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JAMMING AVOIDANCE IN THE ELECTRIC FISH *EIGENMANNIA*: HARMONIC ANALYSIS OF SEXUALLY DIMORPHIC WAVES

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SUMMARY

1. The present report shows an *intra*specific, sexually dimorphic variation in harmonic content and waveform, as well as intensity, of the Electric Organ Discharges (EODs) in the green knife fish, *Eigenmannia* (Figs 2, 11). There is a close correlation between harmonic content of the EODs and waveform (as defined by the ratio of intervals between zero-crossings in the two half-waves of one EOD cycle; Fig. 3). The aim of the following experiments was to determine whether the fish are sensitive to differences in stimulus waveform or harmonic content.

2. Stimulation with electric fields of various waveforms but equal peak-to-peak amplitudes at frequencies close to the fish's frequency elicited the Jamming Avoidance Response (JAR) which is an EOD frequency change increasing the frequency difference (Watanabe & Takeda, 1963). The strength of JARs to distorted square wave and sawtooth stimuli was 25 % smaller than that elicited by sine wave stimuli (Fig. 6). Undistorted square waves elicited stronger responses than sine waves, while undistorted sawtooth waves were the least effective (Table 1). The differences in response strength were proportional to differences in the intensity of the fundamental frequency or first harmonic, f_1, of the stimulus waveforms.

3. Subharmonic stimuli of nine artificial or synthesized natural waveforms at frequencies near one-half or one-third of the EOD resting frequency elicited responses only when a strong higher harmonic, or overtone, of the stimulus was close to the EOD fundamental frequency (Fig. 7). Stimuli of different waveforms, but identical spectral amplitudes, elicited similar responses not significantly different from each other, at stimulus frequencies near one-half (Table 3) and near the EOD resting frequency (Fig. 10).

4. *Eigenmannia's* JARs to synthesized male EODs at frequencies close to the fish's frequency were weaker than those to female EODs of equal peak-to-peak amplitude. The weaker response was proportional to the weaker intensity of the first harmonic of the male EOD (Fig. 12). A stimulus frequency near one-half of the EOD baseline frequency evoked opposite results, as the second harmonic, f_2, of the male EOD was relatively four times stronger than that of the female EOD (Table 4).

Dedicated to the 60th birthday (1984) of Dr Thomas Szabo.

Key words: Jamming avoidance response, electric organ discharge, signal waveform, harmonic content, Fourier analysis, sexual dimorphism, *Eigenmannia*.

5. *Eigenmannia* responded to jamming signals as if it performed a limited spectral amplitude (Fourier) analysis, determining the intensity of that stimulus harmonic (at least up to the third) enclosed within a narrow frequency band centred on its own EOD fundamental frequency. The assessment of that harmonic was independent of stimulus waveform, peak-to-peak amplitude, or power, demonstrating linear filtering of the stimulus wave.

6. Because of *Eigenmannia's* sensitivity to the harmonic content of the stimulus wave, as also demonstrated in subharmonic experiments, the natural variation of EODs in harmonic content may serve in species and mate recognition.

INTRODUCTION

Lissmann (1958) suggested that the weakly electric organ of some tropical fish, among them the South American knife fish *Eigenmannia*, provides the energy for an active electrolocation system. This has been confirmed subsequently and extensive study has been made of the physiology of signal production (Bennett, 1971*a*) and perception (Bennett, 1971*b*; Szabo & Fessard, 1974; Bullock, 1982). Much less is known about the second role of *Eigenmannia's* Electric Organ Discharge (EOD, Fig. 2), that is communication between individuals (Hopkins, 1974*a*), with the notable exception of the Jamming Avoidance Response (JAR; Watanabe & Takeda, 1963; Larimer & MacDonald, 1968; Bullock, Hamstra & Scheich, 1972; Scheich, 1977; Heiligenberg, 1980). The JAR is a reflex-like frequency-shift in the presence of stimulus frequencies close to the sender's frequency. In an experimental situation, this JAR aids the fish in maintaining efficient electrolocation (Heiligenberg, 1977); little is known, however, about the biological context and significance of this response.

Nothing is known about the behavioural significance of the rich species divergence of EOD waveforms and their marked differences in harmonic content in sympatric groups of gymnotoids (Kramer, Kirschbaum & Markl, 1981). The same is true concerning a sexual dimorphism of *Eigenmannia's* EOD presented in this paper (Figs 2, 3, 11; short report Kramer, 1983). The purpose of the present study was to find out whether differences in waveform or harmonic content of stimuli are perceived by the electrosensory system, as measured by the JAR.

According to Bullock *et al.* (1972) comparison of the effectiveness of square, sinusoidal, triangular and sawtooth waveforms in eliciting JARs showed 'very little difference' in stimuli close to the EOD frequency (△1F stimuli); unfortunately, no data were presented. At one-half EOD frequency (△½F stimuli), however, only the sawtooth waveform with its strong second harmonic (which was close to the EOD frequency) elicited JARs.

Gottschalk (1981) concluded that a temporal feature of the EOD, a shorter duration between zero-crossings in the head-positive compared with the head-negative half-waves (see Fig. 2), is essential for eliciting JARs at △½F stimulus frequencies. A sawtooth wave, as used by Bullock *et al.* (1972), only possesses this temporal feature if it is distorted (as, for example, in Fig. 5), or if the wave is offset by a d.c. component.

It is not possible to draw conclusions from this conflicting evidence because information about the stimuli (waveforms and Fourier amplitude spectra) and the strengths of responses is lacking or incomplete. Also, it is difficult to understand why sensitivity for differences in waveform or harmonic content should be detectable in Δ½F stimuli only, but not in the behaviourally more important Δ1F stimuli.

In no electric fish species is it known whether *spectral* or *temporal* properties of tone-signals, including *Eigenmannia's* sexually dimorphic EOD, provide the cues evoking a behavioural response (see also Scheich, 1977; p. 223). The present experiments focused on the fishes' sensitivity for the variation of harmonic content and shape of stimulus waveforms to determine which one of the two conflicting models of signal processing (also known as frequency domain and time domain mechanisms; see Scheich, 1977) is the one used by *Eigenmannia*.

MATERIALS AND METHODS

Eigenmannia species are gregarious and all of them appear to hide among vegetation or under cover during the day but swim into the open water at night (Steinbach, 1970; personal observations near Manaus/Amazonas). Seven animals of the still un named *E. 'sp. III'* (10.5–13 cm, determined by F. Kirschbaum; see also Kramer *et al.* 1981) were tested. The experimental aquarium (52 × 25 × 28 cm high; conductivity $100 \pm 5\,\mu S\,cm^{-1}$; 26·7 ± 0·2 °C) was provided with a porous pot (length, 17·5 cm; inner diameter, 3·3 cm; wall, 0·3 cm) open at one end. For large fish a porous pot of greater size was used (length, 33 cm; inner diameter, 6·5 cm; wall, 1·2 cm). The experimental aquarium was placed in a larger tank (80 × 50 × 50 cm high) containing earthed tap water. The water was heated and an air bubbler in each aquarium prevented the build-up of temperature gradients. Mechanical disturbances from the floor of the building were attenuated by air-cushions underneath the feet of the experimental table.

The fish remained within the porous pot most of the day (L:D, 12:12). The shelter was covered with coarse plastic mesh to prevent the fish from accidentally leaving. (The pot was left open for one animal, with no effects upon the results.) The fish were set free and fed on frozen *Chironomus* larvae before dark.

The EOD was differentially recorded head-to-tail by a pair of silver ball electrodes connected to a wideband preamplifier (0·1 Hz–100 kHz). The EOD frequency was measured under computer control using an electronic counter (Hewlett Packard model 5308A) in the 'period average' mode (measurements accurate to 0·0004 % or 0·002 Hz). In any experiment, the EOD frequency was measured twice per second for a period of 2 min. The baseline EOD frequency was determined as the average of 120 measurements taken during the first minute. During the second minute, the stimulating field (measured with Ag/AgCl-electrodes within the porous pot while the fish was removed) was applied across the fish by a pair of silver ball electrodes positioned symmetrically about opposite the middle of the fish. With this electrode arrangement the recording was almost free from stimulus artifact (Bullock *et al.* 1972). However, the use of a longitudinal stimulus gradient with respect to the fish is also possible (Watanabe & Takeda, 1963) at low stimulus intensities.

The stimulating field (envelope rise time 400 ms) was generated by a synthesizer/function generator (Hewlett Packard model 3325A) connected to a computer. The stimulus frequency, F_{Stim}, was automatically adjusted to 2·0 ± 0·002 Hz below the

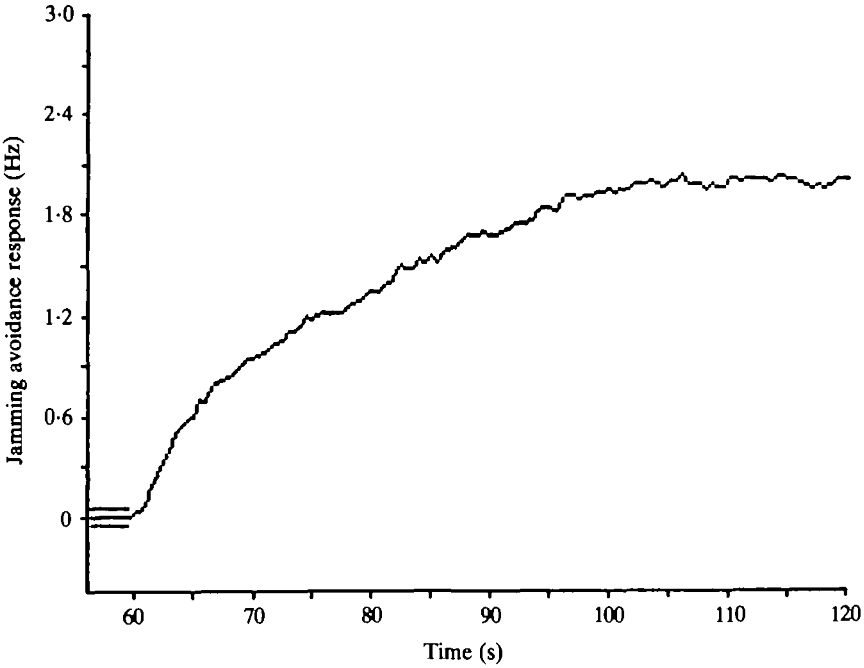

Fig. 1. Time course of the JAR in *Eigenmannia sp. III* shown as the average curve of 10 response curves (similar curves were obtained for *E. lineata*). Onset of a sinusoidal stimulus 2 Hz below the resting frequency ($\Delta F = 2$ Hz) is at '60 s'; the resting frequency (= 0 Hz frequency change by definition), as determined during the first 60 s of the experiment, is shown with standard deviation. Quite often the frequency change is steeper at first than shown in this example. With a negative ΔF (stimulus frequency higher than fish frequency) the response curve would be a mirror image reflected about the abscissa, but the response strength is very often different for identical ΔF values of opposite sign. Stimulus intensity = −60 dB re: 29·6 mV_{p-p} cm^{-1}; stimulus rise time = 400 ms.

baseline frequency of the fish ($\Delta F = F_{Fish} - F_{Stim} = 2$ Hz) by computer (choice of ΔF: see below and Results). The fish began to increase its EOD frequency smoothly within less than a second after onset of stimulation (JAR), approaching a plateau after about 40–60 s (Fig. 1). The JAR was measured as the mean frequency change 40–60 s after stimulus onset, and as the integrated frequency change after stimulus onset relative to the baseline EOD frequency. As the results obtained with these two methods were similar, only one method (the first) was adopted for presentations in Tables and Figures.

As the stimulus frequency remained fixed, ΔF increased continuously during the fish's response. Frequency difference clamping (constant ΔF; Bullock *et al.* 1972) was not used because active frequency following between pairs of fish is unknown under natural conditions. With the frequency difference clamp an optimal ΔF of 3–4 Hz has been demonstrated (Bullock *et al.* 1972). Therefore, with the present initial ΔF of 2 Hz, the fish's response produced an increase then decrease in effectiveness of the stimulus.

An analogue-to-digital (A/D) converter (12 bit, 100 kHz) connected to a computer was used to record stimulus and EOD waveforms as computer files. The waveforms were drawn by a digital plotter connected to a computer (Figs 2, 5, 8, 9, 11). Fast Fourier analysis was done by calculation from a set of 1024 data points, obtained by A/D-conversion of the waveforms at 10-kHz sampling rate.

For JAR experiments with 12 *E. lineata* (identified by F. Kirschbaum) some modifications of the above methods and additional techniques were used (Figs 4B, 10, 12; Tables 1–4). A microprocessor-controlled digital-to-analogue (D/A) converter connected to a computer generated 'natural' stimulus signals obtained by A/D-conversion of EODs (8 bit, 1 MHz) or 'artificial' stimulus signals calculated by computer. This D/A converter had 8-bit resolution, and synthesized waveforms at the rate of 500 000 voltage steps s^{-1}. Frequency and amplitude of synthesized waveforms could be controlled on-line to the experiment; the frequency difference ΔF was either $\pm 2\,\mathrm{Hz} \pm \frac{1}{8}\,\mathrm{Hz}$. Stimulus rise time was again 400 ms. Carbon rod (3·3 × 0·4 cm) electrodes positioned as before were used for both stimulation and recording.

Statistical tests were calculated according to Siegel (1956) and Sachs (1978); all *P*-values are two-tailed.

RESULTS

Sexual dimorphism in EOD waveform

Based on earlier observations (Hopkins, 1974*b*), Gottschalk (1981) first suggested a sexual dimorphism in EOD waveform for four *Sternopygus* sp., similar to the one proposed for *Eigenmannia* in the present study (Fig. 2). He also noted that the EODs of 11 *Eigenmannia* varied from 0·61 to 0·87 in what he called the 'P/N ratio', which is the durations of the Positive over the Negative half-waves of one EOD cycle. However, he could not be sure of the sex of his *Eigenmannia* (see also Westby & Kirschbaum, 1981).

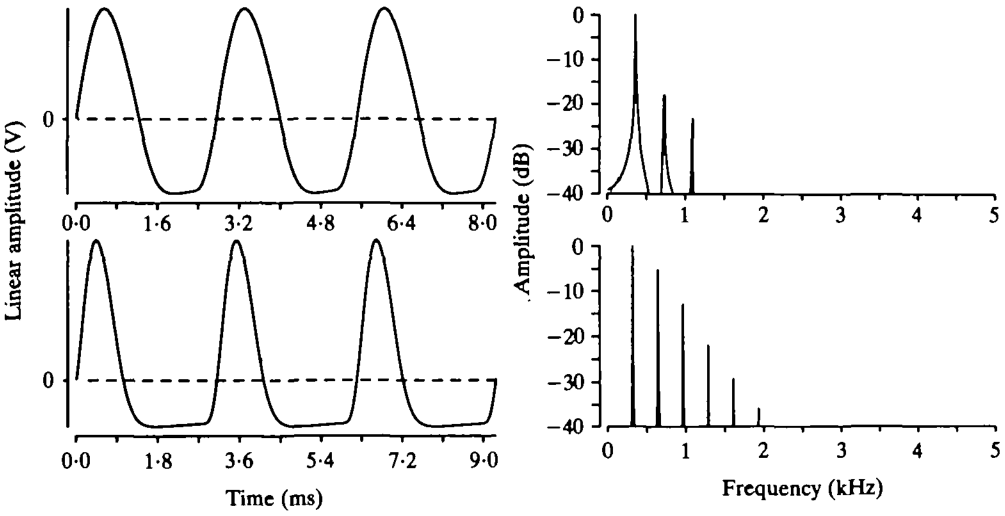

Fig. 2. Electric organ discharges (EODs) of *Eigenmannia sp. III*, left, with Fourier amplitude spectra, right. The ordinates of the left diagrams are arbitrary linear amplitudes (V), of the right diagrams amplitudes expressed as dB attenuation relative to the strongest spectral component of each waveform. Top: female (11 cm); bottom: male (20·7 cm). Note the almost sinusoidal EOD of the female, characterized by weak harmonic content, as compared with the EOD of the male with its marked head-negative d.c. phase and strong harmonic content. (The distortions of some of the spectral peaks are artifacts of the digitizing and Fourier transform procedure.)

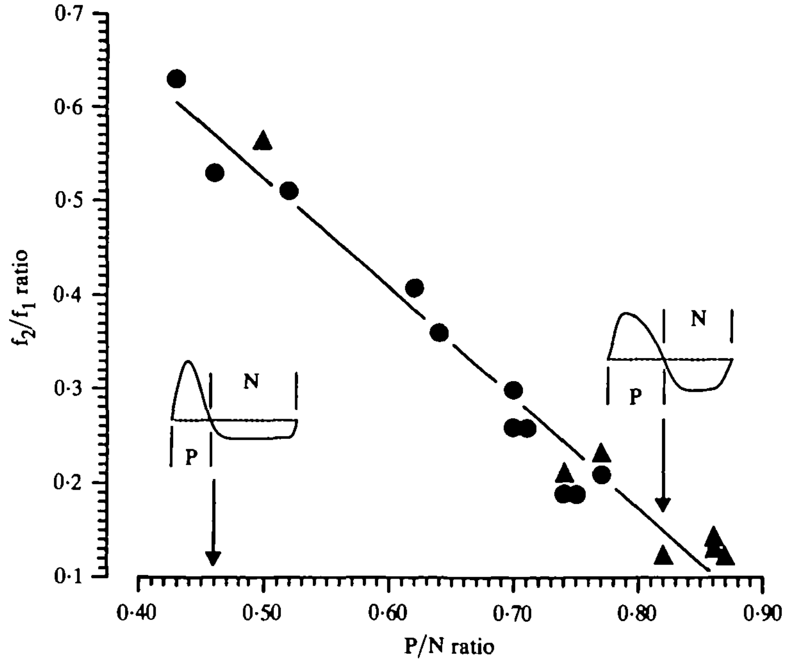

Fig. 3. The intensity of the second harmonic, f_2, of *Eigenmannia's* EOD as a function of a temporal waveform parameter, the P/N ratio (as introduced by Gottschalk, 1981). The intensity of the second harmonic is expressed as the intensity ratio of the second over the first harmonic, f_2/f_1. The first harmonic, or fundamental frequency, is the strongest component, hence $(f_2/f_1) < 1$. Circles, *E. lineata*; triangles, *E. sp. III*. Each point is one fish. The same negative correlation holds for both species ($r = -0{\cdot}983$; difference from zero correlation significant at $P < 0{\cdot}001$). The male-like EOD waveform with its lower P/N ratio (left inset) is associated with a strong second harmonic, and a female-like EOD with its higher P/N ratio (right inset) with a weak second harmonic (compare with Figs 2, 11). Young fish all show high P/N ratios; the transition zone to adult male EODs is estimated to be around P/N = 0·6, or an f_2 intensity of about 0·4. A least squares regression line is fitted to the data ($y = -1{\cdot}17x + 1.1$).

In the present study a much greater range of P/N ratios (0·50 to 0·97) was found in 11 *Eigenmannia 'sp. III'*. Histological examination of two fish showed that one with a P/N ratio of 0·82 was female, and one with a value of 0·5 was male (Fig. 2).

The P/N ratios of the EODs (Fig. 11) of 18 *E. lineata* (probably Gottschalk's species), ranged from a very low 0·40 to 0·82. The four fish with P/N values up to 0·52 clearly were males, as judged by their large body sizes between 30 and 37 cm, which is about twice the size of adult females (F. Kirschbaum, personal communication; Kutz, 1980). Two of the latter (15 and 16·5 cm) were gravid with eggs and had P/N ratios of 0·63 and 0·77, respectively. Thus it appears that in *E. lineata* P/N ratios of the EODs of females are above about 0·6, while those of males are below, with a region of overlap from about 0·59 to 0·63 due to half-grown males with regressed gonads (all animals could be sexed by size and/or by *in vivo* inspection of the gonads through the translucent skin according to F. Kirschbaum, personal communication).

Small fish of either sex all tend to have high P/N ratios; as they grow the P/N ratio decreases. This is also clearly seen in EOD recordings from laboratory-bred *Eigenmannia* during ontogenetic development (Kirschbaum & Westby, 1975). The exact age or size when males begin to develop the EOD waveform characteristic for their sex has still to be determined but it occurred between 11 and 20 cm in either species, and might be linked to the onset of sexual maturity.

There is a close correlation of the P/N ratio with harmonic content, as measured by the intensity ratio of the second over the first harmonic (or fundamental frequency), f_2/f_1 (Fig. 3). The lower the P/N ratio the stronger is the second harmonic (correlation coefficient $r = -0{\cdot}983$; $P < 0{\cdot}001$). Thus the simple P/N measurement allows the assessment of the relative intensity of the second harmonic, using the least squares regression line of Fig. 3.

'P/N ratio' and 'f_2 intensity' do not express the same thing in different ways. Their relationship may be a fortuitous consequence of the way the shape of the EOD waveform varies, but is certainly not generally true for all wave-shapes. For example, the f_2 intensities of the distorted sawtooth (Fig. 5) and the undistorted sawtooth (Fig. 8) are nearly identical in spite of very different P/N values (0·5 and 1, respectively).

Compared with the intensities of the fundamental frequencies, f_1, the intensities of the second harmonics, f_2, of male EODs can be four times stronger than those of female EODs (f_2/f_1 intensity ratios = 0·56 and 0·13 for the *E. sp. III* male and female of Fig. 2, and 0·69 compared with 0·19 for the *E. lineata* male and female of Fig. 11).

In full-grown individuals there is also a marked sexual dimorphism in EOD intensity. The EODs of large males, measured differentially head-to-tail, were much stronger than those of adult, ripe females [about 120 and 100 mV_{p-p} (p–p, peak-to-peak] ($N = 2$) compared with 16 mV_{p-p} ($N = 2$), and still less for all other females]. Westby & Kirschbaum (1981) have formally shown the positive correlation between body length and EOD amplitude in *E. virescens*.

Hopkins (1974*a*), gives a discharge frequency range from 260 to 650 Hz (corrected to 27 °C, using a Q_{10} of 1·5; Watanabe & Takeda, 1963; Enger & Szabo, 1968) for 61 *E. virescens* caught in the wild; Westby & Kirschbaum (1981) measured a range of 250–560 Hz for 148 fish in the laboratory. Hopkins as well as Westby & Kirschbaum found a significant difference, but wide overlap, between the discharge frequency distributions of both sexes (although that difference was of opposite sign in the two studies); both concluded that sex recognition by a statistical difference is unlikely. With body lengths ranging from 13·5 to 23 cm even the largest males analysed by Westby & Kirschbaum (1981), although sexually mature, were still far from fully-grown. Hopkins only states that his fish were sexually mature or in reproductive condition. (According to data from Kirschbaum, 1979, *E. virescens* grows as large as *E. lineata*. Due to the confused taxonomy of the genus *Eigenmannia*, it appears that until recently, *E. lineata* has often been called *E. virescens* in the literature; see also Kramer *et al.* 1981.)

Based on four full-grown *E. lineata* males (larger than 30 cm) and two ripe females (15 and 16·5 cm) I suggest that in *full-grown* fish, there is a clear-cut sex difference in discharge frequency: the males discharged at low frequencies (from 268 to 364 Hz), and the females at higher frequencies (from 420 to 487 Hz; 27 ± 0·2 °C). Six juveniles (three of each sex) had an intermediate frequency range of 347–455 Hz. The above suggestion, of course, needs further support.

Westby & Kirschbaum (1981) observed full gonad development and spawning in their subadult group of fish not showing a sexual dimorphism in discharge frequency (by control of environmental factors in the laboratory; Kirschbaum, 1979).

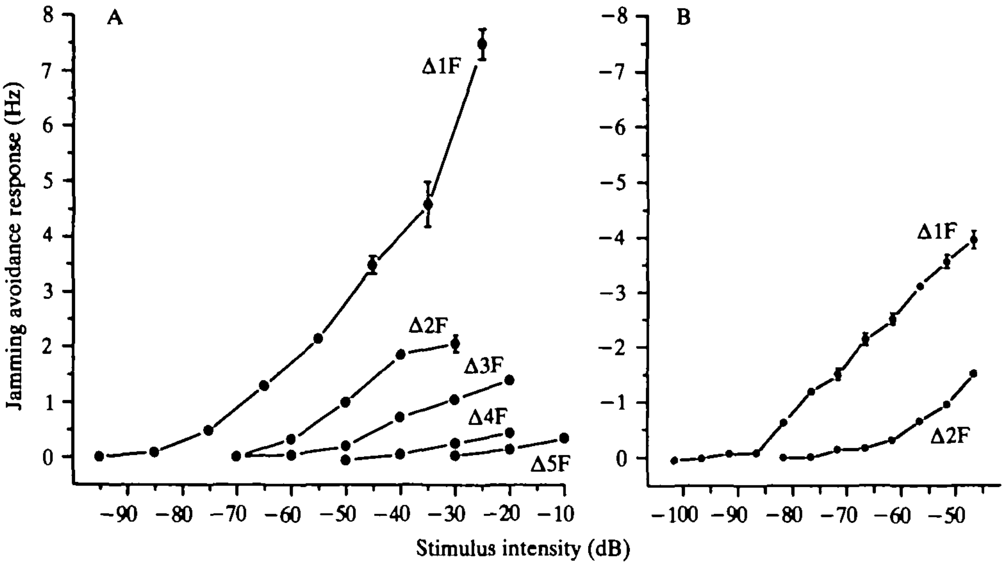

Fig. 4. Response as function of intensity of a sine wave re: 29·6 $mV_{p-p}cm^{-1}$. Each point is a mean of at least 10 measurements. Standard errors are either shown or are too small to be drawn. Δ1F curves: stimulus frequency was 2 Hz below (B, above) the EOD baseline frequency (first harmonic). (A) *Eigenmannia sp. III.* Δ2F curve: stimulus frequency was 2 Hz below two times that frequency (the second harmonic); and so on. (B) *E. lineata.* Δ2F curve: stimulus frequency was 4 Hz above the second harmonic of the EOD.

Therefore, a sex difference in discharge frequency cannot be an essential cue in the reproductive behaviour of *E. virescens*, even if shown in *full-grown* fish. (The suggested sex difference may, however, play a role in male competition for females.)

Time-dependent changes in JAR and stimulus/response curves

According to Bullock *et al.* (1972), there is neither habituation nor facilitation of the JAR, although on many occasions a short 'settling down' period had been observed. In the present experiments using sinusoidal stimulation, the JAR habituated significantly at an inter-trial interval of 4 min (Spearman rank correlation $r_s = -0{\cdot}158$; $P < 0{\cdot}01$; $t = -2{\cdot}756$; df = 298) but not of 10 min ($r_s = -0{\cdot}139$; $P = < 0{\cdot}1$; $t = -1{\cdot}386$; df = 98) and of 25 min ($r_s = -0{\cdot}026$; $P > 0{\cdot}2$; $t = -0{\cdot}256$; df = 98) at the chosen intensity (−55 dB re: 29·6 $mV_{p-p}cm^{-1}$; cf. Fig. 4). Up to the fifth repetition, habituation was preceded by sensitization at 4-min intervals ($r_s = 0{\cdot}366$; $P < 0{\cdot}01$; $t = 2{\cdot}726$; df = 48); subsequently, rather strong habituation was detected ($r_s = -0{\cdot}235$; $P < 0{\cdot}001$; $t = -3{\cdot}876$; df = 258). For each interval a series of experiments was run on 10 subsequent days; the number of repetitions per day was 30 for the experiment with 4-min intervals, and 10 for the experiments with 10- and 25-min intervals.

Watanabe & Takeda (1963) concluded that the magnitude of the response was roughly linearly related (proportional) to the logarithm of the stimulus intensity over a range of about 30 dB above threshold (higher stimulus intensities were not investigated). There was large variation of responses which these authors thought was due to the technical difficulty of maintaining initial frequency differences at constant values in successive experiments.

Bullock *et al.* (1972) obtained similar results with the precise frequency-clamping technique, and presented them in a double-logarithmic plot (their Fig. 5, p. 30) in which 'a straight line sometimes was obtained over most of the range'. A straight line with slope n would indicate that a power function, $y = x^n$, underlies the relationship between stimulus intensity, x, and response strength, y. When exploring also high stimulus intensities these authors found that 'stronger stimuli usually depress the response'.

In the present experiments using an unclamped stimulus frequency like Watanabe & Takeda (1963) but with automated △F-control, the JAR was approximately proportional to the logarithm of the stimulus intensity over a range of at least 40 dB (Fig. 4, △1F curves), similar to the Watanabe & Takeda plot (their Fig. 7). Variation of responses, as measured by standard errors, was often too small to be shown in these stimulus/response curves. No depression of responses was observed over the whole range of intensities investigated (approximately 65 dB above threshold; Fig. 4A, △1F curve). Despite this very high intensity, a plateau was not reached.

A straight line in a semilogarithmic plot like Fig. 4 shows that an exponential function, $y = a^x$, best approximates most of the relationship between stimulus intensity, x, and response strength, y (△1F curve). This input-output relationship is found in most sense organs, and is known in psychophysics as the Weber-Fechner Law. Within certain limits, a given percentage of change in stimulus intensity evokes the same increment in response strength, independent of absolute stimulus intensity.

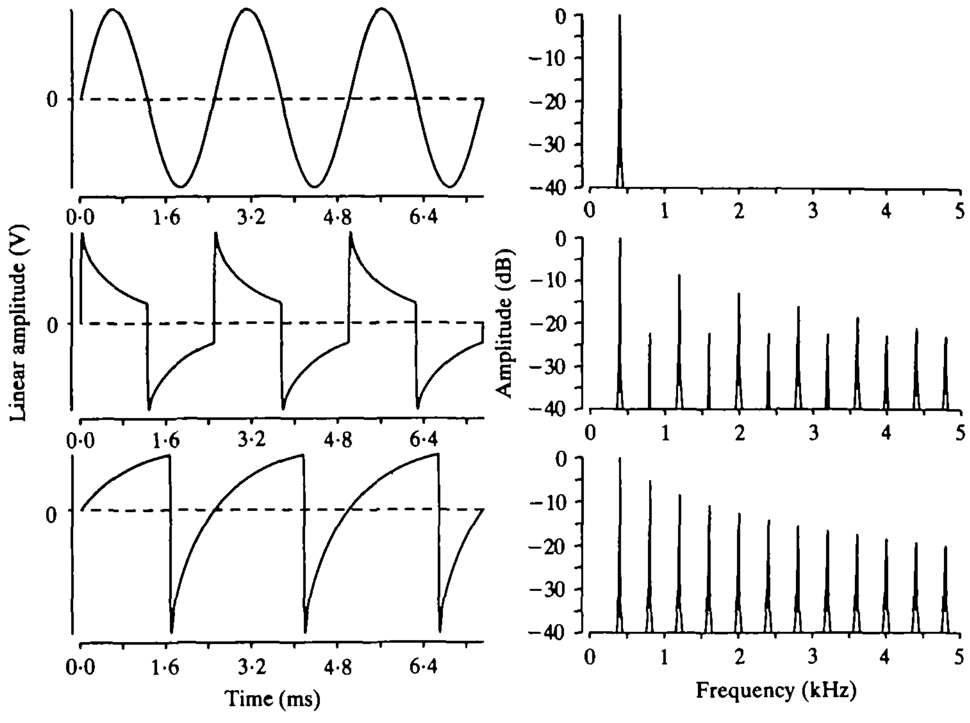

Fig. 5. The sine, the distorted square (middle) and the distorted sawtooth waveforms (bottom) used as stimuli in JAR experiments with *Eigenmannia sp. III*, as recorded from the water, left, with Fourier amplitude spectra, right. Axes as in Fig. 2. Square and sawtooth waves were distorted by a transformer separating the stimulus electrodes from the stimulus generator.

From pilot experiments it was clear that the degree of habituation increased markedly with rising stimulus intensity. Therefore, the inter-trial interval of 25 min was made progressively longer above an intensity of −55 dB, using a 24-h interval at the highest intensities.

The JAR is also elicited by sinusoids close to low integer multiples, or higher harmonics, of the EOD frequency (Watanabe & Takeda, 1963), with response strengths decreasing the higher the harmonic (up to the fifth) at constant stimulus amplitudes (Bullock *et al.* 1972). These authors also found that the best ΔF remains at about the same value from the first to the fifth harmonic.

As shown in the present study, stimulus/response curves of higher harmonics are of sigmoid shape; no depression of the responses even at very high intensities was observed (Fig. 4: Δ2F–Δ5F curves)

Dependence of the JAR on waveform

The first experiment investigated whether the JAR depends on waveform and harmonic content of a stimulus at a frequency close to the fish's frequency (Δ1F stimulus). Three different signal functions at identical ΔF values and peak-to-peak amplitudes in the water were used: the sine wave (harmonic content: less than −60 dB), the square wave and the sawtooth functions. Due to a transformer separating the stimulating electrodes from the stimulus generator, the sawtooth and the square waveforms were distorted by frequency-dependent phase-shifts, with little effect on spectral amplitudes (Fig. 5).

With an f_2/f_1 intensity ratio of 0·54, the f_2 component of the sawtooth wave was slightly weaker than that of the male EOD of Fig. 2 (see above), but seven times stronger than the very weak one of the distorted square wave.

The sequence of signals in an experiment was determined as random permutations of the three signals taken three at a time, according to a randomized blocks design (Cochran & Cox, 1957). The stimulus intensity was −60 dB (compare with Fig. 4); the inter-trial interval was 20 min. In control experiments with the stimulating electrodes disconnected, 'responses' were always close to, and not significantly different from, zero [example from one day: −0·01 ± 0·03 Hz (± S.E.) for the sawtooth, 0·03 ± 0·04 Hz (± S.E.) for the square, and −0.05 ± 0.04 Hz (± S.E.) for the sine wave; $N = 10$ for each waveform].

In each fish, the sine wave elicited the strongest responses compared to stimulation with both distorted square waves and the distorted sawtooth of equal peak-to-peak amplitudes ($P < 0{\cdot}001$; paired *t*-test and Wilcoxon matched-pairs signed-ranks test; Fig. 6). These square wave and sawtooth stimuli elicited similar responses in four animals, although in two animals (fish 3 and fish 4) the responses to sawtooth waves were stronger, and in two other animals (fish 1, unrestrained; and fish 6) weaker compared with square wave stimuli. Combined for all fish, the results for stimulation with square waves (mean 1·30 ± 0·09 Hz; ± S.E.) and the sawtooth (mean 1·32 ± 0·14 Hz; ± S.E.) were not significantly different from each other.

Mean JARs elicited by square wave and sawtooth stimulation were 25 % smaller than JARs elicited by sine waves (mean 1·75 ± 0·08 Hz; ± S.E.). This might be explained by different relative intensities of the f_1 harmonics of the stimulus signals which are clearly the most effective components (cf. Fig. 4: Δ1F curve).

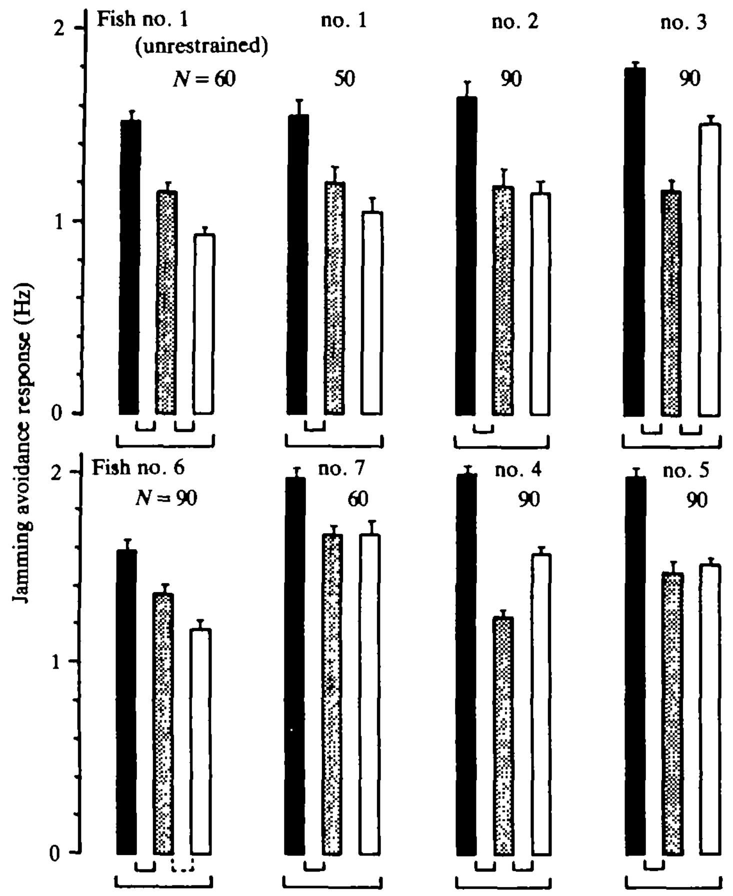

Fig. 6. Jamming avoidance responses to sine (black), distorted square (stippled) and distorted sawtooth waves (white) of equal amplitudes (p–p), shown as means and standard errors, in *Eigenmannia sp. III*. Significant differences as revealed by paired statistical tests indicated by horizontal square brackets ($P < 0{\cdot}001$; broken line bracket: $P < 0{\cdot}01$). Stimulus intensity: −60 dB. The stimulus frequency was 2 Hz below the EOD baseline frequency. *N* is the number of experiments per waveform. The sine wave elicited the strongest responses in each fish.

Relative f_1 intensities were measured by low-pass filtering of an amplified 400-Hz signal as recorded from the water; cut-off frequency of the 48 dB/octave electronic filter set at 350 Hz ($V_{\mathrm{r.m.s.}}$-measurements with Bruel & Kjaer model 2610 precision voltmeter; r.m.s., root mean square). The f_1 intensities were 0·60 and 0·50 for square wave and the sawtooth compared with 1 for sine waves. The JARs obtained on square wave stimulation of unity intensity were not statistically different from expected JARs as calculated for Δ 1F sine wave stimulation of 0·60 intensity ($P >> 0{\cdot}05$). Apparently, the effect of the square wave can be fully ascribed to its fundamental frequency component f_1 alone.

JARs on sawtooth waves of unity intensity were slightly stronger than expected JARs in five animals (by a mean 0.29 Hz; $P < 0{\cdot}01$ in each fish). This could be evidence for a higher harmonic of the sawtooth wave having an additional effect on the JAR. The strong f_2 component had a relative intensity of 0·27 compared to the sine wave of unity intensity and fundamental frequency.

Table 1. *JARs to undistorted waveforms of equal amplitudes (p-p) (shown in Fig. 8) in* Eigenmannia lineata

	Stimulus signal (Δ1F)		
	Sine	Square	Sawtooth
Female no. 1 ($N = 38$)	−3·01 ± 0·1	−3·24 ± 0·1 −3·19	−2·52 ± 0·09 −2·64
Male no. 5 ($N = 32$)	−5·19 ± 0·14	−5·73 ± 0·15 −5·49	−4·36 ± 0·1 −4·54
Female no. 5 ($N = 39$)	−3·83 ± 0·06	−4·06 ± 0·06 −4·05	−3·42 ± 0·06 −3·35
Male no. 9 ($N = 37$)	−3·06 ± 0·06	−3·23 ± 0·05 −3·23	−2·82 ± 0·06• −2·68
Male no. 10 ($N = 48$)	3·36 ± 0·08	3·58 ± 0·08† 3·56	2·94 ± 0·06 2·94

$\Delta F = -2$ Hz ($+2$ Hz for male 10); stimulus intensity; −58·1 dB which is approximately 30 dB above threshold.

Upper figures: observed JARs with standard error (Hz); lower figures: expected JARs, as calculated for a pure sine wave of the intensity of the f_1 component of each waveform, based on the JAR observed to a pure sine wave.

N is the number of experiments per waveform.

Note highly significant differences among observed JARs between waveforms ($P < 0{\cdot}001$, except † where $P < 0{\cdot}05$ compared to the sine wave), but insignificant differences between observed/expected JARs $P > 0{\cdot}05$; •: $P > 0{\cdot}01$).

The intensities of the f_1 harmonics relative to the sine wave (0 dB) were as follows: f_1 (square) = + 1·73 dB; f_1 (sawtooth) = − 3·74 dB.

Five *E. lineata* were also tested with nearly undistorted square and sawtooth waves of equal amplitudes (p–p) applied through the D/A converter for the flat phase response of its output circuit (Fig. 8). Here, the square wave elicited the strongest responses, followed by those to sine and by still weaker ones to sawtooth waves (all differences significant at $P < 0{\cdot}001$ except one where $P < 0{\cdot}05$, Table 1). Stimulus/response curves for the first two harmonics are shown in Fig. 4B.

With relative amplitudes of the f_1 harmonics of the sine, the square, and the sawtooth waves of Fig. 8 at 1·00, 1·22 and 0·65, the response differences could be fully ascribed to these f_1 intensity variations (differences observed−expected JARs insignificant with $P > 0{\cdot}05$ except one comparison where $P > 0{\cdot}01$; Table 1). The response differences could not be related, however, to peak-to-peak amplitudes (which were equal), nor to power (as determined by r.m.s.-values: 1·00 for the sine, 1·36 for the square, and 0·83 for the sawtooth waveforms as measured from the water).

Effect of subharmonic stimuli on the JAR

Watanabe & Takeda (1963) found 'the effect of half-frequency (sine wave) stimulation ... very weak, if present'. The present results show that sine waves and also square waves near one-half fish frequency do not elicit a response at all, not even a very weak one (Fig. 7; Tables 2–4). This also holds true for one-third frequency stimulation with sine waves (Fig. 7B).

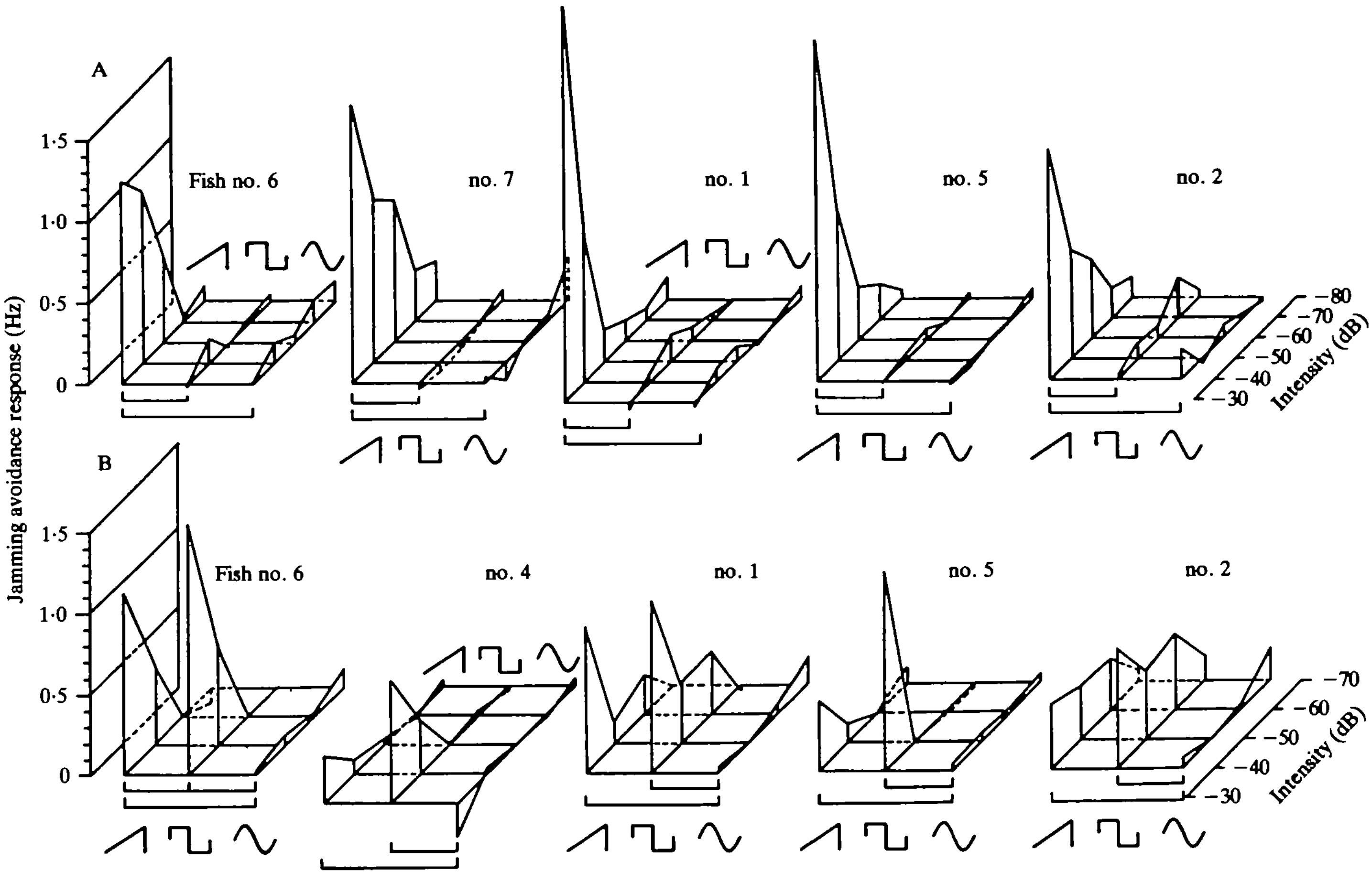

Fig. 7. Jamming avoidance responses to subharmonic stimuli of three waveforms of equal amplitudes (p–p), the sine, the distorted square and the distorted sawtooth waves as shown in Fig. 5, in *Eigenmannia sp. III*. Each point is the mean of 10 experiments. The z-axis is the stimulus intensity. (A) The stimulus frequency was 2 Hz below one-half EOD frequency ($\Delta\frac{1}{2}F$). Square brackets indicate significant response differences, as shown by paired statistical tests for the highest stimulus intensities ($P < 0{\cdot}001$). Note that JARs were elicited only by the sawtooth wave with its strong second harmonic. (B) The stimulus frequency was 2 Hz below one-third EOD frequency ($\Delta\frac{1}{3}F$). Square brackets indicate significant response differences as shown by paired statistical tests for the highest stimulus intensities ($P < 0{\cdot}05$). JARs were evoked by the square and the sawtooth waveforms, as both contained strong third harmonics.

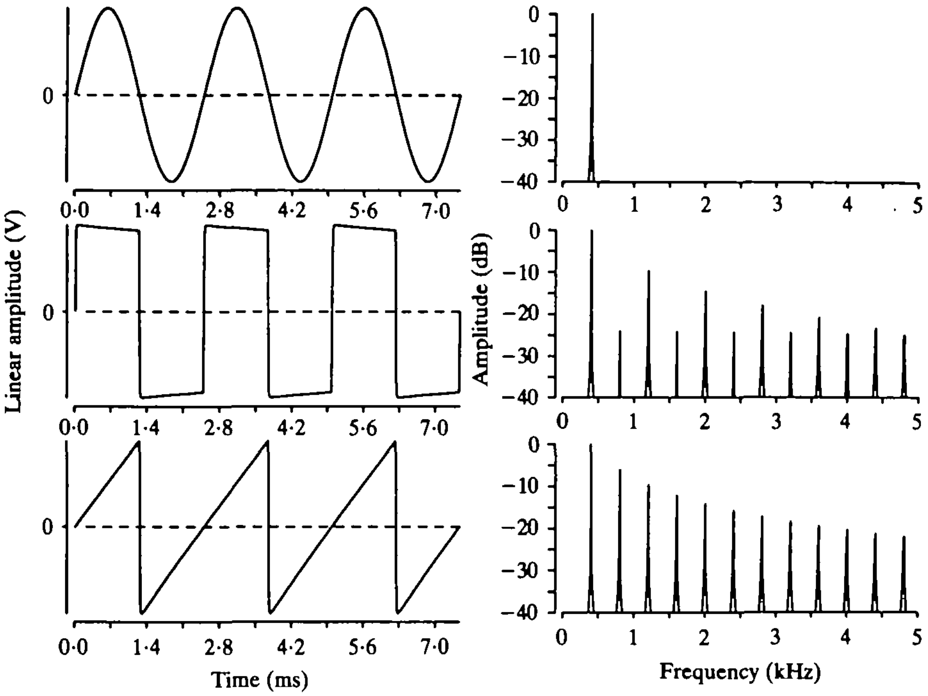

Fig. 8. The sine, the square and the sawtooth waveforms used as stimuli in JAR experiments with *Eigenmannia lineata* as recorded from the water, left, with Fourier amplitude spectra, right. Axes as in Fig. 2. Waveforms were synthesized by a microprocessor-controlled D/A-converter.

The idea originally expressed by Bullock *et al.* (1972) that the effectiveness of a $\Delta\frac{1}{2}F$ sawtooth stimulus is due to its own second harmonic will be further tested here using various waveforms, and expanded by experiments with stimulus frequencies close to one-third of the fish's frequency (Heiligenberg, Baker & Matsubara, 1978, also described several effective subharmonic stimuli but did not give results). Only those waveforms should be effective which contain a strong second harmonic (for a $\Delta\frac{1}{2}F$ stimulus), or a strong third harmonic (for a $\Delta\frac{1}{3}F$ stimulus), close in frequency to the EOD fundamental. The frequency difference would be 4 Hz for a $\Delta\frac{1}{2}F$ stimulus 2 Hz below one-half EOD frequency, and 6 Hz for a $\Delta\frac{1}{3}F$ stimulus with the same ΔF of 2 Hz.

In agreement with Bullock *et al.* (1972), and in spite of numerous differences in methods, $\Delta\frac{1}{2}F$ sawtooth stimuli elicited rather strong JARs ($P < 0{\cdot}001$) in each of five *E. sp. III* (Fig. 7A; distorted sawtooth) and five *E. lineata* (Table 2; undistorted sawtooth). This response was graded with stimulus intensity (Fig. 7A).

When presented at $\Delta\frac{1}{3}F$ frequencies, both the distorted square wave (with P/N = 1) and the distorted sawtooth wave were effective; the sine wave again was not (Fig. 7B). Both effective signals had a strong third harmonic, f_3. Although the responses to square waves were stronger than those to sawtooth waves, these differences were not significant at N = 10 (except fish 6: $P < 0{\cdot}02$), reflecting the small intensity difference of less than 2 dB between the f_3 components (0·18 in the sawtooth and 0·22 in the square wave, compared to 1 for the f_1 of the sine wave, all of equal peak-to-peak amplitudes).

Responses to sawtooth waves were stronger when they were presented at $\Delta\frac{1}{2}F$ compared to $\Delta\frac{1}{3}F$ frequencies (except fish 1 where there was no difference). There may be two reasons: (1) there is an intensity difference of about 4 dB between the f_2 component of the $\Delta\frac{1}{2}F$ stimulus and the f_3 component of the $\Delta\frac{1}{3}F$ stimulus; (2) the effective ΔF relative to the EOD fundamental was 4 Hz for the f_2 component of the $\Delta\frac{1}{2}F$ stimulus and 6 Hz for the f_3 component of the $\Delta\frac{1}{3}F$ stimulus. Responses decline with an increasing value of an unclamped ΔF (Watanabe & Takeda, 1963), although at a slow rate above 4 Hz (B. Kramer, in preparation).

Table 2. *JARs with standard error (Hz) to undistorted, sub-harmonic waveforms of equal amplitudes (p-p) as shown in Fig. 8, in* Eigenmannia lineata

	Stimulus signal ($\Delta\frac{1}{2}F$)		
	Sawtooth	Square	Sine
Male no. 7 ($N = 10$)	− 2·11 ± 0·09	0·09 ± 0·08	− 0·02 ± 0·05
Female no. 3 ($N = 8$)	2·92 ± 0·21	− 0·06 ± 0·09	− 0·11 ± 0·05
Female no. 5 ($N = 10$)	− 2·10 ± 0·05	− 0·03 ± 0·02	0·05 ± 0·03
Male no. 9 ($N = 10$)	− 1·33 ± 0·06	0·07 ± 0·05	0·01 ± 0·04
Male no. 10 ($N = 10$)	1·67 ± 0·1	0·04 ± 0·06	0·00 ± 0·06

$\Delta F = -2$ Hz (+ 2 Hz for female 3 and male 10) relative to one-half EOD baseline frequency.
Stimulus intensity: − 56·6 dB.
N is the number of experiments per waveform.
Only sawtooth waves evoked responses significantly different from zero ($P < 0·001$).

Table 3. *JARs with standard error (Hz) to subharmonic ($\Delta\frac{1}{2}F$) stimuli of equal fundamental frequency intensities in* Eigenmannia lineata

	Stimulus signal ($\Delta\frac{1}{2}F$)		
	f_2 phase 0°	f_2 phase 90°	Sine
Male no. 7 ($N = 10$)	− 1·40 ± 0·08	− 1·50 ± 0·06	0·17 ± 0·07
Female no. 3 ($N = 10$)	4·33 ± 0·15	4·39 ± 0·14	− 0·05 ± 0·03
Male no. 9 ($N = 10$)	− 1·49 ± 0·06	− 1·58 ± 0·06	− 0·04 ± 0·04
Female no. 5 ($N = 10$)	− 2·36 ± 0·03	− 2·42 ± 0·05	− 0·02 ± 0·04
Male no. 10 ($N=10$)	2·13 ± 0·12	2·25 ± 0·11	− 0·01 ± 0·09

The stimulus signals were a pure sine wave and two computer-synthesized waveforms each composed of two sine waves, of fundamental frequency, f_1, and its second harmonic, f_2 (Fig. 9). These latter two signals had identical Fourier amplitude spectra and power but different waveforms because of different phase relations.
$\Delta F = -2$ Hz (+ 2 Hz for female 3 and male 10) relative to one-half EOD baseline frequency.
Stimulus intensity: − 58·1 dB.
N is the number of experiments per waveform.
The two signals containing an f_2 harmonic elicited similar responses (differences insignificant, $P > 0·05$), while the sine wave was ineffective. This shows that in an effective $\Delta\frac{1}{2}F$ stimulus a second harmonic is required, but that its phase, hence form of the complex wave, is irrelevant.

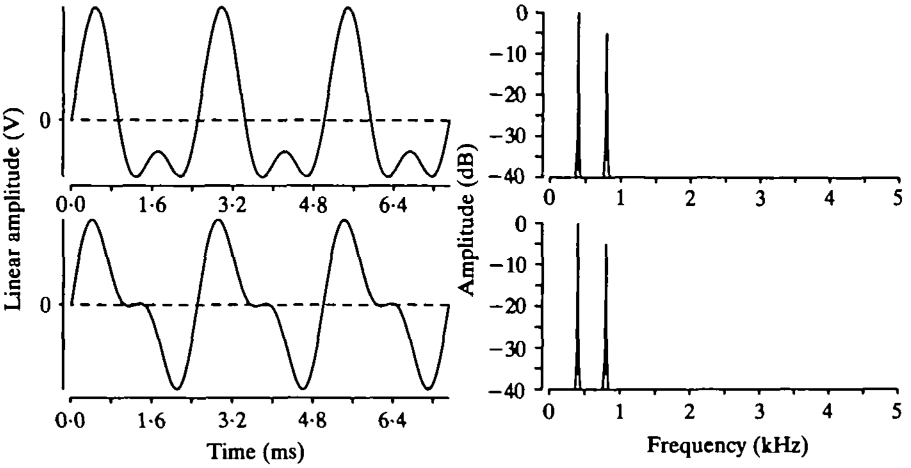

Fig. 9. Computer-synthesized stimulus waveforms as recorded from the water, left, composed of two superimposed sine waves of fundamental frequency, f_1, and its second harmonic, f_2, of weaker amplitude (−5 dB). Right: Fourier amplitude spectra. Axes as in Fig. 2. Top: the phase difference of the peak amplitude of the f_2 harmonic relative to that of the f_1 harmonic is 0°. Bottom: the phase difference is 90°. Note that the spectral amplitudes of both waveforms are identical.

As the distorted sawtooth waves (Fig. 5) had a P/N ratio of 0·5, the effectiveness of this stimulus (although not that of the $\Delta\frac{1}{3}F$ square wave) might be explained by Gottschalk's (1981) 'temporal feature' hypothesis. Therefore, the experiment was repeated in *E. lineata* using true (nearly undistorted) sawtooth and square waves, both with $P/N = 1$ (Fig. 8), and the sine wave. As in the previous experiment, only sawtooth waves elicited JARs ($P < 0{\cdot}001$; Table 2). No responses were obtained to undistorted square and sine waves (differences from zero were insignificant, $P > 0{\cdot}05$). These results show that Gottschalk's 'temporal feature' is not required in an effective subharmonic stimulus.

Irrespective of stimulus waveform and subharmonic frequency, for a given initial ΔF the JAR was apparently determined by the intensity of that stimulus harmonic which was close to the EOD fundamental frequency.

This was further tested in *E. lineata* using two signals with identical spectral amplitudes and power but different waveforms, containing strong second harmonics of equal intensities (phase differences of the f_2 harmonics of 0° and 90°, Fig. 9; explained in the next section). For comparison the sine wave was also used with equal intensities of f_1 harmonics among the three signals which were presented at $\Delta\frac{1}{2}F$ stimulus frequencies. As expected, JARs were only obtained to the two signals containing their own second harmonics (differences from zero significant at $P < 0{\cdot}001$); these JARs were of nearly equal strengths (difference insignificant, $P >> 0{\cdot}05$; Table 3).

Independence of the JAR to changes in phase differences of harmonic signal components

To distinguish whether it is the intensities of harmonic signal components or waveform characteristics, such as the time between zero-crossings, which determine the JAR at $\Delta 1F$ stimulus frequencies, experiments were performed using stimuli of identical spectral amplitudes but different phase relationships of the constituent harmonics, and hence different waveforms.

In the simplest case, only two harmonically related sine waves, the fundamental frequency, f_1, and its second harmonic, f_2, are superimposed, according to

$$y = \sin \omega t + a \sin (2\omega t + \phi),$$

where $\omega = 2\pi f$, f = frequency, t = time, a = amplitude, ϕ = phase difference relative to peak amplitudes. Phase differences of 0° and of 90° result in the two waveforms shown in Fig. 9, calculated by computer.

The f_2 components of both signals had relative intensities of 0·56 (or −5 dB) compared with the fundamental of relative intensity 1 (or 0 dB). Unlike the waveform with a 90° phase difference where P/N = 1, a phase difference of 0° leads to an asymmetrical waveform with respect to intervals between zero-crossings (P/N = 0·60). The third waveform used was the sine wave; the three signals had identical f_1 intensities (−58·1 dB), hence differed in peak-to-peak amplitudes. These were 1·00, 1·18 and 1·37 for the sine wave, and the signals with 0° and 90° phase difference values, respectively. The relative energy contents, as determined by $V_{r.m.s.}$-measurements, were 1·00 for the sine wave and 1·15 for the two other waves.

Six *E. lineata* (three of each sex) were insensitive to these differences in phase relationships and waveform, and peak-to-peak amplitudes and power, as measured by the JAR ($P > 0{\cdot}05$; Fig. 10). The response strength appeared to be exclusively

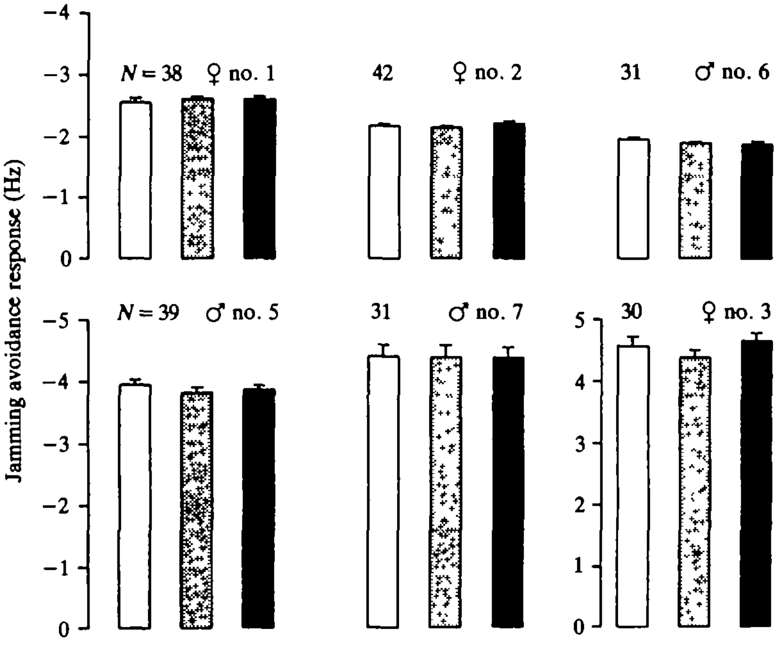

Fig. 10. Jamming avoidance responses to computer-synthesized stimuli of three waveforms of equal intensity of their f_1 harmonics, shown as means and standard errors. The stimulus waveforms are the sine wave (black), and the two waveforms with their f_2 components differing in phase, as shown in Fig. 9. Stippled: phase difference = 90°. White: phase difference = 0°. *N* is the number of experiments per waveform and fish. Response differences are insignificant, showing that the intensity of the f_1 harmonic determines the response strength.

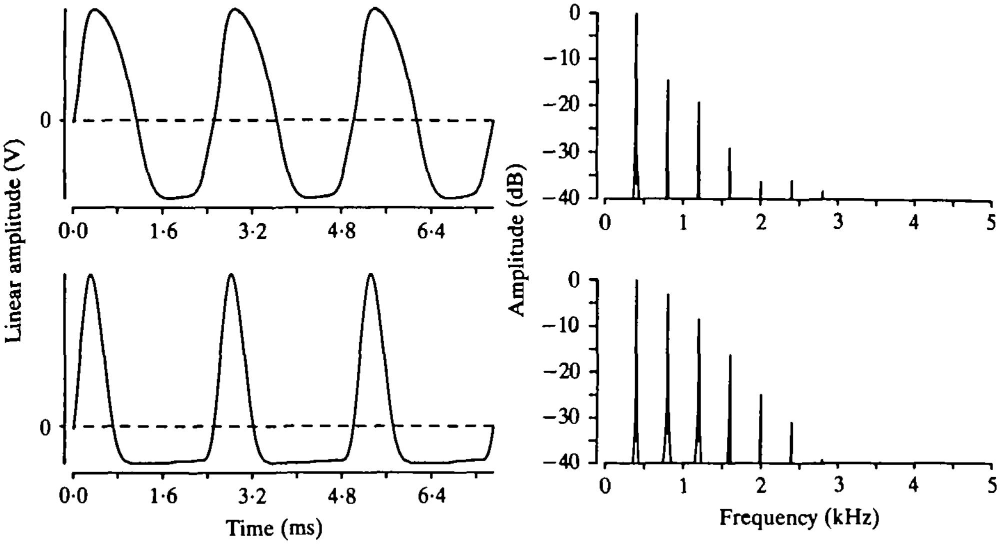

Fig. 11. Computer-synthesized female (above) and male (below) EODs of *E. lineata* used as stimuli in JAR experiments, as recorded from the water, left, with Fourier amplitude spectra, right. Axes as in Fig. 2.

determined by the intensity of the f_1 harmonic which was the only parameter (besides ΔF) in common to all three signals.

The human ear can distinguish an audio signal of the sine wave immediately from those of the two other waves, but cannot discriminate between the latter two.

Effect of the sexually dimorphic EODs on the JAR

From the previous experiments weaker responses to male EODs compared with female EODs can be predicted, provided both EODs are presented as $\Delta 1F$ stimuli (or ΔnF stimuli, but not as subharmonic, or $\Delta \frac{1}{n}F$, stimuli; n being a low integer), and at equal peak-to-peak amplitudes. The reason for this is the stronger harmonic content of the male's EOD with its relatively weaker f_1 intensity compared with the female's EOD.

E. lineata's stimulus/response curves for $\Delta 1F$ and $\Delta 2F$ sinusoidal stimuli (Fig. 4B) are similar to those of *E. sp. III* with the difference that the horizontal shift of the $\Delta 2F$ curve with respect to the $\Delta 1F$ curve was more than 25 dB in *E. lineata* and less than 20 dB in *E. sp. III*. After accounting for the difference in ΔF (2 Hz in Fig. 4A, 4 Hz in Fig. 4B) this would still mean a higher relative sensitivity to $\Delta 2F$ frequencies in *E. sp. III* compared with *E. lineata*. The JAR obtained on a stimulus with an initial $\Delta F = 4$ Hz is weaker by 1–3 dB compared with $\Delta F = 2$ Hz (B. Kramer, in preparation). .

The above prediction of stronger responses to female compared with male EODs was tested in nine *E. lineata*. A/D-converted EODs of a large male (33·5 cm) and of a female *E. lineata* (16·5 cm) gravid with eggs were used for computer-generated playback (Fig. 11). For comparison, the sine wave was also used with peak-to-peak stimulus intensities equal among the three signals (− 56·6 dB). In these synthesized male and female EODs, relative f_1 intensities were 0·71 and 1, respectively; P/N ratios were 0·40 for the male and 0·82 for the female EOD. As stated earlier, the f_2 harmonic of the male EOD was relatively stronger than the female's by a factor of almost 4 in terms of the f_2/f_1 intensity ratio.

Two large males included in the test group (males 2 and 4; 33·5 and 35 cm in length) were different from smaller fish in consistently displaying very weak JARs (Fig. 12), but they often gave 'short rises' of less than 2 s. A 'short rise' is a discharge frequency increase followed by a decrease to the resting frequency and has been observed in dominant fish during agonistic behaviour (Hopkins, 1974*a*). Very weak JARs and many 'short rises' were also found in two other large males (not shown in Fig. 12; B. Kramer, in preparation). For these large males, as well as for the two adult females (nos 1 and 2), ΔF had to be negative in order to elicit responses at all. Also in the other fish, a negative ΔF evoked stronger responses than a positive ΔF, except in female

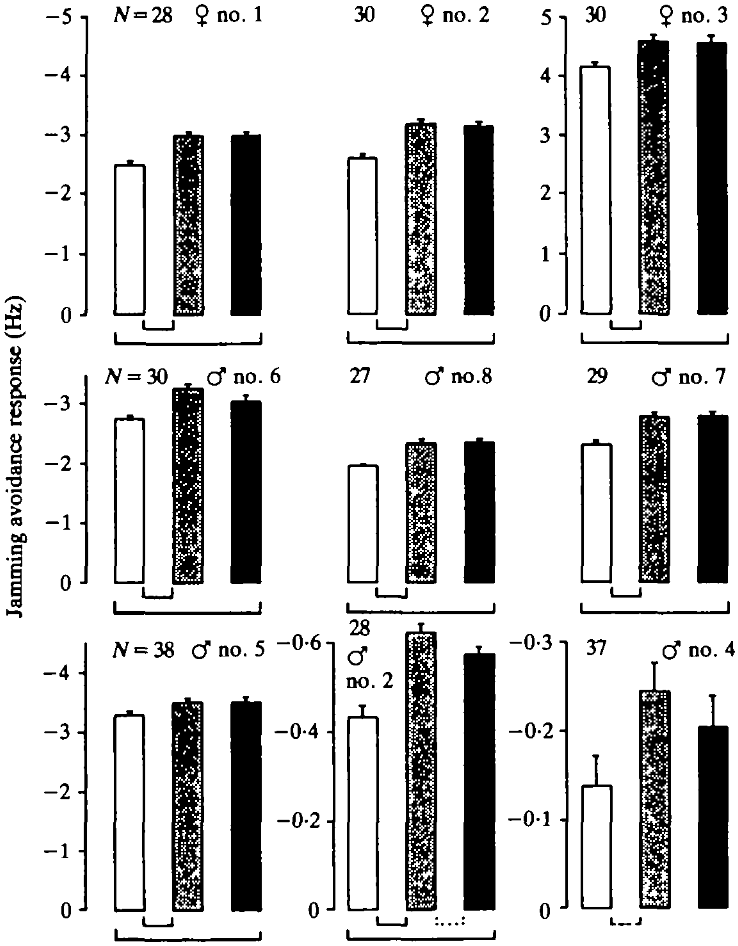

Fig. 12. Jamming avoidance responses, shown as means and standard errors, to computer-synthesized stimuli of three waveforms of equal amplitudes (p–p). The stimulus waveforms were the sine wave (black), male EODs (white) and female EODs (stippled). Significant differences of responses, as revealed by paired statistical tests, indicated by square brackets ($P < 0·001$; broken line bracket: $P < 0·01$; dotted bracket: $P < 0·02$). *N* is the number of experiments per waveform. Note that the male EOD evoked weaker JARs than both the sine wave and the female EOD which had stronger f_1 harmonics.

3 (the only immature female, 8·7 cm in length). Only weak differences in response strength dependent on the sign of ΔF have been reported previously for *Eigenmannia* (Watanabe & Takeda, 1963; Larimer & MacDonald, 1968).

In each fish, male EODs elicited the weakest responses compared with female EODs (a mean difference of 19 %; $P < 0{\cdot}001$, except large male 4 where $P < 0{\cdot}01$) and sine waves (a mean difference of 16%; $P < 0{\cdot}001$ except again male 4 where the difference was not significant; Fig. 12). The responses to female EODs and sine waves were similar. Only in large male 2 was a significant difference observed: his responses to female EODs were even slightly stronger than those to sine waves ($P < 0{\cdot}02$).

The mean difference between responses to male EODs and sine waves was 0·39 ± 0·04 Hz (± S.E., $N = 7$; the two large males nos 2 and 4 not considered because of their extremely weak responses). This agrees with the expected difference (on average 0·31 Hz) calculated on the assumption that the intensity of the f_1 component determines the response alone. (The difference was insignificant with $P > 0{\cdot}05$ in each fish; an insignificant difference was also found for the two large males.)

Opposite results were obtained with the stimulus frequency close to one-half of the EOD frequency. Here, male EODs elicited the strongest responses, female EODs significantly weaker ones ($P < 0{\cdot}01$) and sine waves no responses at all (Table 4). This response pattern reflects well the intensity differences of the second harmonic (which is absent in a sine wave).

In nature it is probably common for a female discharging at the high-frequency tail of the species' distribution (500–650 Hz at 27 °C; see above) to meet an adult male with a frequency close to one-half (250–325 Hz) that female's frequency, while the reverse – a female discharging near one-half the male's frequency – should be rare. In the first case (considered common) the female would give a good response to the male's EOD (Table 4) because the male's strong f_2 harmonic would be close to the

Table 4. *JARs with standard error (Hz) to computer-synthesized, subharmonic male and female EODs (Fig. 11), and sine waves of equal amplitudes (p-p), in* Eigenmannia lineata

	Stimulus signal (Δ½F)		
	Male EOD	Female EOD	Sine
Female no. 3 ($N = 10$)	1·11 ± 0·19	0·38 ± 0·05	0·04 ± 0·04
Female no. 4 ($N = 10$)	− 1·33 ± 0·06	− 0·64 ± 0·06	0·004 ± 0·04
Male no. 5 ($N = 10$)	− 3·57 ± 0·14	− 2·02 ± 0·15	0·25 ± 0·19
Male no. 9 ($N = 10$)	− 1·44 ± 0·06	− 0·95 ± 0·04	0·04 ± 0·05
Female no. 5 ($N = 10$)	− 2·39 ± 0·05	− 1·62 ± 0·06	− 0·02 ± 0·02

ΔF = − 2 Hz (female 3: + 2 Hz) relative to one-half EOD baseline frequency.
Stimulus intensity = − 56·6 dB.
N is the number of experiments per waveform.
Paired statistical tests show that responses to male EODs were significantly ($P < 0{\cdot}01$) stronger than to female EODs.

female's fundamental frequency, and hence most effective. In the second case (considered rare), the male's EOD fundamental would be close to the female's second harmonic, and hence of little effect on the female's JAR (see Fig. 4, Δ2F curves).

Two (out of two) human subjects discriminated acoustic play-backs of the EODs of Fig. 11 in 30 choice tests without error ($P < 0{\cdot}001$, binomial test) after about 5 min training (tested by sequentially paired audio playbacks of male and female EODs at 400 Hz for 3 s each, with envelope rise time = 400 ms; each paired playback sequence was determined randomly). There was also clear discrimination of synthesized female and male EODs from sine waves.

DISCUSSION

Signal parameters influencing the JAR

The finding that Δ1F stimuli of various waveforms of equal amplitudes (p–p), differ in their effectiveness of evoking the JAR contrasts with earlier observations (Bullock *et al.* 1972, p. 29) where no such dependence was found for sinusoidal, square, triangular and sawtooth waves.

One reason for this disagreement is the use by Bullock *et al.* (1972) of a stimulus regime which must have caused strong habituation: + and $-\Delta$F stimuli were switched back and forth every 30 s with no rest intervals. The stimulus intensity was very high in the JAR recordings shown, for example 1 $\mathrm{mV_{p\text{-}p}\,cm^{-1}}$ (about $-$ 30 dB in Fig. 4). A second reason was the use of a stimulus period of only 30 s, which in most animals is too short for the JAR to be shown fully. A third reason might be the use of the frequency difference clamp which frustrates the fish's attempt to escape from the jamming frequency, eliciting stronger JARs compared to an unclamped stimulus frequency (Watanabe & Takeda, 1963, their Fig. 5). Thus the response strength was probably determined by the balancing effect of a 'restoring force tending to shift back the fish to its resting frequency' (Bullock *et al.* 1972), and habituation, rather than by differences in stimulus waveforms.

Analysis of the present results showed that it was not the shape of the waveforms which determined the JAR. Signals presented at Δ1F stimulus frequencies were effective according to the intensities of their f_1 components, not peak-to-peak amplitudes, power nor waveform characteristics (such as the P/N ratio; see above). Therefore, the undistorted square wave was more effective (Table 1), and the distorted one less effective (Fig. 6) than the sine wave at constant amplitudes (p–p).

The crucial importance of the f_1 component intensity of a Δ1F stimulus was also seen in the results obtained with synthesized male and female EODs (Fig. 12) and with two waves of different forms but identical Fourier amplitude spectra when compared with the effectiveness of the sine wave (Fig. 10). Among the latter three signals, the only parameter in common was the intensity of the f_1 component; accordingly, the response strengths were not significantly different from each other. Response strength was determined by the intensity of that stimulus harmonic which was enclosed within a narrow frequency band centred on the fish's EOD frequency.

A qualification of this statement is necessary here. Five out of eight experiments with *E. sp. III* (Fig. 6), and one out of five *E. lineata* (Table 1) gave slightly stronger responses to distorted and undistorted sawtooth waves, respectively, than had been expected from the f_1 intensities of these stimuli. It was speculated that in these cases a higher harmonic, especially the strong f_2 component, had an additional effect on the JAR (the f_2/f_1 intensity ratio of the sawtooth is one-half, or -6 dB). However, a small additional effect due to a higher harmonic could be masked by 'noise' (random variations in response strength to identical stimuli) superimposed on the fish's response. Therefore, to explore this question a stimulus wave with a much higher f_2/f_1 intensity ratio than one-half should be used. In a pilot experiment using a stimulus wave with an f_2/f_1 ratio of 3·2, or $+10$ dB, calculated as explained above, a clear additional effect on the JAR due to the f_2 component of the stimulus was obtained in one *E. lineata* (B. Kramer, unpublished). There seems to be a threshold value for the f_2/f_1 intensity ratio of a stimulus wave: with this ratio greater than about one-half (apparently somewhat higher in *E. lineata* which was found to be less sensitive than *E. sp. III* for frequencies twice its EOD frequency; Fig. 4) the f_1 intensity of a stimulus wave, although still predominant, no longer alone determines the JAR, and an additional effect due to its f_2 component is observed. (The threshold ratio of the f_2 component, as suggested here, should not be confounded with the threshold intensity of a stimulus about twice the EOD frequency which can be read from the $\Delta 2F$ stimulus/response curves in Fig. 4.) Male EODs with their high harmonic content come close to these suggested threshold ratios; therefore, the effect should be of little importance in intraspecific jamming avoidance behaviour with $\Delta 1F$ stimuli (Fig. 12). This does not imply, however, that assessment of harmonic content (or of the f_2/f_1 ratio) was impossible, nor that it was irrelevant in the context of another behaviour (see below).

Experiments with subharmonic stimulus frequencies showed that the effective harmonic of the stimulus wave need not be its fundamental frequency, as suggested earlier by Bullock *et al.* (1972) for a $\Delta\frac{1}{2}F$ sawtooth wave. Responses to $\Delta\frac{1}{2}F$ and $\Delta\frac{1}{3}F$ stimuli of nine waveforms, including synthesized EODs, were obtained only when the signal contained a harmonic close to the EOD frequency which was sufficiently strong. That harmonic was the f_2 component in $\Delta\frac{1}{2}F$ stimuli, and the f_3 component in $\Delta\frac{1}{3}F$ stimuli. Response strength was correlated with the intensity of that harmonic. Further support was the observation of identical responses to two waves differing in form (or phase relationships of the constituent harmonics) and P/N ratios, but not in terms of the Fourier amplitude spectrum, when presented as $\Delta\frac{1}{2}F$ stimuli.

An especially illuminating result was obtained with the natural, sexually dimorphic EOD waveforms. Their effectiveness reversed with stimulus frequency. Female EODs were more effective than male EODs when presented as $\Delta 1F$ stimuli, but much less effective than male EODs when presented as $\Delta\frac{1}{2}F$ stimuli, according to their intensity differences in f_1 and f_2 components (Fig. 11).

Gottschalk (1981) concluded that a specific temporal feature of the EOD, $P/N < 1$, is necessary in an effective subharmonic ($\Delta\frac{1}{2}F$) stimulus. He further concluded that the JAR to a $\Delta\frac{1}{2}F$ stimulus is a maximum function of what he called 'phase quotient', defined as $P_{Stim}/(T_{EOD} - P_{Stim})$, that is the duration ratio of the positive half-wave of the stimulus P_{Stim} and of the EOD period T_{EOD} reduced by P_{Stim}. According to Gottschalk, maximal responses are obtained with a phase quotient of 1, while no responses are obtained with a phase quotient of greater than about 5.

These conclusions are incompatible with the present results, for two waveforms were effective $\Delta\frac{1}{2}F$ stimuli, and a third an effective $\Delta\frac{1}{3}F$ stimulus, although their P/N ratios were 1, and hence their phase quotients infinity. These waveforms were the undistorted sawtooth (Table 2), the waveform with an f_2 phase difference of 90° (Table 3) and the distorted square wave at $\Delta\frac{1}{3}F$ stimulus frequency (Fig. 7B). Unfortunately, Gottschalk did not give waveforms nor amplitude spectra of his stimuli in which one cycle was composed of two monopolar square pulses of opposite polarity 'wave-shaped' by filtering, and of equal or different durations. Even so it is clear that in his $\Delta\frac{1}{2}F$ stimuli, a reduction of the phase quotient from infinity to 1 (or, still in Gottschalk's terminology, lowering of P/N from 1 to 0·33, corresponding to $P_{\mathrm{Stim}} = \frac{1}{2}T_{\mathrm{EOD}}$) caused the f_2 component to rise to maximum intensity. (The f_2 component is the effective harmonic in a $\Delta\frac{1}{2}F$ stimulus.) An inverse relationship between P/N ratio and intensity of the f_2 harmonic was seen in the natural EOD (Fig. 3), Gottschalk's model. The presumed dependence of the JAR on the phase quotient in Gottschalk's stimuli is probably explained by intensity variation of the f_2 component.

Sensitivity to different spectral phase functions of stimulus pulses with identical spectral amplitudes, and discrimination, has been reported in *Hypopomus artedi*, a gymnotid with a pulse discharge (Heiligenberg & Altes, 1978). Unlike wave-discharging fish such as *Eigenmannia*, pulse-discharging fish receive EODs from conspecifics unaltered by superposition with their own EODs, except very few coinciding EODs. With the stimulus-field gradient in the fish's long axis (that is, parallel to the fish's own field), a weaker EOD rate increase was obtained on stimulation with polarity-reversed EOD-like stimulus pulses than with pulses of normal polarity. (In nature a polarity reversal occurs when the discharging fish reverses its head-to-tail orientation with respect to the receiving fish.) Polarity reversal is equivalent to a shift of all spectral phase values of 180°. Responses to EOD-like stimuli with intermediate phase values fell in between the extremes (only the latter were significantly different from each other).

Sensitivity differences instead of true discrimination of waveform patterns may explain the data: a slightly more intense stimulus (p–p) with a less effective phase value would obviously give the same response strength compared to a weaker stimulus (p–p) with a more effective phase value.

This phase sensitivity, or sensitivity for the polarity of the main voltage transient of the stimulus pulse, may be expected from the known sensitivity difference of tuberous electroreceptors to cathodal and anodal voltage steps (Bennett, 1967). The behavioural effect would probably disappear with transversal stimulation with left and right side electroreceptors facing opposite polarities of the stimulating field.

Hopkins & Bass (1981) report phase-sensitivity and waveform recognition in an African pulse-discharging mormyrid, '*Brienomyrus brachyistius triphasic*'. These authors used similar techniques of modifying natural EOD waveforms by shifting all spectral phase values. Play-back experiments were made in the field at night during the natural time of activity of the free-living fish. I think the conclusions of these authors would be better supported by demonstrating male recognition of female EOD waveforms in the laboratory under more stringent control or definition of, for example, stimulus field amplitudes and geometry with respect to the receiving fish, mechanical disturbances, interference from other electric fish, specificity of response criterion, and experimental design (such as the randomized blocks design). If confirmed, response differences to EOD-like stimuli of different phase shift values could still be due to similar reasons as discussed above (regarding the conclusions of Heiligenberg & Altes, 1978).

Phase sensitivity in the sense of true pattern discrimination or recognition of stimulus pulses, varying in waveform but not Fourier amplitude components, is unfortunately not established beyond doubt in electric fish, in spite of the affirmative views held in several recent review or textbook articles (for example, Heiligenberg & Bastian, 1984, pp. 564–565; Hopkins, 1983, pp. 137, 142). These are all based on the above-mentioned two short reports (Heiligenberg & Altes, 1978; Hopkins & Bass, 1981) which are unfortunately not fully documented because of limitation of space. As in the acoustic communication system of frogs we must carefully avoid assuming 'a property of a communication signal ... functionally significant merely because it is species-specific and stereotyped ...' (Doherty & Gerhardt, 1984). However, I do not rule out the possibility of waveform recognition of pulse-like EODs, nor the possibility of EOD discrimination or recognition based on, for example, sex-specific differences in spectral amplitudes, as present in the *Brienomyrus* species investigated by Hopkins & Bass (1981), and in the wave-discharging fishes *Sternopygus* (Hopkins, 1974*b*) and *Eigenmannia* (Figs 2, 11). The sex differences in these three examples are due to different EOD pulse durations, different fundamental frequencies of tone-signals, and different harmonic content of tone-signals, respectively. (However, in full-grown *E. lineata*, but not in juvenile or subadult *E. virescens*, there seems to be a sex difference also in fundamental frequency; see above.)

In mormyrids there is ample evidence for encoding of species-specific information by inter-discharge time interval patterns. For example, in *Gnathonemus petersii* playback experiments using two intraspecific discharge patterns accompanying attack and rest, evoked a host of significantly different electrical and motor behaviour patterns in the stimulated animals (Kramer, 1979). Lücker (1982, 1983) showed that *Petrocephalus bovei* preferred its species' EOD interval patterns over those of other species when one of these was played back simultaneously with its own species' pattern in a randomized blocks experimental design. The natural EOD waveforms had been eliminated in both cases by the use of square pulses or single sine wave cycles. In *G. petersii*, there is no sex difference in EOD waveform (B. Kramer & M. Westby, in press).

Sensory mechanisms of the JAR

The tone-discharging *Eigenmannia* cannot perceive the stimulus wave directly. The fish detects its presence as modulations of its own EOD 'carrier' frequency, even when the stimulus is one thousand times weaker (Scheich & Bullock, 1974). The interaction of two beating frequencies produces modulations in amplitude and time intervals between zero-crossings of the combined signal which depend on relative signal levels, ΔF and waveforms (Scheich, 1977). Electroreceptors of two types reflect these periodic variations within a beat cycle (Scheich, Bullock & Hamstra, 1973; Scheich, 1977; Bastian & Heiligenberg, 1980). *Eigenmannia's* exceedingly high frequency difference resolution, among other things, makes a true frequency analysis of the stimulus unlikely; instead, the principle of time domain analysis of afferent electrosensory input is supported by the evidence (Scheich, 1974).

What can be inferred about sensory processing, although not investigated at the electroreceptor level, from the present experiments? First, the stimulus wave clearly appears to be bandpass-filtered and analysed harmonically before mechanisms of time domain analysis can come into play. The fish were able to extract the intensity of any harmonic (at least up to the third) close to their EOD frequency from any waveform, whether the frequency was subharmonic or not. This is what should be expected from the known properties of electroreceptors (T- and especially P-receptors) which are approximately tuned to the EOD frequency, resembling broad bandpass filters (Scheich *et al.* 1973; Hopkins, 1976; Scheich, 1977; Viancour, 1979). These properties also explain the progressively reduced sensitivity of the JAR for frequencies that are two, three or more times higher than the EOD frequency.

Second, the present results show that the fish are insensitive to the waveform of a stimulus although waveform-dependent information is present in a beat (Scheich, 1977). This second conclusion, of course, follows from the first. Different waveforms of identical spectral amplitudes elicited similar responses (Fig. 10) although the resulting beat patterns must have been quite different (see also the beat pattern analyses presented by Gottschalk, 1981).

The fish apparently do not (or, more likely, cannot) use all of the information theoretically available. The waveform-dependent information would become accessible only after exceedingly complex computation, as the local waveform of the fish's own EOD varies considerably along the fish's body (wave-discharging apteronotids: Bennett, 1971*b*; Hoshimiya, Shogen, Matsuo & Chichibu, 1980; Bastian, 1981; pulse-discharging gymnotids: Bastian, 1977). The interaction of a male's and a female's own EOD with, for example, a sine wave of identical amplitude and frequency difference is also certain to produce quite different beats, reflecting differences in waveforms of the fishes' own EODs only.

The results above show that it is not possible, as has been tried by Gottschalk (1981), to predict the JAR from the beat waveform pattern produced by two superimposed electric fields containing higher harmonics. The filter properties of the electroreceptors (Scheich *et al.* 1973) render such an approach futile. This is most clearly seen in the case of subharmonic stimuli.

A long standing puzzle may be resolved when taking this into account. Heiligenberg *et al.* (1978) explained the ineffectiveness of a $\Delta\frac{1}{2}$F sine wave by the alternating 'motion' in a graph representing the joint amplitude and phase modulations of the beating combined signal, lacking the smooth rotation found in effective ΔnF signals (their Figs 7 and 8, reminiscent of the Lissajous figures in Watanabe & Takeda, 1963). This was later supported by an electroreceptor study. P-units, and still more so their more central representations, E- and I-units, were unable to follow the rapid amplitude modulations near the animal's own EOD frequency which characterize subharmonic beats (Heiligenberg & Partridge, 1981).

An ineffective, scrambled graph would, however, also result from the $\Delta\frac{1}{2}$F waveforms containing strong second harmonics which were all found to elicit JARs. A crucial test of the hypothesis would be to determine whether the required smooth rotation in the amplitude-phase state-plane was observed in P- and T-unit responses, reflecting beat amplitude and phase modulations *after* filtering, with one of the effective $\Delta\frac{1}{2}$F waveforms.

The EOD sex difference and the JAR

The prediction of weaker JARs to male EODs compared with female EODs of equal peak-to-peak amplitudes was confirmed (Fig. 12). This was even seen in two large males which would only show tiny JARs of a fraction of a Hz with the 'good' (negative) sign of ΔF. Sine waves and female EODs elicited similar responses, demonstrating that a sine wave is a good model of a female EOD at $\Delta 1F$ stimulus frequencies. The weaker JARs to male than to female EODs could be fully ascribed to the weaker f_1 intensity of the male EOD.

In an adult pair of *Eigenmannia*, the great sex difference in signal intensity (see above) should add to the male's very low, and the female's high tendency, to respond with a JAR (Fig. 12). At least at closer contact the male's EOD intensity should be sufficient for the female to detect the male's strong f_2 harmonic.

The behavioural threshold of *Eigenmannia* to a sine wave twice its EOD frequency is 10 times that to a sine wave near its fundamental frequency (Knudsen, 1974). The same result was obtained electrophysiologically for primary afferents (Hopkins, 1976), and approximately the same value is derived from the JAR stimulus/response curves (Fig. 4).

Eigenmannia's behavioural threshold-frequency curve does not possess a secondary dip at the second harmonic of the EOD frequency as found in *Apteronotus* (Knudsen, 1974). Knudsen stressed a correlation between the presence of this threshold dip and the strong second harmonic of the EOD of *Apteronotus*. The second harmonic of *Eigenmannia* male EODs (Figs 2, 11) was stronger than that of Knudsen's *Apteronotus* EODs. Therefore, such a correlation is unlikely, unless adult *Eigenmannia* males possess behavioural threshold-frequency curves quite different from those determined in two *Eigenmannia* of unspecified size or sex (Knudsen, 1974; his Fig. 5). These animals were probably females or immature males, as judged from their EOD waveforms (shown in Knudsen, 1974; his Fig. 6).

Eigenmannia's ability to detect the strong f_2 component of the male EOD was demonstrated in a subharmonic ($\Delta \frac{1}{2}F$) experiment: the male EOD elicited two to three times stronger JARs than the female EOD of equal amplitude (Table 4). In nature it is probably common for some females to meet full-grown males discharging close to one-half their own frequencies (see above).

Males and females might be able to recognize each other from their EODs by their differences in harmonic content even in the absence of a sexual frequency dimorphism (absence shown in a large group of *Eigenmannia* containing only subadult, but sexually mature, males; Westby & Kirschbaum, 1981), or sex-specific frequency modulations. Preliminary evidence for the latter is Hopkins' (1974*a*) observation of females giving long series of frequency modulations of unknown significance in the presence of males.

The 'long rise' is a discharge frequency modulation similar to the JAR with positive ΔF; it was seen in subordinate or retreating fish (Hopkins, 1974*a*). The lack of a JAR to a positive ΔF in adult fish (B. Kramer, in preparation) probably indicates conflicting requirements of electrolocation and electrocommunication in a sensori-motor system sharing both functions.

Species recognition by EODs has quite recently been discussed in terms of filtering out other species' EODs by electroreceptors tuned to the EOD frequency assumed to vary across individuals within largely unique, species-specific ranges of fundamental frequencies (Hopkins & Heiligenberg, 1978; Hopkins, 1983). Such a mechanism had been found insufficient in the face of extensive and multiple interspecific overlap of EOD frequency ranges in a sympatric group of gymnotoids (Kramer *et al.* 1981). In individual *Eigenmannia*, 'best frequencies' (BF) of tuberous electroreceptors, which were of a single type, ranged by about 125 Hz at 19–21°C (Viancour, 1979); this range of best frequencies might even be greater at a more natural temperature (29 ± 1°C for the Amazon above the confluence of the Rio Negro with its 30–31°C water; Sioli, 1983, p. 27).

The discovery of a sexual dimorphism in harmonic content of *Eigenmannia*'s EODs opens the possibility of mate recognition by EODs of constant and not sexually dimorphic frequencies, a mechanism different from that suggested in *Sternopygus* with its sex-specific difference in fundamental frequency by about one octave (Hopkins, 1974*b*). (A similar, although less pronounced, sex difference due to the low frequency of *full-grown* males is, however, suggested above. Reproduction was observed in a subadult group of fish not showing a frequency sex difference; Westby & Kirschbaum, 1981.) Mate recognition by EODs of constant frequencies, if it exists, cannot rely on fundamental frequency alone. As a true waveform recognition is unlikely, the f_2/f_1 intensity ratio (or a similar measure of harmonic content) becomes a prime candidate. Differences in harmonic content might be perceived as distinct electrical 'timbre' patterns.

One of the sensory requirements for timbre (or stimulus quality) perception, a set of differently tuned electroreceptors in the same fish, seems to be met (Viancour, 1979; see above). What we do not know is whether there is integration of input across electroreceptor fibres with different best frequencies, producing the sensation of timbre in a way analogous to the mechanisms underlying timbre sensation in the auditory system (for example, Roederer, 1975). For this proposal it is not necessary that receptors should be tuned to the first, second, and so on harmonics; a continuous distribution of receptor best frequencies over the range indicated by Viancour (1979) would also allow assessment of at least the first two harmonics.

I am now testing whether *Eigenmannia* distinguishes male and female EODs with their great differences in harmonic content.

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