The Jamming Avoidance Response
of High Frequency Electric Fish

I. General Features

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Summary. 1. The J.A.R. is a reflex shift in the frequency of discharge of their electric organs by high frequency electric fish (Gymnotidae: *Eigenmannia, Sternarchus*) when stimulated by an alternating current in the water, with a frequency close to the fish's. The shift is in the direction of increasing the difference (ΔF) between its frequency (F_{fish}) and that of the stimulus (F_{stim}). The significance of this behavior is presumed to be the maintenance of a private frequency for the object-detection function of the electric system, when another fish of nearly the same frequency approaches.

2. The pathway (Fig. 1) includes a high precision pacemaker unit in the medulla under the tonic influence of electroreceptors. The simplicity of the relevant parameters and the convergence on one command unit in a complete piece of quantifiable social behavior attracts attention to the J.A.R.

3. The latency, time course, form, asymmetry, and variability, the effects of temperature, anesthesia, mechanical and electrical disturbance, light, salinity and spontaneous background changes, and the absence of effect of sound are described (Figs. 2, 3, 4, 5).

4. *Eigenmannia* will usually shift F_{fish} up for a $-\Delta F$ and down for a $+\Delta F$, rather symmetrically; *Sternarchus* will only shift upwards and gives no response to a $+\Delta F$.

5. Experimentally isolating parts of the system indicates that the fish does not compare the stimulus frequency with its pacemaker frequency directly but must receive both through the same set of electroreceptors.

6. The stimuli of opposite effect, when given simultaneously cause an intermediate response, i.e. both stimuli are effective.

7. The response survives section of the posterior branch of the anterior lateral line nerves bilaterally and, with slightly raised threshold and latency, of the supraorbital and maxillary branches as well, leaving only the mandibular. It survives partial lesions of the corpus cerebelli and valvula and complete transection in front of the mesencephalon. Lesions of the torus semicircularis of the mesencephalon cause loss or gross abnormality of the J.A.R.

8. The ΔF sensitivity, dynamic range and other properties suggest that the biological significance of preserving a private frequency lies in the need of unknown brain mechanisms, that analyze the fish's own field for object detection, to function over a considerable range of distance from object to fish and therefore of voltage of a signal clearly the fish's own.

9. Evidence from bringing two or more fish together, whose separate frequencies are close, suggests the J.A.R. is used in natural social situations.

A. Introduction

The electric organ discharge frequency of the so called high frequency weakly electric fish of the genera *Eigenmannia* (ca. 300 Hz) and *Sternarchus* (ca. 900 Hz) was for years regarded as so constant that sensory input could not change it. The discharge was regarded as a regular oscillation which could be influenced only by temperature. It had apparently very little neurobiological interest in respect to control since both frequency and amplitude seemed to be fixed (Lissmann, 1951, 1958, 1961; Coates, Altamirano and Grundfest, 1954; Grundfest, 1957; Fessard, 1958; Keynes, 1957). This view was only tempered by the fact that *Gymnarchus* and some of the high frequency gymnotids can arrest the discharge for periods of several to many seconds. However, when it resumes, the frequency is immediately normal, within the period of one cycle.

The situation was drastically altered by the discovery of Watanabe and Takeda (1963) that there is one form of stimulation which regularly elicits a smooth, graded change in the frequency of electric discharge of an intact, unanesthetized *Eigenmannia*. This form of stimulation is a weak oscillatory electric current of a frequency slightly different from the fish's own. The response is a shift of a few Hz in the direction that increases the difference $(\varDelta F)$ between the fish frequency (F_{fish}) and the stimulus frequency (F_{stim}). This response was analyzed further by Larimer and MacDonald (1968) and, because of its presumed biological significance for the animal, called the "jamming avoidance response" by Bullock (1969). Other forms of transient response involving shifts of electric organ discharge frequency have been described by Larimer and MacDonald (1968), Erskine *et al.* (1966) and Bullock (1969).

The jamming avoidance response (J.A.R.) is attractive as an object of study because it is apparently a normal and complete behavioral act, it is elicited by social stimuli, it is quite reproducible, tonic and subject to very accurate quantitative measurement. It is graded and labile in ways that suggest evaluation by higher brain centers of the significance of stimulus parameters, and it is possible to know virtually the complete output of the relevant command system as we can rarely expect even in simple behavioral acts. The responsible input can be ascribed entirely to one sense modality (others may influence it under some conditions) and it seems possible to approach a complete knowledge of the actual input to the central nervous system relevant to this behavior. Finally the discharge has been found to be commanded cycle by cycle from a center in the medulla whose cells are true pacemaker neurons and are electrically coupled such that they normally act together as a single physiological unit (Szabo and Enger, 1964; Bennett, Pappas, Gimenez and Nakajima, 1967; Bennett, 1968). The commands emanating from
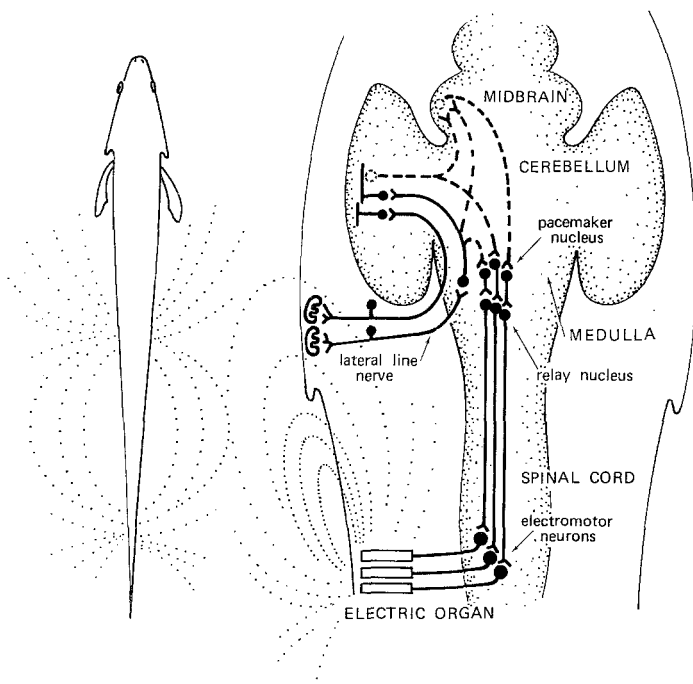
Fig. 1. Diagram of the anatomy of the J.A.R. system. Dashed lines are hypothetical connections. (See also paper II, Fig. 1)

the pacemaker center are relayed through internuncials in the caudal medulla and again through electric motoneurons in the spinal cord, thence to the electric organ (Fig. 1). Nevertheless, extra-corporeal electrodes in the water outside the intact fish recording the electric organ discharge quite faithfully measure the frequency of the discharge of the command unit in the brain.

The present study undertakes to assess the properties of the jamming avoidance response in the two main genera where it is known, *Eigenmannia* and *Sternarchus* belonging to different subfamilies of the South American family of knife fishes, the Gymnotidae. In the following paper quantitative experiments allow some conclusions relevant to the specifications of the system between electroreceptors and medullary pacemaker centers.

B. Materials and Methods

The species used are, we believe, *Eigenmannia virescens* and *Sternarchus albifrons* (sometimes called *Apteronotus albifrons*). Occasionally other species of *Sternarchus*, especially *S. leptorhynchus*, but possibly also others have been used; their

identification is difficult and we have observed no differences in their be-
havior. Specimens, usually between 14 and 24 cm in length, were obtained from
tropical fish dealers and kept in the laboratory for long periods. *Eigenmannia* was
normally kept several to a tank and fed on live brine shrimp; *Sternarchus* was kept
one to a tank in five gallon aquaria and fed on a mixed diet, chiefly living earth-
worms. The temperature of home tanks and of experimental chambers has been
maintained between 25 and 28° C. These details are given because although we have
not systematically varied these conditions we believe they might significantly in-
fluence the jamming avoidance response in some respect.

The experimental chambers used and the conditions of recording and stimu-
lating were generally similar to those described in Bullock (1969). Most experiments
were done in a chamber $26 \times 12.5 \times 12$ cm (3.9 liter) with a central compartment
for the fish of $22 \times 6.5 \times 3$ cm defined by plastic screen. An air bubbler maintained
circulation of water. Two pairs of electrodes were built into the chamber, one into
the ends, one into the sides. The end electrodes, on the extension of the anterior-
posterior axis of the fish were usually used for recording the fish's discharge. The
side electrodes, transverse to the fish, were usually used for stimulation, they were
either carbon rods approximately opposite the middle of the fish and positioned
symmetrically to reduce stimulus artifact in the recording, or stainless steel plates
the full length and height of the fish compartment to make a nearly homogeneous
field. The fish was prevented from approaching the anterior-posterior electrodes
closer than 15 mm, to keep the recorded amplitude more nearly uniform. The fish
was maintained between 35 and 55 mm from either of the side electrodes, to keep
it in a relatively uniform part of the stimulus field.

The basic measurement made, electric organ discharge frequency, has been
done by gating a 10 MHz precision electronic clock with successive fish discharges.
Every interval or every n intervals is thus estimated to a resolution, in the case
of *Sternarchus*, with the shortest intervals, ca. 1 msec, of ca. 1 in 10 000. The
number of clock pulses between fish discharges was counted digitally and the last
eight binary bits converted to an analog voltage and displayed, giving 256 counts
full scale. The careful control of electrical and electrochemical interference and of
the trigger which detects fish discharge by zero crossings, has permitted a useful
full scale sensitivity of 0.5% of the interval duration; this is readable on the paper
record to 0.01%. When greater resolution was required the duration of an epoch
defined by 2 to 128 intervals was measured, allowing a useful sensitivity to smaller
than 0.001%. The output of the precision interval measurement could be read and
photographed from a cathode ray oscilloscope or written out on a slow paper chart
or fed to a PDP-8/L computer that averaged the responses (frequency shifts), inte-
grated area under the curves and controlled the stimulus regime.

An electronic circuit that uses the output of the fish-interval-measurement to
control the stimulus frequency was used and will be referred to as a frequency dif-
ference clamp. After setting its gain to track the fish's changes in frequency with
zero difference, any desired stimulus frequency, expressed as a positive or negative
difference from that of the fish in Hertz (hereafter ΔF) could be set with precision
dials to 0.05 Hz.

The difference clamp as used is imperfect in two ways. First it updates stimulus
frequency at the end of a chosen interval which is often set to be every four fish
intervals, unless maximum time resolution and hence modulo 1 is selected. For
Sternarchus then, about every four milliseconds the stimulus frequency is readjusted
to match the most recent estimate of fish frequency (for *Eigenmannia* about
every 12 msec). This will ordinarily be a trivial error since most frequency changes
are slow. The same is true of the second imperfection: across the full scale of the

interval plotter, when the control system gain is set carefully at a certain frequency, there can be an error of up to a 0.25 Hz in tracking a fish response of 10 Hz, or 0.03 Hz in a response of 1.0 Hz in *Sternarchus* firing at 1 kHz (for *Eigenmannia* at 250 Hz the errors for the same responses are about 1.0 and 0.07 Hz, respectively). This is usually a negligible error since it means that the stimulus may be only a small percentage off of its ostensible ΔF value.

Temperature is well known to influence the frequency of the ongoing discharge (Enger and Szabo, 1968; Coates *et al.*, 1954; Lissmann, 1958; Grundfest, 1967). The Q_{10} is not high—typically about 1.5 in the range of normal temperatures, but since we are looking for small changes in frequency as a result of stimulation, the temperature has been closely controlled. The plastic fish chamber is maintained in a large (57 l) regulated water bath, both the water in the chamber and the water in the bath being well stirred. The temperature control system cycles every few seconds and its action is not reflected in temperature fluctuations of the fish chamber, whose time constant is about an hour. Temperature changes in the fish chamber include drifts of long period (> 30 min) and fluctuations of short period. The worst measured rate of temperature drift in the fish chamber was less than 1×10^{-3} °C/min. Over an hour, during favorable times of the day, the excursion is unlikely to exceed 0.02 °C. The short term fluctuations in the fish chamber are not more than 6×10^{-4} °C peak to peak over many minutes. No correlation was observed between the small recorded temperature fluctuations and the fish's frequency fluctuations.

C. Results

I. General Properties of the J.A.R.

1. Form of the Response

A good way to see the jamming avoidance response is shown in Fig. 2. Here an A.C. stimulus voltage simulating another fish is maintained by the frequency difference clamp at a ΔF of 3 Hz, first 3 Hz above and then 3 Hz below the experimental fish's frequency, for about 25 sec each. Starting within a small fraction of a second (see Section on Latency below) the fish responds by shifting its frequency unerringly in the correct direction towards escape or increasing the difference frequency. The time course of this shift is not shown completely in this figure but the half time is commonly between 10 and 15 sec, and 90% of the full shift is typically achieved within 25 to 35 sec.

The form of the frequency shift is often a simple curve approximating an exponential but it is also quite often steeper at first and slower in the second half. Commonly there is a systematic asymmetry between the time course of the upwards and of the downwards shifts.

Fig. 3 shows another form of stimulation, a sinusoidally modulated stimulus frequency that spans the F_{fish}. The exact form of the response is dependent not only on the span but on its symmetry around the response, the voltage and the modulation frequency. The example illustrated is unclamped, i.e. the F_{stim} is unaffected by the fish's response but we also used the clamp and sinusoidally modulate the ΔF added to
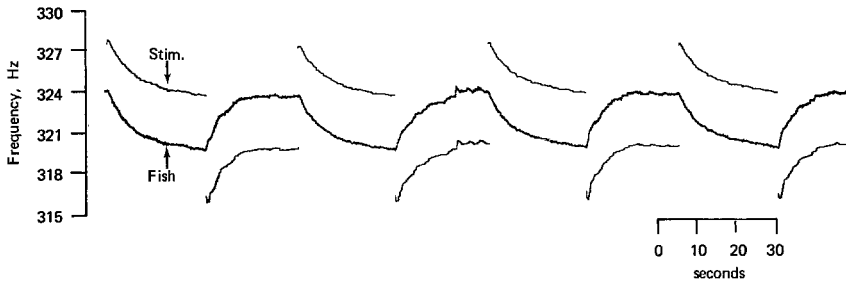
Eigenmannia, Jamming Avoidance Response,
−70 db

Fig. 2. The jamming avoidance response (J.A.R.) of *Sternarchus albifrons* stimu-
lated at about 30 db above threshold with alternately higher and lower stimulus
frequencies *clamped* at ΔF (difference from the fish) $= \pm 4 \mathrm{Hz}$ by a frequency
difference clamp. The alternation occurs automatically about every 25 sec. The
stimulus frequency and the fish frequency are each measured by an interval plotter
operating in modulo four, that is, counting high frequency (10 MHz) precision clock
pulses during four successive intervals and repeating this for each four, without
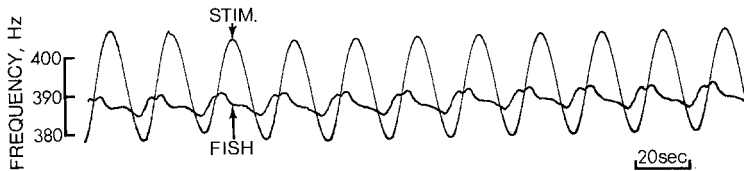dead time

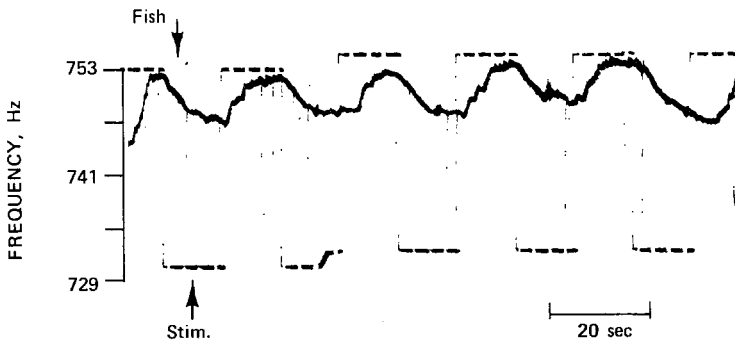Fig. 3. J.A.R. to sinusoidal FM stimulation, *Eigenmannia, unclamped*

Fig. 4. The "negative J.A.R." in *Sternarchus, unclamped.* A normal response in
the escape direction but somewhat depressed by the high intensity (60 db above
estimated threshold) is abruptly replaced by a reverse or following effect when the
intensity is switched 10 db higher. At the 40th sec the mean frequency of the stimulus
was adjusted upwards to avoid the possibility that the fish would increase its
frequency above the stimulus. This fish was engaging in an unusually high degree of
chirping activity at this time

the F_{fish}. All these types of experiment are considered parametrically in the following paper.

While the response is nearly always in the direction of escape there can occur the opposite, namely a shift towards the stimulating frequency, which we call the "negative J.A.R.". This is more likely to occur when the intensity of the stimulus is high and the frequency difference clamp is not in use (Fig. 4), but even under these conditions it is rare.

The J.A.R. is often very consistent when a regime of stimulus switching, back and forth every half a minute, is continued for many minutes. The amplitude and form of the frequency shifts are repeated with little variation. However, on many occasions there is a substantial "settling down" period with up to 50% fluctuation in the magnitude and some variation in the form of the response. Consistent responses then supervene after a few minutes. Often the first response or several responses following a period of rest (of the order of an hour) is the largest. Subsequent ones diminish to a stable plateau of about half the magnitude of the first response. The decline cannot properly be called habituation; it does not dishabituate with changes in amplitude or timing. The response regains maximum height only after a long rest. Once it has settled down, the height of response for each intensity and ΔF is repeatable in a "good" fish for many hours, even though one changes the intensity or ΔF or gives short rests. Some specimens are erratic in amplitude and in spontaneous frequency, in the fractional percent range. Spontaneous fluctuations of the baseline discharge frequency are considered below (2f).

No sign of facilitation of the amplitude of the J.A.R. by successive stimuli has been seen although we have not exhaustively tried all possible parameters to elicit it. A regime designed to elicit facilitation if it can occur was to apply stimuli in twos or three's, each stimulus of moderate intensity (e.g. -70 db), optimal ΔF (e.g. 3 Hz) and 2 to 10 sec duration; the stimuli of a pair or triplet were separated by a short interval, T_1, which was systematically varied from 2 to 30 sec; the interval, T_2, between pairs or triplets was long, to allow rest, e.g. 2 min.

2. Factors that Might Influence the Response

a) Vibration and Sound. Tapping on the aquarium can sometimes alter the response. In certain specimens of *Sternarchus* it has been noted that tapping increases the amplitude of a J.A.R. that has stabilized and reduces drastically the incidence of chirping (Bullock, 1969) which in such specimens is likely to be frequent. These effects are very prompt upon the initiation of tapping and persist through 3 mins or more of continuous tapping, giving way to the initial condition of amplitude

and of chirping within a few seconds of the cessation of tapping. This is virtually the only indication of access of another sense modality to the J.A.R., although it is only one of many indications that this response is labile and subject to the central excitatory state.

In view of the sensitivity to tapping and of the close relationship of electroreceptors and mechanoreceptors as parts of the acousticolateralis system of lower vertebrates, one wonders whether fluid-borne sound has access to the electric discharge pacemaker center. The J.A.R. is a convenient and sensitive end-point with frequency specificity. Therefore we have tried to elicit such a response by air borne sound, including tones at fish frequency plus or minus a ΔF of 3 Hz. Avoiding vibration by any contact between sound source and fish chamber, no response has been seen even to very loud sounds. The same is true for tones close to or far from the fish's frequency.

b) *Anesthesia*. Anesthesia can gradually abolish the J.A.R. and can do so in a graded manner. This response fails under the progressive action of tricaine methanesulphonate (MS 222, Ayerst Laboratories, Inc.) at about 30 parts per million, a dose producing no obvious effect on fin movements, opercular breathing movements, responses to touch, or the presence of discharge of the electric organ, which fail in that order as concentration is increased to about 150 p.p.m.

Quite remarkable is the effect of this anesthetic upon the resting discharge frequency in the absence of any stimulation. This frequency is normally maintained steadily (within 0.1% per hour) for many hours and even days at constant temperature. However, even very small concentrations of MS 222 depress the resting frequency and this effect is smoothly graded over a range of more than 120:1 (120 parts per million to 1 part per million) (Fig. 5). There may occur spontaneous, slow increases and decreases in discharge frequency, of the order of 1% with a period of 10 to 150 sec when the concentration has risen to ca. 40 p.p.m. During most of this depression the J.A.R. is still elicited nearly normally. It drops out at about 30 parts per million. The fish lies on its side at 40–80 and ceases fin movements at 60–100 parts per million; cessation of opercular movements requires slightly higher concentrations and of the pacemaker, still higher concentrations, 80–130 or more, depending on the rate of application and duration of each dose.

c) *Temperature*. The effect of temperature has not been studied upon the J.A.R. itself but is well known for the resting frequency and is not very great.

A typical Q_{10} in the range of temperatures here used, 25 to 28 °C, as given by previous authors and also confirmed by us, is in the neighborhood of 1.5, falling steadily towards 1.0 in the low 30's °C and
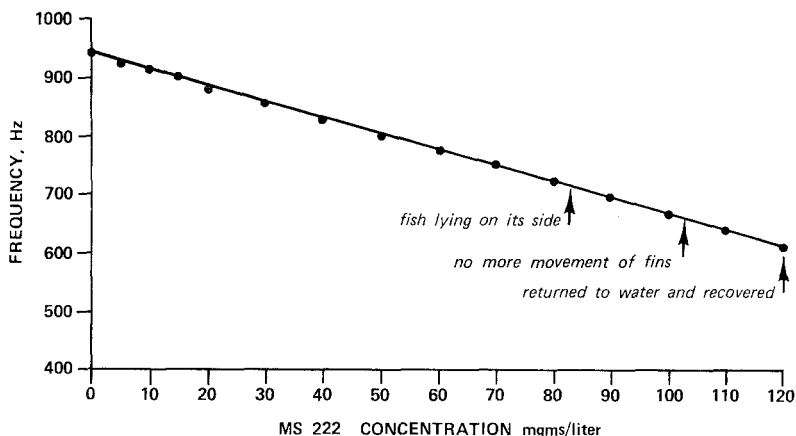
Fig. 5. Effect of the anesthetic MS 222 in different concentrations (parts per million) on the *resting discharge* frequency of *Sternarchus*. The drug was added in small increments to the bath and in each dose caused a frequency shift to a new plateau level. That is, the fish was not steadily failing. At 80 parts per million the fish ceased to hold the normal upright position and lay on its side, a sign of light anesthesia. At 100 parts per million all movement of fins stopped, but the opercular movements for breathing could last longer. At a little higher concentration than that reached here, the electric discharge would have suddenly ceased. All these changes are reversed with fresh water

increasing towards 2 and above for temperatures below 20 °C. Some of the smallest responses to stimuli given below could be imitated by a temperature jump of 0.01 to 0.02 °C and the figures given below for background fluctuation of the discharge interval expressed as standard deviation of individual interval lengths would be produced by temperature jumps of 1 or a few thousandths of a degree C. But such temperature jumps never occured in the short periods of the fluctuations or responses concerned.

d) *Salinity.* We find over a range of resistivity from 200 to 15 000 Ohm·cm, made up by diluting fish Ringer's solution with deionized water (= 0.2–0.0045 Ringer's) that *Sternarchus* and *Gymnotus* electric organs act as nearly constant current generators, in approximate agreement with Harder et al. (1964) and Larimer and MacDonald (1970). The peak voltage of discharge seen by electrodes some centimeters away, in the water, increases very close to linearly with resistivity. This is presumably due to the high skin resistance in series with the internal generator.

This means that the distance of just threshold detection of one fish by another will be a function of water resistivity. The experimentally measured threshold for J.A.R. in terms of voltage gradient actually

measured in the water near the fish was found to conform to this expectation over a certain range. From 2–200 k Ohm · cm of specific resistivity the threshold increased close to proportionally with resistance (*Eigenmannia*, three specimens). From 200–2 000 Ohm · cm the threshold increased less than expected or actually decreased with rising resistance. These were short term tests, i.e. acute exposures to various dilutions of fish Ringer's solution by deionized water. (Deionized water 150 to 375 k Ohm · cm; our tap water = 850 Ohm · cm, our aquarium water = 520–2 000 Ohm · cm; 1/3 fish Ringer's = 250 Ohm · cm, at 22–25 °C.)

Since the J.A.R. is the result of mixing the fish's own discharge, which is stronger and varying in voltage with the load (water conductivity), and the stimulus, which is much weaker and not varying in voltage with the load, this result in the low salinity range is as though the threshold were a certain ratio of the two voltage gradients. This is equivalent under these conditions to saying the threshold is a certain current. There is no obvious explanation for the results in the high salinity range but one must conclude the proportionality or constant current threshold is not necessarily true over whole physiological range of salinity of the milieu, since the fish live, in aquaria at least, in the 500–2 000 Ohm · cm range.

Electrolyte content and hence conductivity varies widely in the natural waters occupied by gymnotids in South America. Gessner (1962) gives values as low as 6 microSiemens (28 °C) (166 k Ohm · cm) for the extremely electrolyte-poor black water rivers like the Rio Negro.This is the locale of many of the experiments on social interaction and J.A.R. in sternarchines reported by Bullock (1969). Values up to 62 μS (16 k Ohm · cm) (28 °C) are given for the Solimões, just above the confluence of the Rio Negro, in September. Still higher conductivities must be expected on the island of Marajo, near the mouth of the Amazon, in the dry season. In the laboratory we have kept *Sternarchus*, though not for long periods, in salinities as high as three-tenths Ringer's solution.

The electric organ discharge frequency need not be altered by salinity at least over the range tested, 247–2 000 Ohm · cm, but there may be a transient drop in frequency in *Eigenmannia*, probably equivalent to Larimer and MacDonald's response to a sudden change in external resistance, and perhaps dependent on the rate of change of the salinity.

Water conductivity must be expected to have an effect on the sensitivity, resolution and useful range of an active electroreceptor system though the present paper does not deal with the object detecting function.

e) Light. Ordinarily one sees no change in the ongoing frequency of the electric organ in these genera when illumination is turned on or off. But in some individuals darkening brought about a decline in frequency

by about 0.5% in 10 seconds and re-illumination caused a return to the former frequency in about one minute. The decline in the dark may be associated with increased swimming activity that looks like exploratory probing. We believe the optic input has no direct access to the pacemaker but if it results in a marked change in activity or arousal, the pacemaker may be affected.

f) Spontaneous Fluctuations of Frequency. Since dependable responses can be shifts of the fish's frequency of less than 0.1%, it becomes interesting to examine just how steady the unstimulated fish discharge frequency is. This varies considerably. *Eigenmannia* can be more variable and occasionally exhibits spontaneous changes of 20 to 30%; these are usually slow, irregularly progressive over hundreds of seconds. Ordinarily however spontaneous fluctuations as much as 1% will not be seen in dozens of animals observed for several hours each. In one specimen of *Sternarchus* examined carefully over three days, 40 of the 53 frequency determinations made at random times showed a discharge frequency within $\pm 0.1\%$ of the mean value, after compensating for temperature fluctuations of the bath, the other 13 samples were below the mean by 0.2–0.4%.

Both genera are quite capable of rather abrupt large changes and do exhibit them from time to time apparently spontaneously, under conditions or for reasons that we have been unable to discern. Sometimes but not always these changes are accompanied by locomotor signs of arousal (Larimer and MacDonald, 1968). Marked changes in arousal state seem to be accompanied by frequency shift. Increased arousal is commonly associated in *Eigenmannia* with decrease in frequency.

Following some forms of disturbance, frequency changes are somewhat more likely although not at all certain. Sharp tapping on the substratum, the approach of a metal object in the water, the closing of a circuit that shorts together two electrodes near the fish, or tactile stimulation may be followed by irregular frequency change or by a shift to a new plateau which can be a fraction of a percent or several percent removed from the previous frequency. Or there may be no change at all.

Sometimes the resting frequency is quite "wobbly". This can be a quasi-periodic fluctuation, for example, with a 4 sec period and as little as 0.04% peak to peak amplitude, or it can take the form of irregular wanderings whose waves are mainly tens of seconds long and from tenths of a percent to several percent in height. Individuals show behavior that is unique or difficult to find in other specimens. In one *Eigenmannia*, over and over again, as he turned end for end in the long, narrow fish chamber, the resting frequency of discharge briefly declined 0.2–0.5%, in slowly developing and slowly returning cusps of

ten seconds total duration. In others, no visible behavior correlated with
a transient shift or change from smooth to "wobbly" frequency. In
several specimens of *Eigenmannia* there have occurred quasi-periodic,
sudden increases in frequency, by 0.5–1% in less than 0.3 sec, slowly
falling back to the same "resting" level, usually within $\pm 0.05\%$.

One of the conditions quite often accompanied by "wobbly" fre-
quency is the rising phase of the J.A.R. (Figs. 1, 10, 11). This has been
noted in both *Eigenmannia* and *Sternarchus*, but especially in the latter.
The falling phase of the J.A.R. is commonly much smoother, indeed
quite markedly free of variation.

However, the great majority of the observations of *Eigenmannia*
and even more frequently of *Sternarchus* reveal a steadily maintained
discharge frequency that fluctuates by such a small amount that special
methods are required to measure it. Discharges counted per second or
any fixed period of this order of magnitude generally fluctuate by no
more than one count which is the inherent error of such counting.

If we plot every interval to a resolution of 1 part in 10 000 in *Ster-
narchus*, the standard deviation over a thousand intervals during the
usual quiet discharge that lasts most of the time can be as low as
0.012% which is 0.14 microsec. Three additional samples of 7 500 inter-
vals each gave S.D. values of 0.16, 0.16 and 0.17 microsec and interval
histograms that are quite symmetrical and Gaussian. The condition of
minimum fluctuation has been illustrated elsewhere (Bullock, 1970) in
connection with a discussion of the reliability of neurons.

This same illustration (in Bullock, 1970) shows the end of a "song"
or "bout" — initially irregular, abrupt and sputtery, $< 1\%$ departures
from the smoother resting frequency, becoming more and more regular,
and at times, for a number of seconds (thousands of cycles), exhibiting a
patterned and systematic sequence of preferred intervals (Fig. 6).
"Bouts" or "songs" have been seen over and over in a few indi-
viduals of *Sternarchus*, going through a predictable series of stages
from sputtering to patterned and finally decelerating and diminishing
sinusoidal modulation of frequency, followed by two short "beeps" and
then resumption of the normal state of minimum fluctuation. We have
not learned how to elicit or when to expect these bouts of complex
interval succession and hence have not analyzed them in detail. Short
loops of the zero-crossing interval-plotter records on magnetic type
have been examined in an analog frequency analyzer and show a mixture
of at least two frequencies modulating the fundamental *Sternarchus*
rhythm of about 1 kHz. It cannot be excluded yet that these "bouts"
are epochs of desynchronization or decoupling of a small group of the
pacemaker neurons in the medullary center, from the majority, nor-
mally electrotonically coupled.

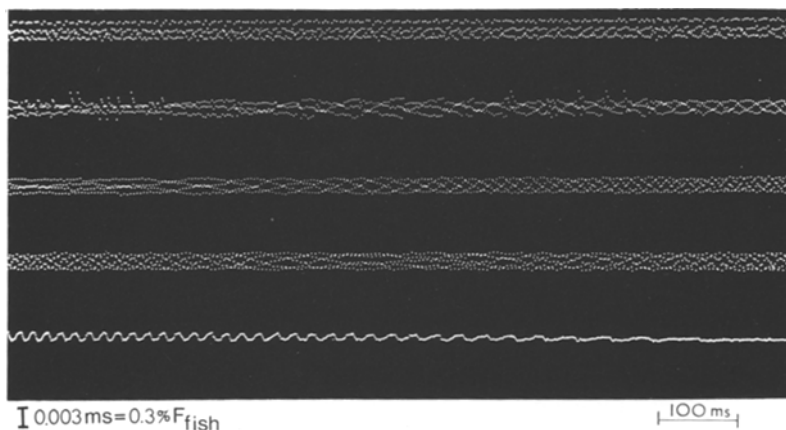I 0.003 ms = 0.3% F_{fish} ⊢ 100 ms ⊣

Fig. 6. High resolution modulo 1 record (every interval individually plotted) of
spontaneous fluctuations; Sternarchus. Several states are illustrated, with minimal
fluctuation (standard deviation of a sample of 1000 intervals = 0.012% = 0.14 μsec),
with simple sinusoidal fluctuation, with complex patterned fluctuation (preferred
intervals) and with irregular "large" fluctuations of ca. 0.5%

II. Experiments on the Pathway

1. Separation of Inputs

The frequency difference clamp is one way of interfering with the
normal control of ΔF. Another way is to take advantage of the facts that
(a) the response is a relation between two inputs, the fish's frequency and
the stimulus frequency and (b) electroreceptors are widely distributed
over the head, trunk and tail whereas the electric organ is in the trunk
and tail. One can prepare a rubber diaphragm cut to fit the fish closely
just behind the operculum and mounted in a framework such that the
head of the fish is in one compartment and the trunk and tail in another.
Electrodes in the posterior compartment pick up the electric organ
discharge at full intensity whereas electrodes in the anterior compartment
detect the electric organ discharge some 50 db weaker, representing
escape of the electric organ current presumably through the tissues of
the fish that connect the two compartments. Stimuli can now be delivered
in the anterior compartment and will be similarly attenuated in the
posterior. Under these conditions stimuli at optimal ΔF and moderate
intensity do not evoke a J.A.R. That the fish is however willing and
able to respond is shown by leaking a small amount of the voltage from
the electric organ discharge into the anterior compartment, whereupon
a normal J.A.R. is evoked.

This experiment shows that the two input frequencies must be
received over the same set of afferent fibers, that is from the same

moiety of the body. It also means that the information available in the brain as to the frequency of the electric organ discharge being commanded from the pacemaker center in the medulla is not adequate for combining with the stimulus to the anterior compartment, but the same information delivered into the water of the anterior compartment is. This experiment is difficult to repeat since it depends upon a good fit between the rubber dam and the fish and upon a cooperative specimen that does not struggle. It was quite satisfactory on only one specimen of *Sternarchus* and partially successful on two others.

Still another and more readily repeated method, which answers nearly the same questions is to curarize the fish and thus stop the electric organ discharge, while recording the command of the pacemaker center in the medulla with a microelectrode. This method is useful in *Eigenmannia* where there is a curare-susceptible junction in the electric organ, whereas in *Sternarchus* there is no such junction, the electric organ consisting of expanded and specialized nerve endings rather than postsynaptic cells.

In *Eigenmannia* a dose of gallamine triethiodide (Flaxedil) of 0.05–0.1 mg per 5–10 gm fish, intramuscularly, just abolishes the electric organ discharge, while the command from the pacemaker center continues normally. Even a stimulus of optimal ΔF delivered into the water around the fish fails to evoke a J.A.R. whereas if a second sinusoidal voltage at the frequency of the pacemaker discharge is injected into the water, a nearly normal J.A.R. is elicited. Once again the information available in the brain from the electric organ command center is not adequate for combination with the stimulus of optimal ΔF, but the commanded information converging on the same electroreceptors with the stimulus frequency (ΔF from the command) is adequate.

This leads to the next logical step. If we deliver stimuli of two different frequencies to the curarized fish, neither stimulus being close to the fish's own frequency, but arbitrarily chosen and only a few Hz apart, one at a moderate intensity, the other 20 or more db weaker, the combination is effective in causing a shift of the medullary pacemaker discharge. This is true for *Eigenmannia* between limits of about 150 and 600 Hz. The best ΔF is about 6 Hz. The responses are abnormal in that both $+$ and $-\Delta F$ (the sign arbitrarily given by the weaker minus the stronger stimulus) cause a small rise of the fish pace. The fish did not seem able to distinguish between $+$ and $-$ defined in this way.

2. Multiple Stimuli

A different question is what response will a normal, uncurarized fish make to several simulated, invading fish, that is to two or more strange rhythms close to its own. If one stimulus is a positive and the other a

negative ΔF of the same stimulating value, the result found is that the fish does not respond or changes its frequency only very slightly and irregularly up and down by a small amount. If the ΔF and intensity of one stimulus is adequate to drive the fish's frequency up by 4 Hz and the other stimulus is adequate by itself to drive the fish's frequency down by 2 Hz, the combination will result in an increase in the fish frequency by about 1 Hz. In short two stimuli at the same time apparently result in approximate algebraic summation of the responses to the stimuli separately. This should be a common situation especially for *Eigenmannia* which tends to aggregate.

3. Section of Lateral Line Nerves

In eight specimens of *Eigenmannia* the posterior branch of the anterior lateral line nerve has been sectioned on both sides just as it passes dorsal to the operculum, thereby denervating all electroreceptors of the trunk and tail. Within six hours, the fish having recovered from the MS 222 anesthesia, they were tested for J.A.R. In most cases the response was virtually normal. In a few individuals it was somewhat subnormal, weak, altered in form, long in latency and adapting. Specimens with sham operations otherwise equal but without cutting the nerve showed normal J.A.R. After two or three days of recovery, the nerve sectioned animals that were initially abnormal showed nearly normal responses.

In an additional four *Eigenmannia* a more extensive denervation was performed. Six nerves were cut: the posterior branch of the anterior lateral line nerve, the supraorbital nerve and the maxillary nerve, on both sides. This leaves virtually only the mandible still innervated. Even these animals had a J.A.R. but it was higher in threshold by 10 db or more and appreciably longer in latency than normal. Evidently lateral line input is important but a fraction of the full complement of receptors suffices to mediate a high threshold J.A.R.

4. Lesions of the Brain

Complete or nearly complete transections of the brain in the diencephalon or at its anterior limit were performed on five *Eigenmannia*. Tested after 1 to 3 days the J.A.R. appeared normal.

Localized lesions on eight *Eigenmannia* have involved the cerebellum and structures below it. With small lesions of the corpus cerebelli alone or small lesions involving both corpus and valvula, the J.A.R. has been slightly abnormal but survives. Larger lesions still not damaging most of the corpus or valvula but encroaching somewhat on the torus semicircularis under the cerebellum cause loss or gross abnormality

of the J.A.R. The series however is till too small and analysis too meager to permit systematic statements about the relation of the structures involved to the functional deficits.

D. Discussion

I. Nature of the Response

The J.A.R. is merely the most convenient and reproducible of several forms of evidence that the high-frequency, "constant" frequency gymnotids have in fact constant control of the frequency with several forms of integration and evaluation of input, converging on the pacemaker center in the medulla. The several parameters that can influence independently the discharge frequency and the response to stimuli suggest that the J.A.R. is not a simple reflex but involves weighting functions that might be expected to involve structures at least as high as the midbrain. The convergence of evaluated input to a single command unit whose controlled parameter is so accurately measurable and the relative simplicity of the input modality, together with the possible involvement of the elaborate cerebellum and specialized midbrain centers, make this an attractive object of study as a model of the central control of behavior.

The form in which the response was displayed by Watanabe and Takeda (1963) who discovered it and by Larimer and MacDonald (1968) (Fig. 7) plots the initial stimulus ΔF against the final fish frequency
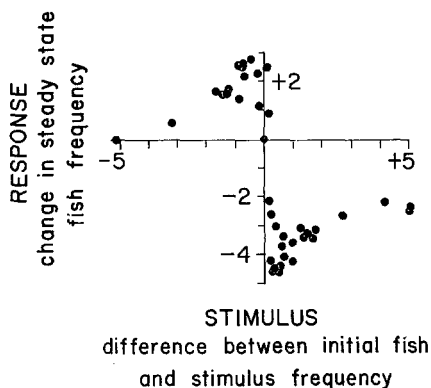

Fig. 7. Stimulus/response relation as plotted by Watanabe and Takeda (1963); *Eigenmannia, unclamped.* Each point is one J.A.R. at plateau; the stimulus onset is an intensity step from subthreshold to a moderate voltage. Note frequencies are plotted as differences from resting frequency, not differences between stimulus and fish at the plateau

change in the unclamped steady state. This results in the response appearing larger, the smaller is the ΔF ("error signal") and the input-output curve approaches the vertical in slope. The frequency difference clamp has revealed that there is a most effective stimulus (ΔF) (paper II, Fig. 4) which is about 4 Hz, considerably more than the minimum effective ΔF (< 0.2 Hz). The points of large response at small ΔF's in the Watanabe and Takeda plot are explained by the fact that the small initial ΔF resulted in a weak response in the direction of increasing the ΔF, which therefore became a better stimulus and the ΔF soon rose to best frequency and hence elicited the best response.

The J.A.R. is a tonic, slowly rising response, smoothly graded over a wide range of output and an even wider range of input, integrating over time and, when they are present, over separate stimuli. It is only one of a set of responses that involves changing the frequency of the electric organ discharge. The others, including chirps ("pings" of Larimer and MacDonald, 1968) irregular fluctuations, and in *Eigenmannia* a sometime response to general arousal or activity, are much less understood both as to biological significance and adequate stimuli.

II. Neuronal Pathways and Other Structures Involved

Fig. 1 shows the structures known or presumed to be involved in the J.A.R. The pacemaker nucleus in the medulla and the internuncial nucleus just behind it are known and have been studied by penetrating microelectrodes (Bennett *et al.*, 1964, 1967; Bennett, 1968a; Szabo and Enger, 1964). These and the electric-organ motor neurons have been studied electron microscopically as well (Bennett *et al.*, 1967). The electric organs and their control have been extensively studied (Grundfest, 1957; Keynes, 1957; Fessard, 1958; Bennett, 1961, 1970). The electroreceptors, inferred from behavior (Möhres, 1957; Lissmann, 1958; Machin, 1962; Lissmann and Machin, 1958; Machin and Lissmann, 1960), have been described physiologically (Bullock *et al.*, 1961; Fessard and Szabo, 1961; Hagiwara *et al.*, 1962; Hagiwara and Morita, 1962; Szabo, 1963; Harder *et al.*, 1964, 1967; Hagiwara *et al.*, 1965a, b; Bullock and Chichibu, 1965; Bennett, 1968b; Szabo and Fessard, 1965; Suga, 1967a, b; Szabo, 1967; Szabo and Hagiwara, 1967) and histologically at both light microscope and electron microscope levels (Szabo, 1965; Harder, 1968a, b; Wachtel and Szamier, 1966; Lissmann and Mullinger, 1968; Derbin and Szabo, 1968; Szamier and Wachtel, 1969, 1970).

The receptors types described for *Sternopygus* (Bullock and Chichibu, 1965) are probably relevant and apply to the high frequency species that exhibit a J.A.R.; those species are otherwise known with respect to receptor types, from the studies of Hagiwara and Morita (1963) and Hagiwara *et al.* (1965b). It seems safe to conclude that the classes

of electroreceptors relevant to the J.A.R. are (a) the afferent units
which have been referred to as probability coding and (b) those which
have been called phase or latency coding, among the tuberous receptors.
Possibly (c) the frequency coders which form the other ("ampullary")
class histologically, are also involved in slow beat-frequency stimulation.
Microelectrode studies on these and central units under similar conditions
will be reported in separate papers (Scheich *et al.*, in preparation).

As Fig. 1 shows, the afferent fibers are said to enter and terminate
in several parts of the medulla, cerebellum and midbrain. However,
recent work by tracing degenerating fibers from cut lateral line nerves
in mormyrids shows no fibers proceeding to the midbrain or even to
the cerebellum proper, apart from the anterior and posterior lateral
line lobes (Karten, personal communication). The properties of second
or early higher order units in the lobus lateralis of the medulla, a struc-
ture of cerebellar organization, have been described by Enger and Szabo
(1965) in response to stationary and moving objects of dielectric and
conducting character.

For the most part the pathways and organization of central influence
upon the pacemaker center in the medulla are still only conjectural
(dashed lines in Fig. 1). Because of its size and histological specialization
as well as its primary lateral line input the cerebellum is a logical candi-
date for involvement. The same factors suggesting an extensive analog
display on a much folded sheet might be a reason to expect that the
cerebellum is primarily involved in the object detection function, that
is to say, the analysis of the position of the body relative to the environ-
ment and therefore that the specialized social response of the J.A.R.
may involve the cerebellum relatively less.

III. Biological Significance of J.A.R.

The J.A.R. is dependent upon and in a sense required by the great
steadiness of the normal background discharge. Presumably there are
several ways of meeting the contingency that other discharging fish of
about the same frequency approach close enough to risk "jamming"
the object detection system, for which electric organs, electroreceptors
and central analyzing mechanisms were supposedly evolved (Lissmann,
1958). One is to pay attention to each discharge and the shape of the
instantaneous field it sets up. Another, combined with this, is to make
the intervals between discharges somewhat irregular, reducing the chance
that several discharges in succession will be, within a given allowance,
coincident. These are the properties of the numerous low frequency
electric fish. Another way may be optimal if separate selection pressures
increase the mean frequency of the discharge output or alter the input
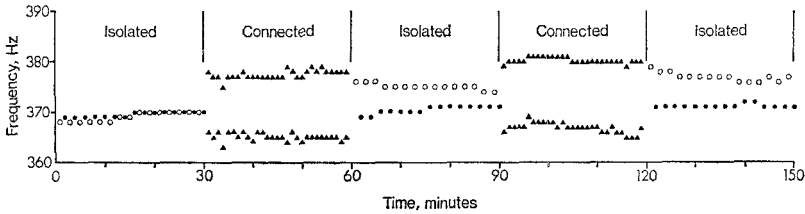analyzer in the brain to integrate a number of successive intervals. This

Fig. 8. Two individuals (*Eigenmannia*) selected from a large number for nearly equal electric organ discharge frequency, kept in separate aquaria and measured to ± 0.5 Hz, alternately isolated and connected by a pair of wires. Measurements of isolated fish are by actual count for 10 sec, of connected fish by fast Fourier analysis of 1.3 sec of the combined signals, tape recorded. Similar behavior occurs when the fish are placed together in the same tank. The two symbols represent the two individuals when isolated; when connected they cannot be distinguished and a common symbol is used

might be to look, as it were, through a narrow band filter and pay attention only to mean input frequency close to the output discharge frequency. In this case, the more regular the discharge, the narrower can be the receiving filter.

The success of this system of relatively high frequency and regular discharge will be greater with two more properties. One is that the mean frequencies of individual fish vary quite widely. This is seen in the range of about 300 Hz within the species in both *Eigenmannia virescens* and *Sternarchus albifrons*. The other is the active avoidance of other individuals whose frequency is too close. We have no evidence of locomotor spacing out specific to the frequency difference, though it has not really been looked for. The J.A.R. accomplishes the same thing.

The extraordinary regularity may be part of the fish's answer to the contingency of jamming by other fish. It might also be adaptive for the brain mechanisms still only slightly understood (Enger and Szabo, 1965; Scheich and Bullock, in prep.) for processing the electroreceptor input about the environment of the fish. We find and will report elsewhere, a high sensitivity of some brain cells to small differences in phase of input signals; this is aided by regularity. We cannot say whether these parameters are important in object assessment or only in assessing other fish.

To show whether the J.A.R. actually occurs in social situations when the stimulus is not artificial, we have brought fish together that were selected from a large sample to have "resting" frequencies when isolated that lay within a few Hz of each other (Fig. 8). Of 16 pairs of such *Eigenmannia* 14 responded within 60″ by widening the ΔF, two showed no change. The average increase in ΔF was 7.2 Hz. Only 6 of these pairs were followed after reisolating the individuals; 5 of them

2*

decreased the difference between their frequencies, one showed no change after 60″. The average decrease in ΔF was 7.0 Hz. These values of increase and decrease are highly significant. Samples of isolated fish remeasured at intervals > 2 min show some drift, as described above (Section III, A2), but extremely little, apart from temperature changes. The form of the occasional wandering or frequency shift is such that increases and decreases are equally likely. Jumps within 60 sec of more than 1 Hz, are extremely rare.

The wide dynamic range of the J.A.R. is notable. We may propose that it has biological significance for the mechanism of use of the high regularity object detection. The range of 60 or 70 db above threshold over which the J.A.R. is graded implies that a fish will shift its frequency very slightly when another fish is just detectable at maximum distance and most effective ΔF, whereas it will shift its frequency more and more over a range of at least 10 times greater proximity of the foreign fish. Now, what biological significance can it have that the frequency difference is increased (avoiding jamming) as the intensity of the foreign fish increases with proximity? The suggestion is that the importance lies in the need of the brain mechanisms that analyze input for object detection to function over a considerable range of distances from object to fish and therefore a wide range of signal voltage.

There is no obvious biological significance that we can suggest for the differences between species such as the asymmetry of J.A.R. in *Sternarchus* compared to its symmetry in *Eigenmannia*.

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