müller and Schwartz 1982). This corresponds exactly to the procedure to increase the responsiveness of *Xenopus* specimens with total lateral line destruction. The finding that *Xenopus* after some partial lesions responds less accurately than without lateral line organs has its parallel in the fact that *Aplocheilus* with only one organ left intact responds to waves by turning always through a constant angle irrespective of the wave direction and again resumes oriented taxis response after destruction of that last neuromast (Müller and Schwartz 1982). I.e. *Aplocheilus*, too, relies more on its lateral line information even if it is objectively wrong than on its other sensory system. The experiment with only one intact lateral line organ shows a difference between *Xenopus* and

*Aplocheilus* in that *Xenopus* with only one occipital stitch intact already turns with the accuracy of its other wave localizing system (Elepfandt 1982). But this difference can be explained by different lateral line organization in these two species. In *Aplocheilus* wave localization by means of the lateral line system is based upon a topological principle, turn angles of specimens with only one intact lateral line organ depend on the location of that organ on the fish (Müller and Schwartz 1982). In *Xenopus*, however, wave localization by means of the occipital lateral line group is made by comparison of the inputs from different stitches, which is no longer possible, if only one of them is left (Elepfandt 1982). Thus, the existence of a second non-visual sensory system for wave localization and the predominance of the lateral line system about that system in species so different as a teleost and a frog indicates that these phenomena might be more widespread than had been assumed so far.

*Acknowledgements.* The work was supported by grant El 75/2-2 of the Deutsche Forschungsgemeinschaft. I thank H. Markl for helpful comments and W.J. Davis for revision of the English manuscript.

## References

- Dijkgraaf S (1947) Über die Reizung des Ferntastsinns bei Fischen und Amphibien. *Experientia* 3:206–208
- Dijkgraaf S (1963) The functioning and significance of the lateral line organs. *Biol Rev* 38:51–105
- Elepfandt A (1982) Accuracy of taxis response to water waves in the clawed toad (*Xenopus laevis* Daudin) with intact or with lesioned lateral line system. *J Comp Physiol* 148:535–545
- Görner P (1973) The importance of the lateral line system for the perception of surface waves in the clawed toad, *Xenopus laevis*. *Experientia* 29:295–296
- Görner P, Moller P, Weber W (1984) Lateral-line input and stimulus localization in the African clawed toad *Xenopus* sp. *J Exp Biol* 108:315–328
- Kramer G (1933) Untersuchungen über die Sinnesleistungen und das Orientierungsverhalten von *Xenopus laevis* DAUD. *Zool Jb Physiol* 52:629–676
- Müller U, Schwartz E (1982) Influence of single neuromasts on prey localizing behavior of the surface feeding fish, *Aplocheilus lineatus*. *J Comp Physiol* 149:399–408
- Murray RW (1955) The lateralis organs and their innervations in *Xenopus laevis*. *Q J Microsc Sci* 96:351–361
- Schwartz E (1965) Bau und Funktion der Seitenlinie des Streifenhechtlings (*Aplocheilus lineatus* Cuv. u. Val.). *Z Vergl Physiol* 50:55–87
- Schwartz E (1971) Die Ortung von Wasserwellen durch Oberflächenfische. *Z Vergl Physiol* 74:64–80
- Shelton PMJ (1970) The lateral line system at metamorphosis in *Xenopus laevis* (Daudin). *J Embryol Exp Morphol* 24:511–524
- Sommerfeld A (1970) Vorlesungen über Theoretische Physik II. Mechanik der deformierbaren Medien. Akademische Verlagsgesellschaft, Leipzig