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The Functional Significance of Frequency Modulation Within a Wave Train for Prey Localization in the Surface-Feeding Fish *Apopocheilus lineatus* (Cyprinodontidae)*

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Summary. The physical properties of water surface waves and the responses of the topminnow *Apopocheilus lineatus* to normal and altered single wave trains were investigated.

1. A single immersion of any object into the water or a short air blow onto the water surface produces surface waves containing wave cycles of different amplitudes and frequencies. Such wave trains are characterized by a downward frequency modulation, the degree of which depends on source distance but not on initial stimulus intensity (Figs. 1 and 2).

2. When stimulated with single wave trains (clicks) *A. lineatus* is able to determine the source distance (Fig. 4). This ability is independent of wave amplitude and thus also of frequency range.

3. When presented click signals the topminnows move on an average of 6.1 ± 1.9 cm (mean and S.D.) towards the wave center, which is 6.5–7.5 cm away from them, or 11.8 ± 3.3 cm at a source distance of 14.5–15.5 cm. However, presentation of a wave signal at a source distance of 7 cm, the frequency modulation of which resembles a click signal originating at a source distance of 15 cm, causes the fish to move forward 10.8 ± 4.5 cm (Fig. 5).

4. *A. lineatus* also reacts to altered single wave trains, which are upward frequency modulated. But there is no or only a weak distance determination (Fig. 6).

5. For different kinds of wave production the frequency modulation within a click may be slightly different at identical source distances (Fig. 7). But, in general, looking at the first 7–9 wave cycles (which are used by *A. lineatus* for prey localization) the frequency modulation in a single wave train mainly depends on source distance, but not on kind of wave production (tested for the source distances 5, 10, and 15 cm, Fig. 8).

6. Long lasting wave signals are preceded by a click stimulus (Fig. 7 right half). Independent of the long lasting wave pattern this preceding click might be used by *A. lineatus* for distance localization.

7. It is assumed that *A. lineatus* analyzes the amplitude spectrum of a wave signal for discrimination of prey and nonprey waves and that the frequency modulation of the first 7–9 wave cycles of a wave train is used to obtain information about source distance.

Introduction

Many fish and aquatic amphibians detect their prey — aquatic, semiaquatic and terrestrial insects — by means of surface waves of the water elicited by the prey’s struggling (Schwartz 1965, 1971; Schwartz and Hasler 1966; Kramer 1933; Görner 1973, 1976; Bleckmann 1980). Localizing responses to ripples on the water surface also exist in the whirligig beetle *Gyrinus substriatus* (Rudolph 1967), the water strider *Gerris remigis* (Murphey 1971a, b; Wiese 1969) and the back swimmer *Notonecta glauca* (Markl and Wiese 1969; Wiese 1972, 1974; Murphey 1973; Lang 1980a, b). Even spiders of the genus *Dolomedes* and *Pirata* are alerted by surface waves caused by insects trapped on the water surface (Berestynska-Wilczek 1962; Carico 1973; Gettmann 1977).

In contrast to predatory insects and aquatic amphibians surface-feeding fish are not only able to determine the direction but also the distance to a wave source if confronted with single wave pulses produced by prey or by dipping a rod into the water (Schwartz 1971; Bleckmann 1980). Whereas the exact determi-
nation of the source direction depends on the interaction of symmetrically located head lateral line organs in the topminnow *A. lineatus* (Schwartz 1965; Rath 1980; Müller 1981), there is no satisfactory explanation for the distance determining ability of surfaceterding fish. Two facts contradict Schwartz's assumption (1965) that *A. lineatus* uses exclusively the information coded in the curvature of a wave front for distance determination:

1. The ability to determine the distance to a wave source is reduced or no longer exist if monofrequent wave signals are presented (Bleckmann 1980).

2. The topminnow *A. lineatus* determines the distance to a wave source even when all lateral line organs involved in surface wave perception except one are removed (Müller 1981; Koschwitz, unpublished). Since it is impossible to measure the curvature of a wave front with one neuromast the information used by *A. lineatus* must be coded within the wave train itself.

Lang (1980a) has pointed out two main types of wave signals produced by prey insects: 1. long lasting wave signals which consist of wave cycles of varying frequencies and amplitudes in an irregular mode. This type of signal is produced by terrestrial insects struggling on the water surface. 2. Single wave pulses, elicited for example by leg movements of water striders or by emerging insect larvae at the water surface.

In this study we investigated the means by which *A. lineatus* succeeds in determining the source distance when single wave pulses are presented which closely resemble those of Lang's type 2. It is shown that the frequency modulation within a wave train contains information about the source distance and that this information is used by *A. lineatus* for distance determination.

### Materials and Methods

For the experiments adult male and female topminnows *Aplodinotus lineatus* (Cyprinodontidae) were used. The fish (body length 6–8 cm) is native to South India and Sri Lanka. The experimental animals were bred and raised in our laboratory.

In order to eliminate visual cues the fish were blinded. After encieation they always held contact with the surface film of the water. For training and testing they were transferred to an experimental tank (45 × 50 cm, water depth 6 cm).

Surface waves were produced by touching the water surface with the tip of a probe (Ø 2 mm–8 mm) mounted on the diaphragm of a loudspeaker (Isophon BPSL 100, 7/9 Watt). For all determination experiments the mode of stimulation was changed by blowing air onto the water surface. For this purpose a perspex disk with a central hole was mounted in front of a loudspeaker (Isophon PSL 300/70/3, 70/100 Watt). The tip (inner Ø1.5 mm) of a glass tube fixed to the hole reached down towards the water surface ending 1 mm above it. The loudspeakers were run by a square pulse generator (Stimi, Hugo Sachs) or with a sine generator (Hi-

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H. Bleckmann and E. Schwartz: Prey Localization in *Aplodinotus lineatus* mediated HG 101 B, 102 B, 103 B, 108 B, 500), voltage output of which could be amplitude and frequency modulated.

Wave recordings were made using a helium-neon laser (Polytec LGK 691) whose beam was reflected from the water surface onto a position sensitive photodiode (UDT, PIN–LSC 4). The laser, photodiode and tip of the glass tube were arranged in a vertical plane. Temporary inclinations of the water surface caused by surface waves deflected the laser beam on the photodiode. Consequently the photodiode signal is not an analogue of the wave form, but of its first differential. After amplification (UDT–301 A) the electrical signal of the photodiode was stored on FM-tape (Tandberg TIR 115). For evaluation of the wave frequencies (amplitude, rise and fall times, propagation speed) a signal averager (Nicolet 1070) was used. In order to ensure that even the very small amplitudes at the beginning of a wave signal could be recognized, in all cases 128 signals were averaged. The amplitude of the waves was determined according to a computing procedure developed by Unbehauen (1980).

In order to simulate a wave signal which at 7 cm source distance resembles the frequency modulation of a click at a source distance of 15 cm, an optimization strategy similar to that described by Rechenberg (1973) was used. First a 70 Hz wave train was generated in which the amplitude modulation at 7 cm source distance equalled that of the 1.5 V click (see below) at 15 cm. Then in order to adjust the described frequency modulation the controls of the function generator (Hi-med) were varied step by step. For the simulated click shown in Fig. 5 about 150 steps in the optimization procedure were used.

The orientation behavior of the animals was recorded using a closed circuit television system and a video recorder (Hitachi SV–612 EK, max. 50 frames/s), which allowed frame by frame playback. A stimulus was given only when the fish was still and in direct contact with the water surface or – in some cases – moved continuously with a steady swimming speed prior to stimulation. The target angle varied between 0° and 130° (0° = medially in front of the fish).

To determine the reaction time (time interval between the arrival of the first wave front at the middle of the fish's head and the beginning of the evoked body movement) the propagation velocities of the wave signals were measured. The reaction time was calculated by counting the number of video frames between the arrival of the wave front at the fish and the onset of the response. The method of counting the video frames was also used to determine swimming duration (time the fish needed to swim the first 5 cm towards the wave source after stimulation).

For each experiment five fish were used.

### Results

**Signal Characteristics**

Touching the water surface with a thin rod or blowing a short air blast onto it produces an unperiodic wave group of several hundred ms duration. Such a wave train, most conveniently produced by a 5 ms square pulse delivered to a modified loudspeaker and consequently called click, consists of waves of different amplitudes and frequencies. Since phase velocity as well as damping of surface waves are frequency dependent (Sommerfeld 1970; Lang 1980a), such a wave train is subjected to a considerable change of its wave pattern during propagation (Fig. 1). After 2–3 cm distance covered there are high frequency waves (up to 190 Hz) only at the signal front because of their
is used for the amplified voltage output of the stimulus generator) are produced, the wave parameters amplitude, slew rate (increase of amplitude with time), range of frequencies and signal length may differ considerably at a given distance from the wave source. In general, when using the same stimulating method but decreasing stimulus intensities, the stimulus amplitude, slew rate, frequency range and stimulus length drop at a given distance from the wave source (Grodd 1977; Bleckmann 1980). Independent of initial stimulus amplitude all waves produced by a given signal intercept the x-axis at nearly the same points (Fig. 2). This was proved for wave signals produced by touching the water surface with a rod (Ø 2, 2.5, 5 and 8 mm) and for wave trains generated by blowing air onto the water surface (analyzed for the source distances 4, 6, 8, 10 and 12 cm (rod) and 5, 10 and 15 cm (air blow: 5 ms)).

**Responses to Normal Signals (Clicks)**

Using monofrequent wave signals it was shown that wave amplitude and slew rate are less important for localizing the wave source. But as with increasing stimulus frequency the distance estimated by the fish decreases (Bleckmann 1980), *A. lineatus* may interpret wave signals containing high frequency parts to mean the wave source is in its immediate vicinity. With respect to the damping characteristics of the water surface this would, from a theoretical standpoint, be only partially understandable, because the frequency range of a wave train depends on the source distance as well as on the kind of wave produced (cf. Bleckmann 1980: Fig. 5).

By presenting click stimuli of different intensities we investigated whether *A. lineatus*’ ability to determine the source distance depends on stimulus amplitude, slew rate and, primarily, on frequency range. Wave trains were generated with square pulses of 4 V, 1.5 V, 1 V, and 0.5 V intensity. The corresponding amplitudes of the waves (peak-to-peak) were between 13 µm (4 V click, source distance 5 cm) and 0.07 µm (0.5 V click, 10 cm). At 15 cm source distance the wave amplitudes produced by the 0.5 V click became subthreshold for the fish and therefore were not determined. All clicks were presented at random within the range 5 to 16 cm. The intensity adjustment of the pulse generator was chosen so that the relation between the above mentioned parameters and the source distance was not equivocal. For example: the maximal amplitude of the 0.5 V click at 10 cm source distance is 0.07 µm, whereas that of the 4 V click at 15 cm is still 1.7 µm. The corresponding upper frequency limits within these wave trains are 50 Hz (0.5 V click, 10 cm) and 83 Hz (4 V click, 15 cm).
The exact development of amplitude and frequency or the intervals between the intercepts on the x-axis were measured for all clicks for the distances 5, 10, and 15 cm from the wave source (Fig. 3).

Reaction time, swimming distance (distance covered towards the wave source from onset of response to standstill or to clearly recognizable forward stretching of the breast fins) and swimming duration were evaluated. Fig. 4 shows the swimming distance as it depends on source distance for all tested stimulus intensities. Control experiments using clicks produced by dipping a rod into the water were carried out. For all fish there was a significant increase in swimming distance with increasing source distance \( t \)-test \( P \leq 0.001 \) which was independent of stimulus intensity. The slope of the regression lines varies from 0.79 to 1.18 for different animals, but there was no trend such as a decrease or increase in relation to the stimulus intensity. Likewise it is true for all fish that there is no difference in their reaction to air-blow clicks of different intensities as compared to rod clicks \( t \)-test, \( P \geq 0.1 \).

In agreement with earlier findings (Bleckmann 1980) the swimming duration decreased significantly with increased source distance for all tested stimulus intensities significantly \( t \)-test, \( P \leq 0.05 \) (prey catching reactions were not considered). For example: the mean swimming duration following the 1.5 V click is 566 ± 122 ms for a source distance of 5–7 cm, but only 410 ± 88 ms for 13–15 cm. Here too, no significant differences exist as compared to the responses to rod clicks \( t \)-test, \( P \geq 0.17 \). In summary, it is evident that the reaction to clicks and the ability to determine the source distance is not dependent on stimulus intensity and thus not on amplitude, slew rate and frequency range of the wave signal.

Since characteristic changes of muscle activities occurred 30 ms before a first oriented response of \( A. \ lineatus \) could be detected on video recordings (Bleckmann and Schwartz 1981), the fish must have received all necessary information about the distance of the wave source at least 30 ms before the end of the reaction time. The horizontal lines in Fig. 3 (top) represent the measured reaction times less 30 ms and show simultaneously which part of a wave signal passes the fish during this period of time. Independent of stimulus amplitude the completion of 7.7 ± 0.8 wave cycles (mean value ± S.D.) is necessary to initiate an orienting response. This is in good agreement with the value of 8.5 ± 0.5 wave cycles measured by Bleck-
mann (1980). The number of wave cycles and therefore their time periods determine the reaction time. Thus it seems possible that the fish obtain information on source distance from frequency modulation within the wave signal.

**Responses to Altered Signals as Test for Explanatory Hypothesis**

*Simulated Wave Signal.* To test this hypothesis a wave signal was produced which at 7 cm source distance largely resembled the frequency modulation of the 1.5 V click at 15 cm source distance. In all sets of experiments the fish were given the simulated wave signal when they were at a source distance of 7±0.5 cm, and clicks of 1.5 V or other intensities as controls over the entire range of 5 to 16 cm in a random pattern. For all fish and for all intensities tested there was no difference between the responses to clicks during the simulation experiments and the experiments in which click stimuli were presented exclusively (t-test, *P*≥0.07). Thus all responses to clicks (source distance 7±0.5 cm and 15±0.5 cm) were pooled and taken as controls for the responses to simulated wave signals. The results are shown in Fig. 5. As a response to simulated wave signals the mean swimming distance of all experimental animals exceeds the source distance. The swimming distance following simulated wave signals at 7±0.5 cm source distance is significantly longer for all fish (10.8±4.6 cm; mean and S.D.; *N*=259) than following clicks at the same source distance (6.2±1.9 cm, *N*=87) (t-test, *P*≤0.007).

However, there is no significant difference for 4 out of 5 fish when the responses to simulated wave signals are compared with those to clicks at a source distance of 15±0.5 cm (t-test, *P*≥0.082). These results emphasize the meaning of the frequency modulation for distance determination.

Comparing swimming durations following simulated signals and clicks at 15±0.5 cm source distance we found a significant difference for 3 out of 5 animals (t-test, *P*≤0.05). Summary of all values results in a swimming duration of 455±76 ms for clicks at the specified source distance and 583±102 ms for the simulated wave signal. This difference is significant at *P*<0.01 (t-test). Since the swimming duration following clicks increases significantly with decreasing source distance, it is evident that the fish were not completely misled. In addition to many reactions to simulated wave signals with swimming distances of 10 to 20 cm, there were cases of only hesitant swimming or no swimming at all, although fin movements usually did show that the fish had perceived the stimulus (number of positive reactions on clicks 94% (*n*=
1963), on simulated stimuli 71.4% (n=363). The difference is significant at $P < 0.001$ ($\chi^2$-test).

Upward Frequency Modulated Wave Signals. As clicks always show downward frequency modulation, the question arises how the fish react to wave signals with upward frequency modulation. To answer this question a wave train was synthesized which at a source distance of 5 to 16 cm met all the requirements mentioned and which did not resemble the frequency modulation of a click anywhere in the test range (inset Fig. 6). Here too, clicks of various intensities were used as controls throughout the experiments in a random sequence. Again there were no differences between the responses to clicks during the experimental sessions with upward frequency modulated signals compared to experiments in which only clicks were presented ($t$-test, $P \geq 0.13$).

In Fig. 6 the reactions of the fish to upward frequency modulated wave signals are shown. In three fish there is no dependence of swimming distance on source distance ($t$-test, $P \geq 0.33$). The remaining two fish reveal a significant increase in swimming distance with increasing source distance ($t$-test, $0.05 > P > 0.035$), but their ability to localize the wave source is only poorly developed (slopes of regression lines 0.54 and 0.64). Most often all fish swam just 4 to 6 cm after stimulus presentation, regardless of the source distance. Two fish sometimes swam beyond the stimulus source, but they appeared hesitant and only rarely showed a clear distance estimate (e.g. a sudden stop or protruding breast fins).

The difficulties in responding to upward frequency modulated wave signals are clearly demonstrated by the difference between swimming duration following these modulated signals (705±241 ms, $n=405$) and regular clicks (521±160, $n=1963$). The difference is significant at $P=0.01$ ($t$-test). With upward frequency modulated wave signals the fish in most cases not only swam too short a distance, but were also hesitant and slow. Considering the fact that the animals showed no reaction in 23.6% of all cases (6% with
clicks) (difference significant: \( \chi^2 \)-test, \( P = 0.001 \)), although here about every fifth reaction was rewarded by feeding too, we must assume that upward frequency modulated signals, just as monofrequent signals (Bleckmann 1980) contain less information about source distance than do clicks.

The Frequency Modulation of Wave Signals Caused by Different Sources

Does the kind of wave production influence the degree of frequency modulation at a certain source distance? First, we compared the frequency modulation of various clicks produced by an air blow and by rods of different diameters (2.5, 5 and 8 mm). Second we investigated whether in long lasting wave trains, as for example produced by terrestrial insects trapped on the water surface, the first 7–9 waves of the signal (= reaction time) also contain information about the source distance. For this purpose long lasting wave signals with a minimum of regularity were generated by driving the loudspeaker with sine- and triangular voltage of considerable rise and fall of amplitude. The rod diameter only slightly effects the wave pattern (Fig. 7). However, there are differences when air-blow clicks or long lasting wave signals are compared with rod clicks. The difference can reach half a wave length for the first 9 wave cycles (always with reference to the 4 V air-blow click). The similarity in the frequency modulation of the first 7–9 wave cycles of long lasting wave signals and clicks was not unexpected. It is certainly caused by the fact that the initial movement of the rod produces a click which precedes the real long lasting wave train.

Comparing the various wave signals analysed at 5, 10 and 15 cm source distance reveals more differences in the frequency modulation of the first 7–9 wave cycles than a comparison of the different signals at the same source distance (Fig. 8). Both, frequency range and frequency modulation, decrease with increasing source distance. Based on such a decrease in frequency modulation a decline in A. lineatus' ability to determine distance occurred as was expected with increasing source distance (Fig. 4).

Discussion

Localization of Wave Source

Independent of amplitude, slew rate and frequency range A. lineatus is able to determine the distance from the wave source if click stimuli are presented. Although water surface waves are subjected to strong frequency dependent damping (e.g. 1.67 dB/cm for 10 Hz and 8.57 dB/cm for 140 Hz; after Lang 1980a), none of the mentioned parameters alone is sufficient for an unequivocal indication of source distance. All these parameters not only change with increasing
source distance, but also depend on the kind of wave production and initial stimulus intensity.

The results of all experiments suggest that the frequency modulation within a wave train is of high significance to distance determination. On the other hand the experiments with the simulated click (Fig. 5) and with the upward frequency modulated wave train (Fig. 6) indicate that the fish were not completely deceived and that there must be an additional minor cue in such wave signals. At least two explanations are possible:

1. Remaining irregularities in the course of amplitude and frequency modulation of the simulated click may be one reason for the differences in the responses to the two signals.

2. Electrophysiological investigations have shown that single neuromasts of A. lineatus are directionally sensitive (Unbehauen 1980). This means that under otherwise identical conditions (target angle, stimulus frequency, stimulus amplitude) the output of the lateral line system of A. lineatus depends on the curvature of the wave front and thus on source distance. Because the width of the head of the fish as the basis of measurement is only about 1 cm, the curvature of the wave front can only – if at all – provide the fish with information about the source distance in the vicinity of the wave source (about 7 cm). These points may explain why the fish were not completely deceived by the simulated click and why for some fish there was still a weak distance dependent graded reaction when frequency upward modulated wave signals or monofrequent wave signals of 30 Hz and 50 Hz (see Bleckmann 1980) were presented.

**Sensory Mechanism**

Behavioral studies have shown that A. lineatus reacts highly sensitively to water surface waves within the frequency range of 10 Hz to at least 250 Hz with the lowest threshold amplitude of 0.013 µm at 100 Hz (Bleckmann 1980). Spike activity recordings of lateral line primary afferents of single head neuromasts of A. lineatus confirmed these values (Bleckmann and Topp 1981). The neuromasts were found to be most sensitive between 80 Hz and 140 Hz when stimulated with monofrequent wave signals of 0.04 µm pp-amplitude. It is remarkable that this frequency bandwidth is also characteristic for prey-indicating wave signals, whereas signals caused by abiotic sources do not at all contain such high frequency waves (Lang 1980a).

Microphonic potentials of the head neuromasts of A. lineatus (Unbehauen 1980; Koschwitz, unpublished) and the spike sequences of their primary afferents (Topp 1980; Bleckmann and Topp 1981) are synchronized to sinusoidal wave stimulation. The synchrony of receptor and neural membrane potential changes in lateral line receptors has been stressed in many studies (for ref. see Kroese et al. 1980). In addition, the responses of neuromasts in Aplocheilus became more intense with increasing stimulus amplitude when high frequency waves were used (Topp 1980). Therefore the topminnow A. lineatus should be able to determine the frequency content or the amplitude-frequency content of a wave signal and to discriminate wave trains containing wave cycles of different frequencies.

The ability of A. lineatus to discriminate frequency was demonstrated recently (Bleckmann et al. 1981). According to this investigation A. lineatus is able to discriminate surface waves of different frequencies if the ratio between the frequencies of the signals is at least 0.15 (e.g. 20:23 Hz or 120:138 Hz). These results support the idea that the frequency modulation within a wave train is used by A. lineatus for distance determination.

**The Reaction to Prey Signals**

According to Lang (1980a) wave trains caused by aquatic and semiaquatic insects consist of single wave pulses which largely resemble the clicks used here. On the other hand, terrestrial insects trapped on the water surface produce long lasting wave signals which may have a very irregular wave pattern. The results with the long lasting artificial wave trains (see Fig. 7) indicate that even for these natural long lasting signals the frequency modulation of the first 7–9 wave cycles may contain information about the source distance. Yet it is difficult to test this assumption, because 64 to 128 wave stimuli would have to be averaged before the amplitude-weak onset of these wave signals would be visible. Such signal averaging, however, is not possible since no uniform trigger point could be referred to in measurements of that kind. On the other hand, for long lasting wave signals the localization of the stimulus source is facilitated by the fact that the fish need only follow the stimulus gradient in order to reach the prey. That they do so can be seen in feeding experiments using living insects.

According to Lang (1980a) and the present study wave signals contain the information prey or non-prey as well as cues about the source distance. Waves caused by prey differ from non-prey waves in that they have higher upper frequency limits and an amplitude maximum which it shifted to a higher frequency range of 12–45 Hz. Due to the damping properties of the water surface, with increasing source distance there is (a) a decrease of the upper frequency limit of a wave signal and (b) a shift of the amplitude
maximum down to lower frequencies (Grood 1977). Therefore information on the kind of wave production and source distance interfere at least partially with each other. As a result the discrimination between prey and non-prey signals should become more and more difficult with increasing source distance. Surface-feeding fish might partly solve this problem by calculating the initial frequency-amplitude content of a wave signal, taking into account the actual source distance and the frequency dependent damping of surface waves.

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