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Primary Lateral Line Response to Water Surface Waves in the Topminnow *Aplocheilus lineatus* (Pisces, Cyprinodontidae)

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Abstract. 1. The function of supraorbital organ II/2 of the head lateral line system of the surface feeding fish *Aplocheilus lineatus* is characterized here by the lateral line nerve response evoked by biologically relevant surface wave trains.

2. A single organ is particularly sensitive to the high frequency, low amplitude cycles at the beginning of a click evoked wave train. By using gated sinusoidal signals it was shown that the following mechanisms are responsible: a. a strong phasic component superimposed on the tonic response component, b. high sensitivity of the organ in the frequency range between 70 and 120 Hz (corresponding to the frequency range of the first cycles of a prey evoked wave), c. the organ is responsive to the acceleration component of wave stimulation ($b \sim f^2$).

4. As the time structure of a surface wave is encoded in a corresponding discharge pattern in the lateral line nerve it is probable that the time structure ('stimulus pattern') of a signal is used by *A. lineatus* to estimate the distance to its source.

Key word: Lateral line – Surface feeding fish – Prey localisation

Introduction

Surface feeding fish localize their prey – normally flying insects fallen on the water surface – by means of surface waves evoked by the prey's struggling. The stimulus sensitive organs are the lateral line organs of the head and body (Schwartz 1965, 1970, 1971).

Although the localization of a wave source direction by *Aplocheilus lineatus* is based on interaction of the bilaterally symmetrical head organs, a distance estimation by the fish is possible when all the organs except one have been removed (Müller and Schwartz 1982). The information about source distance must therefore be encoded in the wave itself.

Both the damping factor and propagation speed of surface waves are dependent on their frequency (Sommerfeld 1970). In general, with increasing wave frequency above 14 Hz, both propagation speed and attenuation increase. In consequence, the frequency amplitude spectrum of surface wave signals is dependent on the propagation distance (Grodd 1977; Bleckmann 1980; Bleckmann and Schwartz 1982).

Although behavioural experiments have been made, there is as yet very little electrophysiological information about the response of the lateral line organs of surface fish to surface waves (Bleckmann and Topp 1981). This study therefore analyses the reaction of a single neuromast of the supraorbital group (group II, organ 2) of the head lateral line system of *A. lineatus* to biologically relevant stimuli (similar to the 'single wave pulse' of Lang 1980) by means of multi-unit recordings from the lateral line nerve.

As the damping characteristics of surface waves mean that the amplitudes and frequency spectra of these quasi-natural stimuli cannot be varied independently further analysis of the organ's response was made using gated sinusoidal stimuli where the carrier frequency (cF), amplitude (A) and steepness of onset (ramp) could be varied. In this experimental series particular attention was paid to the phasic component of the response to the initial cycles of a surface wave as this portion of the signal has been shown in behavioural studies to be particularly important for localization.

As Lang (1980) showed that non prey waves ($f = 14–60$ Hz) differ from prey evoked waves ($f = 70–140$ Hz) in their frequency spectrum, the frequency sensitivity of the lateral line organ was characterised using iso-intensity curves.

Material and Methods

Experimental Animal

For the experiments 27 adult killifishes, *Aplocheilus lineatus*, bred in the laboratory, were used. The lateral line system on the head of *A. lineatus* consists of 3 groups of 3 single neuromasts located dorsolaterally on each side (Schwartz 1965). Multi-unit recordings were made from primary afferent fibres originating from the supraorbital organ II/2 (long axis diverging 5.8° from long axis of body) in response to surface wave stimulation.

Preparation

The fish was anaesthetised with MS 222 (Sandoz, 0.5 g/l, pH 7) and immobilised with an injection of *d*-tubo-curarine-chloride (0.015 mg/g bodyweight). The ramus ophthalmicus superficialis of the truncus supraorbitalis (a branch of the trigeminal facial complex, Müller 1976) which innervates the supraorbital II group of head lateral line organs (Schwartz 1965) was exposed and cut caudal to a point where the fibres

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innervating organ II/2 pass into the skull. The nerve stump was laid over a Ag-AgCl hook electrode that could be withdrawn into a vaseline and oil filled tube. A silver wire was placed in the operation wound to serve as an indifferent electrode.

Data Recording

The recorded spikes were stored on magnetic tape (Tandberg TIR 115; Philips MB 1020). Data analysis (Peri-Stimulus-Time-Histograms, PSTHs) was performed off-line with a Nicolet 1074 signal processor. Measurement series where spontaneous activity varied strongly (more than 4% during the recording period) were discarded. The spontaneous activity was measured 7.4 s after stimulus offset.

The threshold was measured from PSTHs made at different stimulation intensities. Threshold was defined as the intensity that evoked a 20% (high spontaneous activity) to 100% (low spontaneous activity) discharge rate increase above spontaneous rate. For click evoked waves 100 presentations for each PSTH were made; 40–60 presentations for gated sinusoidal signals.

Experimental set up

The animal was placed in a Ringer-filled ('Cortland Ringer', Wolf 1963) experimental tank. Four control fishes which had been kept for 3 weeks in this solution showed no significant difference in prey capture behaviour compared to animals kept in top water. This species is in any case often found naturally in brackish water. The thresholds found in these experiments were also similar to those found by Unbehauen (1980) recording microphonics from organ II/2 in tap water. The spontaneous activity (60 $\pm$ 45 Imp/s; $n = 62$) was similar to that recorded by other authors working on lateral line systems (Harris and Milne 1966; Weber and Schiewe 1976). The fish was placed in a holder that allowed the position of the head to be adjusted to be the same as that of the animal in its natural prey seeking position just under the water surface. When recordings from the nerve were obtained fine adjustment of the head position was made to give the best response to a test stimulus. The point of stimulus was 6–7 cm from the organ along the long axis of the fish. To reduce reflected waves the experimental glass aquarium (50 × 40 × 12 cm) was lined with a foam rubber coated glass beach, inclined at 15° to the horizontal.

Stimulation

Surface waves were produced by a 4 mm plastic disc attached to a thin aluminium tube glued to the cone of a loudspeaker (Isophon BPSL 100). In order to simulate one type of waves ('single wave pulses', Lang 1980) produced by prey at the water surface, a 5 ms click was applied to the transducer to form a surface wave whose frequency and amplitude components varied with distance from the source.

To allow different parameters of the signal to be independently varied a series of experiments was performed with gated sinusoidal signals. In order to avoid switching frequency artefacts the onset and the end of the wave train were relatively flat (narrow bandwidth signals). The repetition rate was 0.9 Hz for click stimuli and 0.09 Hz for sinusoidal stimuli.

Stimulus Recording

The waves were recorded using He-Ne laser (Poytec Pl 691), the beam of which was reflected from the water surface and captured by a position sensitive photodiode (United Detector Technology, PIN-LSC 4). Details of the calibration and measurement of wave amplitude (peak-peak, pp) are given in Unbehauen (1980).

To measure the phase of the stimuli the surface wave was recorded with a resistance probe at the organ (Rudolph 1967). The probe was an electrolytically sharpened tungsten wire placed so that its tip was as close as possible to organ II/2 without touching it. Control measurements with both of the above methods showed identical signal time structure and no detectable nonlinearities in the tungsten probe response. To measure the small amplitude components at the beginning of the click evoked surface wave 100–200 averaging sweeps were needed.

Results

Response to Click Evoked Wave Trains

In the first series of experiments the animal was stimulated with click evoked waves whose frequency spectrum closely resembled natural prey evoked waves ('single wave pulses', Lang 1980). In particular the response of the organ to the initial high frequency components of the signal, which is known to be behaviourally important (Bleckmann 1980; Bleckmann and Schwartz 1982), was studied.

The PSTHs in Fig. 1. show a marked stimulus response pattern. The strong response to the first low amplitude high frequency components of the signal is noticeable. Despite the higher amplitude of the last low frequencly displacement (20 μm as opposed 0.05 μm for the first cycle) the response to the 9th cycle (9 Hz) is only a modulation of spontaneous activity, without any increase in discharge rate (upper response: 2.54 Imp/period; lower response: 1.68 Imp/period). The PSTH shows a broad peak at this point, the maximum of which is only just above the level of spontaneous activity. In all cases (5 animals) the 6th cycle (40 Hz) evokes maximum activity.

The lateral line organ responds to the high frequency, low amplitude components at the beginning of the signal with a higher sensitivity than to the later cycles. The amplitude needed to evoke a suprathreshold response (100% > spontaneous activity) to the first cycle (170 Hz) is < 0.015 μm, to the second (125 Hz) is < 0.02 μm, to the third (100 Hz) is < 0.07 μm and to the eighth (14.5 Hz) is < 0.5 μm. These values were obtained from PSTHs made with different stimulation amplitudes.

Iso-intensity Curves

The previous data show that the lateral line organ is most sensitive to the high frequency initial cycles of the signal. For more quantitative analysis of this frequency selectivity and to decide if organ II/2 is differentially sensitive to the frequencies in prey evoked waves as opposed to those in non prey evoked waves, the frequency response of organ II/2 was measured with iso-intensity curves.

Narrow bandwidth signals with constant end amplitude (A = 3.5 μm, pp), rise time (rt = 800 ms) and duration (t = 1.6 s) but different carrier frequency (cF = 10–120 Hz) were used.

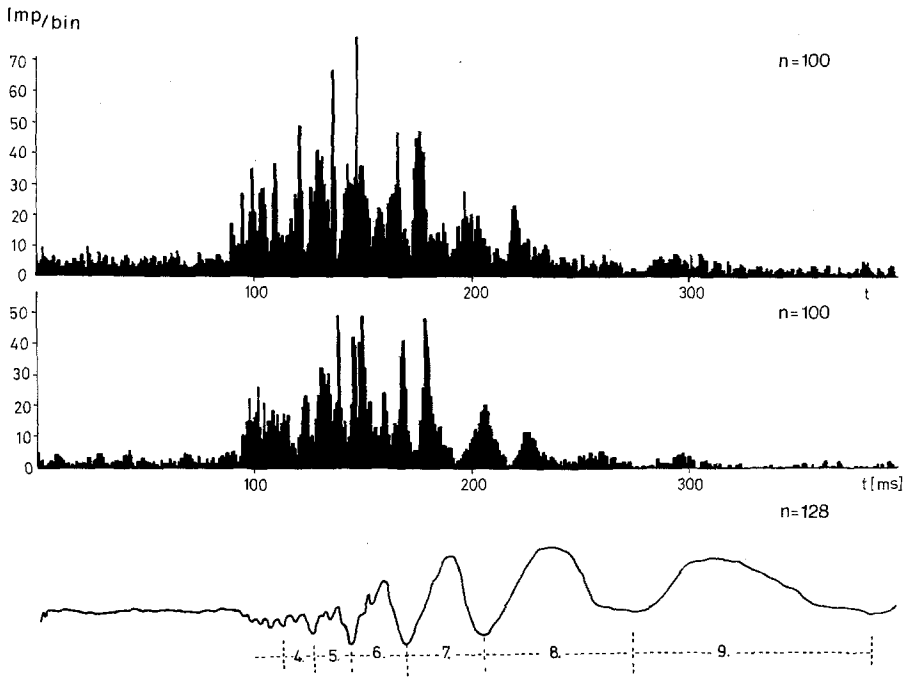

Fig. 1
PSTHs (1 ms bin) from 2 animals (spontaneous activity: *upper response:* 47.8 Imp/s; *lower response:* 21.5 Imp/s) in response to a click evoked wave train (*bottom*) measured at organ II/2 with a tungsten probe. The numbers under the stimulus trace are the individual cycles. Frequency and amplitude (pp) of the cycles (measured with laser/photodiode):

1. cycle: f = 170 Hz; A = 0.05 µm
2. c: f = 125 Hz; A = 0.24 µm
3. c: f = 100 Hz; A = 0.56 µm
4. c: f = 72 Hz; A = 1.70 µm
5. c: f = 55 Hz; A = 3.90 µm
6. c: f = 40 Hz; A = 8.40 µm
7. c: f = 28 Hz; A = 15 µm
8. c: f = 14.5 Hz; A = 27 µm
9. c: f = 9 Hz; A = 20 µm

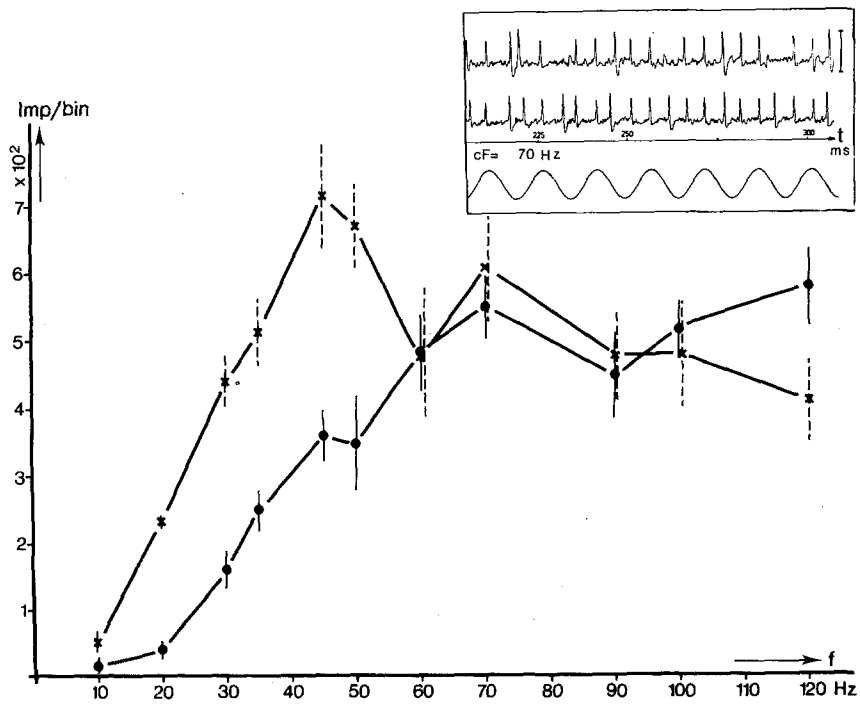

Fig. 2
Mean discharge rate (spikes/300 ms bin; 40 sweeps) of 4 animals as a function of stimulus carrier frequency (*cF*). Measurement points: 300 ms after stimulus onset (●——●; standard deviation: ⧳) and the last 300 ms of the plateau response (×——×; standard deviation: ⧳). It must be noted that the phasic components are for signals about $^1/_3$ of the pp-amplitude. *Inset:* Original recording of the nerve activity to the plateau region of a 70 Hz signal. Signal measured with laser/photodiode. Stimulus: rise time: *rt* = 150 ms; end amplitude: A = 5 µm, pp; duration: *t* = 1.6 s. *Top right:* calibration bar: 800 µV.

When the phasic component (defined as the first 300 ms; $^1/_3$ of the pp-amplitude is reached within this time) is examined it can be seen that the response increases from 10–70 Hz and remains at this plateau level up to 120 Hz (Fig. 2). The 70–120 Hz values are not significantly different (*t*-test, $P > 0.05$). The tonic component of the response (defined as the last 300 ms of the plateau response) increases from 10–45 Hz (*t*-test, $P < 0.001$) and then declines with higher cF (*t*-test, $P < 0.05$). The response for 60–100 Hz cF is however higher than at 10–30 Hz.

Phasic-Tonic Characteristics

The iso-intensity curves do show that the organ is particularly sensitive to the high frequencies present in a prey evoked wave. Therefore it is necessary to analyse: 1. how far the phasic component of the response increases its sensibility to the beginning of a prey signal and 2. to what extent the organ can measure the steepness of onset of the stimulus. A stimulation frequency of 70 Hz was chosen as this frequency allows the steepness of onset and the amplitude to be varied

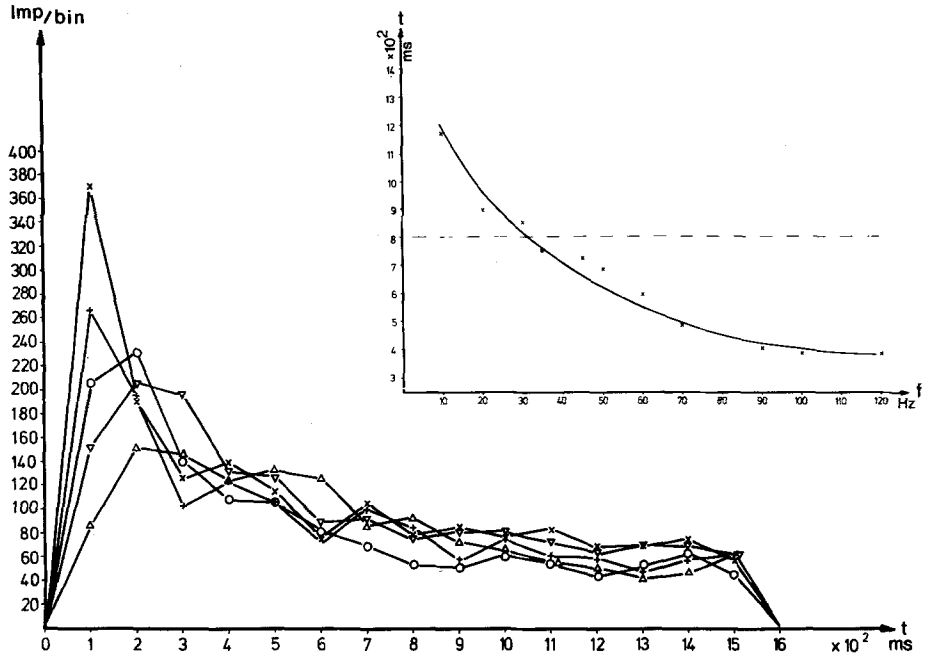

Fig. 3
PSTH response curves to a series with the same end amplitude (A = 3.00 µm, pp) and carrier frequency (cF = 70 Hz), but with different onset steepnesses (rise time: rt = 75–830 ms; stimulus duration: t = 1.6 s). *Ordinate:* Impulses/100 ms bin; 40 sweeps. *Abscissa:* time in ms after stimulus onset. *Inset:* Effect of stimulation frequency on the latency of the phasic component. Stimulus: amplitude: A = 3.50 µm, pp; rise time: rt = 800 ms; duration t = 1.6 s. The dashed line shows the end of the rise time (beginning of the stimulus plateau). *Ordinate:* latency of the phasic response component; *Abscissa:* cF in Hz (△ 1.8 µm/s; ▽ 3.5 µm/s; ○ 7.0 µm/s; + 9.8 µm/s; × 19.6 µm/s

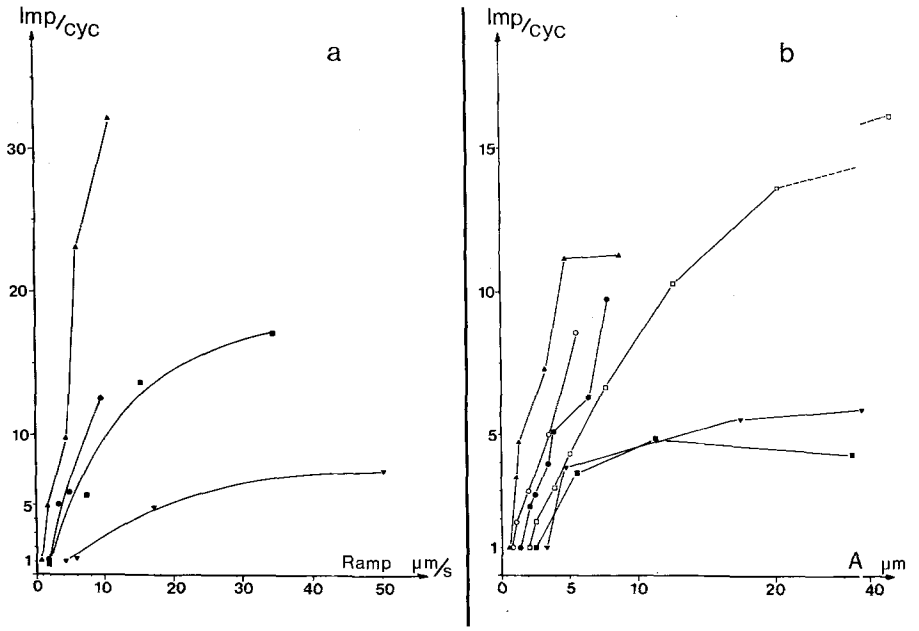

Fig. 4
Responses to onset (phasic, **a**) and plateau (tonic, **b**) response. **a**. Spikes per stimulus cycle as a function of stimulus onset steepness (ramp; onset steepness: ½ pp amplitude devided by rise time) at different cFs. (▼ 20 Hz; ■ 30 Hz; □ 40 Hz; ● 60 Hz; ○ 70 Hz; ▲ 100 Hz)

over a wide range without producing stimulus artefacts at the beginning and end of the signal.

In Fig. 3 a series of PSTHs is plotted as curves. The response is a typical phasic-tonic one. It can be seen that with constant end amplitude (A = 3.00 µm, pp) the phasic component increases with steepness of onset (range: 150–370 spikes/bin/40 sweeps) while the tonic component remains relatively constant (range: 42–68 spikes/bin/40 sweeps).

The latency of the phasic component (time to the initial peak) is a linear function of rise time (rt = 0.77 X + 30.3; r = 0.92) and at latest it occurs ¾ of the way along the ramp.

When the envelope parameters are held constant (A = 3.5 µm, pp; rt = 800 ms) and the cF is changed in the range from 45–120 Hz this latency decreases with increasing stimulus frequency (inset Fig. 3). Below 30 Hz the phasic component occurs after the end of the onset ramp.

Phasic and Tonic Components of the Responses to Different cF Signals

The effect of increasing onset steepness on discharge rate is potentiated by increasing the cF (Fig. 4a). For all cFs the discharge rate monotonically increases with increasing onset steepness of the stimulus. The initial slope of these monotonic curves increases with increasing cF.

The tonic discharge rate evoked by signals of a given pp-amplitude is also increased at higher frequencies (Fig. 4b). The steepness of the response amplitude function is also greater for higher frequencies than for lower. The increase in

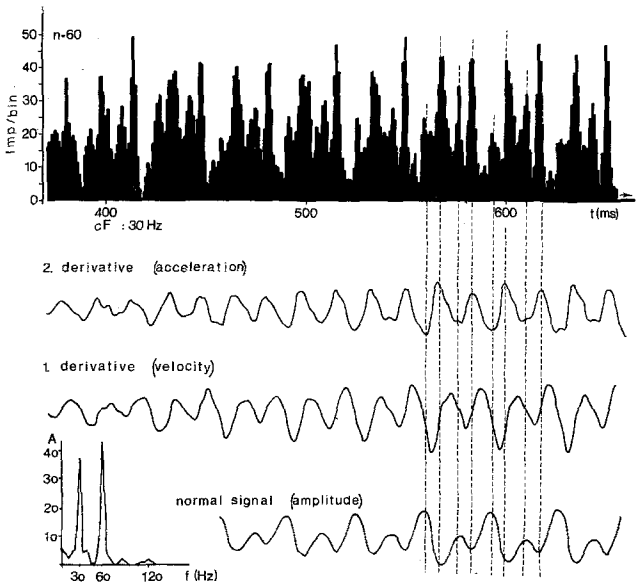

Fig. 5. Section of PSTH in response to the ramp portion of a 30 Hz cF surface wave. PSTH: 1 ms bin; 60 sweeps. *Bottom:* signal measured with the tungsten probe at the head of the animal, together with its first and second derivatives (128 sweeps). *Inset in bottom trace:* frequency spectrum of the 30 Hz cF surface wave. *Ordinate:* relative amplitude (total amplitude 100%). *Abscissa:* frequency in Hz

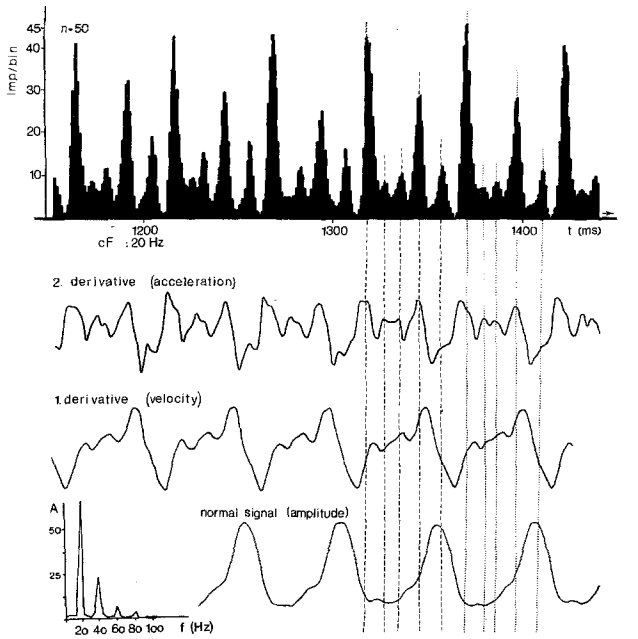

Fig. 6. Section of PSTH in response to a 20 Hz cF surface wave. PSTH: 1 ms bin; 50 sweeps. *Bottom:* signal measured with the tungsten probe at the head of the animal, together with its first and second derivatives (128 sweeps). *Inset in bottom trace:* frequency spectrum of a 20 Hz cF surface wave. *Ordinate:* relative amplitude (total amplitude 100%). *Abscissa:* frequency in Hz.

sensitivity of the organ for both ramp steepness and amplitude is thus greater for higher frequencies than for lower.

Phase Characteristics of the Response

Behavioural experiments suggest that the fish can estimate the distance of a wave source analysing the time structure of the signal. Therefore a series of experiments with 20 and 30 Hz cF wave signals was made to test: if lateral line nerve spikes are locked, to what phase of the signal they are locked and if various frequency components found in the prey evoked signal are coded in their correct phase relationship.

These wave signals, composed of various superimposed waves (mainly first and second harmonics), evoked a response from the lateral line organ which consists of 4–5 peaks of the cF period in the PSTHs (Figs. 5 and 6). In response to a surface wave whose frequency spectrum is composed mainly of the 2nd harmonic (60 Hz, 43%) and the fundamental component (30 Hz, 37%; Fig. 5 inset) it can be clearly seen that 2 peaks are produced by the lateral line nerve for each wave cycle at the cupula. This is also true for the 20 Hz signal whose 2nd harmonic was not so strongly represented (23%–66% cF; Fig. 6 inset).

In the tested frequency range of 10–120 Hz the response of the lateral line nerve in each case was double the frequency at the cupula.

The response to the 30/60 Hz signal gives more information about the correspondence between PSTH peaks and signal components as the response to the 20/40 Hz signal.

With the 30/60 Hz signal the double frequency response makes it impossible to decide if the PSTH peaks correspond to maximal signal amplitude (+sin) or acceleration (−sin). Peaks in the PSTH could correspond to either positive or negative signal maxima. With the 20/40 Hz signal, where the maximum amplitude and acceleration do not correspond it can be clearly seen that the PSTH peaks correspond to the positive acceleration maximum. This shows clearly that organ II/2 responds to the acceleration and not to the displacement or velocity components of 20/40 and 30/60 Hz signals. In addition it is clear that a prey evoked signal composed of superimposed waves can be clearly coded by the lateral line organ provided the acceleration component of each phase is above threshold.

Discussion

Correlation of Lateral Line Response Characteristics to Those of Prey Evoked Signals

When a click evoked wave train is presented to *A. lineatus* the animal shows an orientation reaction after the first 6–9 cycles have passed the head lateral line organs (Bleckmann 1980). This shows that the fish can extract information about the direction and distance of the wave source from the beginning of the wave train. The dominance of the early components is also shown in this study. It can bee seen that two different mechanisms are responsible for this dominance.

First, the head lateral line organ of *A. lineatus* shows a phasic-tonic response (Fig. 3) which has also been shown in other lateral line organs (Görner 1963; Harris and Milne 1966; Kuiper 1967) and in *A. lineatus* II/2 organ using microphonics (Unbehauen 1980). As the phasic response is dominant the sensitivity of the organ is greater at the beginning of a wave train.

Secondly, the organ is more sensitive to the 70–120 Hz high frequency components at the beginning of the signal (Fig. 2). In the range where *A. lineatus* can estimate distance (up to 12–18 cm, Bleckmann 1980) the beginning of a wave train is composed of these frequencies (Fig. 1).

The greater sensitivity of organ II/2 to these higher frequencies is at least partly due to the fact that it responds to the acceleration component of wave signals ($b \sim f^2$)[1].

[1] $b = -4\,A\,\pi^2 f^2 \sin \omega t$; b, acceleration; A, amplitude; f, frequency; ω, phase

The high frequency cycles at the beginning of a wave train are of rather low amplitude. The response to gated sinusoidal signals shows that the capability of the organ to differentiate amplitudes increases with frequency (Fig. 4a, b). Despite the low amplitude at the beginning of the signal the lateral line organ can encode the amplitude of individual cycles. This is consistent with the behavioural data of Waldner (1981) who, using cF stimuli, showed that the ability of *A. lineatus* to discriminate amplitudes also increased with stimulus frequency.

Kroese et al. (1980) working on the lateral line system of Xenopus laevis during large-amplitude steady-state periodical stimulation (0.5–2 Hz) found a correspondence between the extracellular receptor potential, the afferent nerve activity and the acceleration component of the signal.

This study has shown however, that independent of the amplitude of the stimulus the relation between afferent nerve activity and periodic wave displacements is evident. This is shown in Fig. 5 where the section of the PSTH and the wave stimulus are taken from the ramp part of the signal (the amplitude of the signal between 400 and 600 ms after stimulus onset was between 1.25 and 1.9 μm).

That the maximum response is evoked by the 40 Hz cycle of the click evoked wave train does not contradict the frequency sensitivity characteristics obtained with gated sinusoidal signals. The individual cycles in the 70–120 Hz maximum sensivity range are 5 (72 Hz) to 35 (125 Hz) times smaller than the 40 Hz component.

Ability of the Lateral Line Organ to Discriminate Between Prey and Non Prey Signals

Non prey evoked signals such as waves evoked by wind, falling leaves etc. can be clearly differentiated from prey evoked waves on the basis of their frequency spectrum. The highest frequency limit is between 14–60 Hz for non prey waves, with a maximal amplitude in the region of 8–14 Hz. In contrast, prey waves have frequency limits between 70–140 Hz (Lang 1980).

Thus it can be seen that the sensitivity of organ II/2 of *A. lineatus* is 12.5–35 times greater in the prey wave frequency range than in the non prey wave range. Therefore the fish should be able to seperate prey elicited waves from non prey waves at a reasonable distance (about 3 times the bodylength), despite the strong damping of high frequency waves at the water air interface (e.g. 8.6 db/cm at 140 Hz; Lang 1980).

The Role of the Time Structure ('Stimulus Pattern') of a Prey Signal

A click evoked wave train is represented by a double frequency phase locked discharge in the lateral line nerve of *A. lineatus*. This double frequency response is presumably due to the presence of two oppositely polarized hair cell population in the neuromast. The response to narrow bandwidth signals also show this double frequency response between 10 and 120 Hz, with the action potentials be phase locked to the positive acceleration phase of the signal. The distance-dependent wave pattern can produce then a corresponding neural discharge which could be centrally analysed to allow distance estimation on the basis of information from a single organ. This corresponds to the behavioural findings that *A. lineatus* can estimate distance of a wave source using only one lateral line organ (Müller and Schwartz 1982) and that it can use the frequency spectrum of a signal for distance analysis (Bleckmann and Schwartz 1982). The results of these studies suggest that *A. lineatus* analyzes the time structure ('stimulus pattern') of a surface wave signal to estimate the source distance and that the response of individual lateral line organs is particularly suited to such an analysis.

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