7-1-1975

Interactions in the Frequencies of Electric Organ Discharge by Eigenmannia Virescens (Sternopygidae, Pisces) During Social Behavior

Philip Gaddis

Portland State University

AN ABSTRACT OF THE THESIS OF Philip Gaddis for the Master of Science in Biology presented July 1, 1975.

Title: Interactions in the Frequencies of Electric Organ Discharge by Eigenmannia virescens (Sternopygidae, Pisces) During Social Behavior.

APPROVED BY MEMBERS OF THE THESIS COMMITTEE:

[redacted]

Richard Petersen, Chairman

[redacted]

Richard Forbes

[redacted]

Robert Tinnin

The extent to which individuals of Eigenmannia virescens modulate their electric organ discharge frequencies to accommodate the frequencies of others of the same species during social interactions was investigated. Recordings of the fish's discharge frequencies, taken with Tektronix 3L5 and 5L4N spectrum analyzers, showed that, although movements of up to 60 Hz in a day may be made, the frequency movements would be made more or less synchronously by all fish in the group. An apparent preference for, and a tendency of the fish to follow one another in frequency, at frequency ratios of 2:3 (a musical fifth), 3:4 (fourth), and even 4:5 (major third) was observed. The appearance of a circadian rhythm was also noticed.

TO THE OFFICE OF GRADUATE STUDIES:

The members of the Committee approve the thesis of Philip Gaddis presented July 1, 1975.

[redacted]

Richard Petersen, Chairman

[redacted]

Richard Forbes

[redacted]

Robert Tinnin

[redacted]

Laird C. Brodie

APPROVED:

[redacted]

Earl Fisher, Jr., Head, Department of Biology

[redacted]

David T. Clark, Dean of Graduate Studies

July 1, 1975

INTERACTIONS IN THE FREQUENCIES OF ELECTRIC ORGAN DISCHARGE BY EIGENMANNIA VIRESCENS (STERNOPYGIDAE, PISCES) DURING SOCIAL BEHAVIOR

by

PHILIP GADDIS

A thesis submitted in partial fulfillment of the
requirements for the degree of

MASTER OF SCIENCE
in
BIOLOGY

Portland State University
1975

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

The subject of the communication systems that enable aggregations of animals to synchronize their activities has received little attention. The study of animal communication has provided a wealth of detailed descriptions of vocalizations and displays of a more or less intentional nature that are used in agonistic and reproductive interactions - situations involving only a few individuals at once. These mechanisms involve alternating periods of transmission and reception of information by the individuals involved. I suggest that the synchronization of the activities of many animals involves a system in which all may continuously and simultaneously transmit and receive information. The activities of animals are normally associated with acoustic and electric byproducts and tend to be basically periodic. The harmonization of the frequencies of these acoustic or electric byproducts may provide the means of effecting the organization of aggregations of animals.

The glass knife fish, *Eigenmannia virescens* (Cypriniformes: Gymnotoidei) continuously discharges weak electrical pulses into the surrounding water, as do all the members of the suborder. The frequency of discharge is relatively stable and each individual may discharge in a frequency range of from 250 - 600 Hz (Bennett, 1971a). The field produced by these discharges is used for object location and navigation and has supposedly facilitated the nocturnal habits of these fishes (Lissmann, 1958). The discharges are also used in communication and a basic vocabulary of frequency modulations used in agonistic and reproductive interactions has been worked out by Hopkins (1974). These modulations consist of interruptions lasting 20 - 80 msec and frequency rises of 5 - 20 Hz of short (less than 2 sec) and long (2 - 40 sec) duration.

The gymnotoids receive electrical information through two morphologically and functionally different kinds of electroreceptors, termed ampullary and tuberous, both of which are believed to be derived from modified lateral live receptors (Bennett, 1971b). The ampullary receptors are sensitive to d.c. and low frequency potential changes up to 50 Hz. The tuberous receptors are sensitive to higher frequency changes and, in particular, to the fish's own discharges. The tuberous receptors are believed to mediate the object location and navigation functions. The function of the ampullary receptors remains a mystery. Hopkins (1974) has suggested that these receptors could be sensitive to the low frequency components of the frequency interruptions that are used in communication.

Field studies of the gymnotoids in the Amazon Basin have shown Eigenmannia virescens to be a social animal. It has been found in aggregations at the river bottom (Steinbach, 1970) or in protected locations along the banks of smaller streams (Lissmann, 1961). These aggregated individuals disperse during the night while they are presumably foraging solitarily for crustaceans. The aggregations form again at dawn in the same locations. Apparently nothing is known of the frequency interactions that accompany these fish's organization into large groups.

It was my hypothesis that each individual *Eigenmannia virescens* could tune its discharge frequency relative to the others to produce a regularly patterned chord. Any pattern in the harmonic structure of the chord could be the carrier of information that would facilitate their social organization. It was the purpose of this study to examine this chord and monitor it during social organization.

When these two non-dominant fish were placed with another fish whose frequency was not nearly as low as the dominant, the frequencies of all 3 fish dropped 50 Hz over 5 days.

The fish whose frequency was far below the others in group I was much smaller than the others and represented the bottom of the social heirarchy. When this fish was present, the frequency distribution of the group of 6 fish was very similar to that of group III with the same number of fish. As in group III, the fish were spread rather evenly over a 60 Hz interval centered loosely around a fifth above the low frequency fish. Its removal was followed by a drop of 45 Hz by the entire group. By the next day, the group had returned to within 5 Hz of the frequencies shown before the removal of the low frequency fish.

A frequency distribution similar to that found in the early stages of group III appeared to be present in group II but the picture was complicated by the presence of one very small fish whose frequency was very close to that of the low frequency, dominant fish. The amplitude of this fish's discharge was smaller than the others in proportion to the fish's size. The fish was subjected to severe physical abuse by the other, larger fish and was finally removed with its fin in shreds and missing an eye. After the removal of this fish, the frequency distribution of a low frequency dominant with the rest of the group clustered about the fifth above persisted for four days until a new fish was added whose frequency was intermediate between the dominant and the group. This new fish was larger than the resident dominant and quickly assumed dominant status. Over the next six days, the frequency of the new dominant decreased to within 10 Hz of the previously dominant fish who was found dead on the following morning. The frequencies of the other fish also dropped along with the new dominant fish and the original frequency configuration was not reattained.

After the removal of the low frequency, subordinate fish from group I, and after the fish had returned to their original frequency distribution, the dominant fish was removed from the group for a period of 20 minutes. Before its removal this fish had had the highest frequency, topping a 60 Hz interval for the group of five fish at 480 Hz. When this fish was placed in a tank with identical temperature and with several other non-electric fishes, its frequency dropped 95 Hz. In the meantime, the fish of the group shifted upward 2 - 5 Hz but, within 10 minutes, returned to their previous frequencies. During this time, the fish which was thought to be the second fish in the social heirarchy assumed dominance and occupied the hiding place of the dominant fish without contention from the others. This fish had had the second highest frequency and now had the highest.

The original dominant fish was then returned to the group discharging at a frequency of 385 Hz. It immediately went to its hiding place to find it occupied by the number two fish who apparently did not recognize the original dominant fish at its new frequency. After a very short bout of this species' characteristic wrestling, the number two fish yielded the preferred hiding place. During the struggle, the frequencies of the two contestants shifted- the dominant fish from 385 to 394 Hz, and the number two from 460 to 454 Hz. The original 60 Hz interval was thereby reattained. No other frequency shifts were observed in the next hour but the next morning the dominant fish was discharging at 485 Hz - 5 Hz above its original frequency. In order to attain this frequency, the fish must have crossed all the other fish in frequency. The experiments of Watanabe and Takeda (1966) and of Bullock, Hamstra, and Scheich (1972) on the jamming avoidance response of Eigenmannia virescens showed that when the frequencies of these fish are approached to within 3-6 Hz by an artificial frequency of appropriate voltage and amplitude they will reflexly move away in frequency and can be chased as far as 6.5 Hz. It seems that these fish would avoid crossing each other in frequency and this appears to have been the case throughout my studies except for the case just described above.

The frequency differences between individual fish appeared to be more stable than were the absolute values of the frequencies. In order to compare these two quantities, the ratio of the average change in the inter-fish frequency differences to the average change in frequency for all fish in the group were taken over arbitrarily chosen intervals showing large frequency movement and in which the group size remained constant. It is suggested that a ratio less than 1.0 would indicate relatedness in the discharge frequencies. Table I shows these ratios. It can be seen that these ratios are all much smaller than 1.0 indicating the relatedness of the frequencies and the tendency to conserve the frequency differences.

On numerous occasions, and with all three groups, fish were observed at frequencies quite near and sometimes precisely on the values of the 2:3, 3:4, and sometimes even the 4:5 frequency ratios above the low frequency fish. In order to determine the extent of

TABLE I

RATIOS OF THE AVERAGE CHANGE IN INTER-FISH FREQUENCY DIFFERENCE TO THE AVERAGE CHANGE IN FREQUENCY

DATE	RATIO
Group I	
11-22-74	0.085
11-22-74 to 11-23-74	0.025
Group II	
12-38-74 to 12-29-74	0.4
12-29-74 to 12-30-74	0.22
12-30-74 to 12-31-74	0.2
1-3-75 10:00 A.M. to 6:00	0.17
1-3-75 to 1-4-75	0.24
Group III	
3-10-75 12:15 P.M. to 3-11-75 12:30 P.M.	0.16
3-11-75 12:30 P.M. to 3-13-75 8:00 A.M.	0.114

the fish's tendencies to follow these ratios, they were plotted along with the frequencies of the fish. A representative example is given in Figure 1 which shows a period of 8 days from the study of group III. To further visualize this phenomenon of ratio following, the 2:3 and 3:4 ratios were drawn as straight lines in Figure 2 with the frequencies of the closest fish plotted in relation to them over the same interval of time as shown in Figure 1.

It can be seen from these figures that the fish numbered 3 and 6 followed the 3:4 and 2:3 ratios respectively for the entire period shown. Neither fish were seen to cross these harmonic lines, but stayed above them at average distances of 8.2 Hz, S.D. 3.02, for fish 3 and 7.2 Hz, S.D. 4.8, for fish 6. The fit to these harmonic lines was compared to the constancy of the absolute frequency differences. Fish 3 maintained a frequency difference with a S.D. of 3.05. For fish 6, the S.D. was 4.14.

A circadian rhythm with a daytime decrease in frequency that averaged 15.3 Hz was shown by the fish of group III for a period of 9 days. When the dominant, low frequency, fish was isolated from group III after these 9 days of the rhythm, its rhythm damped out and became quite flat. After the seventh day of isolation, daily fluctuations began to reappear but, with only one exception - the seventh day - the daily fluctuations did not exceed 7 - 8 Hz until the 14th day.

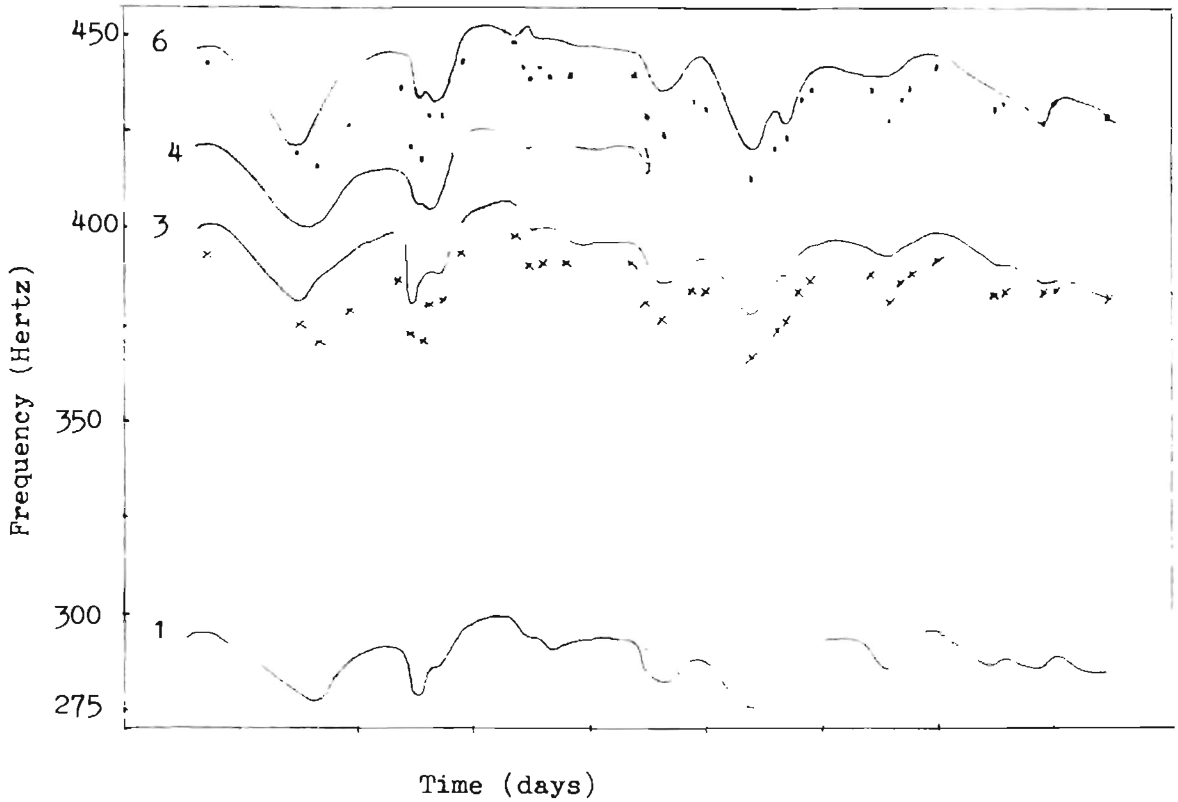

Figure 1. Frequencies of the fish of group III and the values of the 2:3 and 3:4 frequency ratios to the low frequency fish taken over a representative 8 day period. •=2:3, x=3:4

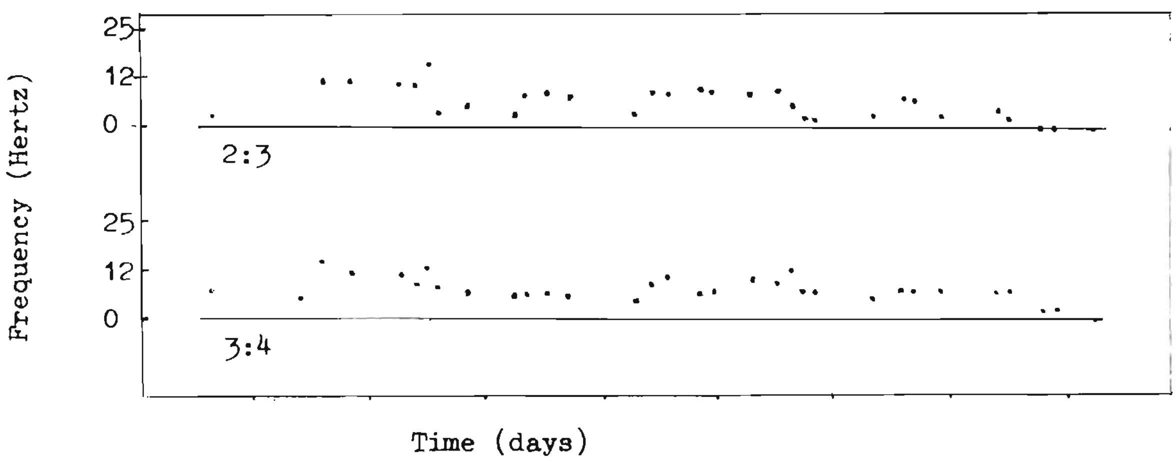

Figure 2. The 2:3 and 3;4 ratios to the low frequency fish drawn as straight lines with the frequencies of the nearest fish taken over the same time interval as Figure 1.

In the final series of experiments with group III, 2 fish that were placed consecutively in a cage in the tank of the originally dominant fish both showed initial frequency movement while the resident fish maintained a relatively stable frequency. The frequency of the first fish dropped 15 Hz in the first 5 hours and stayed at this lower level for the remainder of its stay in the cage. The second fish fluctuated 5 Hz and then stabilized near its original frequency for the rest of its stay. In both cases the frequencies of the fish were held relatively stable after a short period of initial fluctuation. When all 3 fish were placed in the same tank and allowed to interact physically, their frequencies did not remain stable but shifted in a synchronous manner as had those of the other groups.

DISCUSSION AND CONCLUSIONS

When observed over a few hours, the frequencies of solitary fish and fish in groups will usually remain relatively stable as long as social circumstances remain stable. When observed over a day or more, the frequencies may be seen to shift gradually over frequency differences as great as 50 - 60 Hz, may show regular, circadian rhythms of 5 - 25 Hz, or may remain relatively constant. When frequency shifts are observed in groups of constant size, the group will be seen to move as a whole with the inter-fish frequency differences being conserved to a much greater extent than the absolute frequencies.

Short term changes in the level of activity or in the type of activity are not accompanied by persistent changes in frequency. Any changes in group size, however, will be accompanied by rapid changes in frequency that may or may not be in a uniform direction throughout the group. These changes may be quite large - 45 Hz for a group of 5 fish, 95 Hz for a single fish. Removals of individual fish from a group are not followed by consistent changes in the frequencies of the other fish. It is apparent from the results that the removal of certain fish from the group are followed by much greater changes indicating a greater influence by these fish on the frequencies of the group. If a fish's frequency happens to be at a distance that creates a frequency ratio close to 2:3, 3:4, or even 4:5 to another fish or to a group of fish, these frequency distributions will be conserved.

The removal of this distant fish will be followed by large shifts of the frequencies of the rest of the group.

The tendency of these fish to follow small whole number frequency ratios may serve them in providing a reference for the correction of their internal clocks. Being "cold blooded" animals, their pacemakers will be subject to alteration by any changes in the water temperature. (Enger and Szabo, 1968). If two fish that are maintaining a frequency ratio are subjected to a change in water temperature, their frequencies will be changed by a constant amount and will no longer be in the same frequency ratio. The smaller the original whole number ratio, the greater will be the resolution in the ratio change and the greater will be the indication to the fish that the temperature has changed and a correction is required.

The fish do not appear to seek these harmonic intervals actively. Rather, they seem to be arrived at by chance and this will only occur if the harmonic lies within the characteristic frequency range of the fish. The harmonic itself is not followed but is followed at a distance that is in conformance with the fish's jamming avoidance response. It appears that these fish prefer to "listen" to small, whole number frequency ratios, as do humans, with the fifth and fourth being the most comfortable. But it also appears that their reflexive avoidance of potentially jamming frequencies causes them to follow at a small frequency distance. The similarity of fit of the frequencies of fish following these intervals to the absolute frequency difference, however, prevents the conclusion that, once at these ratios, it is the ratio itself and not the frequency difference that the fish use to maintain the interval. In either case, the maintenance of this interval is probably mediated by the tuberous electroreceptors which are receptive to higher frequency potential changes.

If the frequency ranges of the individual fish in a group are such that these luxuriously large intervals are not available to them, they nevertheless will maintain smaller intervals relative to the other fish. The maintenance of these smaller intervals is possibly mediated by the ampullary electroreceptors which are known to be maximally sensitive to frequencies of less than 50 Hz.

SOURCES CONSULTED

Bennett, M.V.L. 1971a. Electric Organs. In Hoar, W.S. and C.J. Randall (Eds.) Fish Physiology Vol.V. pp.354-492. Academic Press, New York and London.

_______ 1971b. Electroreception. Ibid. PP. 493-568.

Black-Cleworth, P. 1970. The role of electrical discharges in the non-reproductive social behavior of Gymnotus carapo (Gymnotidae, Pisces). Animal Behav. Mono., 3: 3-77.

Box, H.O. and Max Westby 1970. Behavior of Gymnotus carapo in a group membership experiment. Psychon. Sci. 21: 27-28.

Bullock, T.H. 1970. Species differences in effect of electroreceptor input on electric organ pacemakers and other aspects of behavior in electric fish. Brain Behav. Evol., 2: 85-118.

_______ and S. Chichibu 1965. Further aspects of sensory coding in electric fish. Proc. Nat. Acad. Sci. 54: 422-429.

_______, R. Hamstra, and H. Scheich 1972. Jamming avoidance response of high frequency electric fish. J. Comp. Physiol. 77: 1-48.

Darwin, Charles 1872. The Expression of the Emotions in Man and the Animals. John Murray Publishers. London

Dewsbury, D.A. 1966. Stimulus-produced changes in the discharge rate of an electric fish and their relation to arousal. Psychon. Sci. 16: 495-504.

Enger, P.S. and T. Szabo 1968. Effect of temperature on discharge rates of electric organs of some gymnotids. Comp. Biochem. Physiol. 27: 625-627

Frey, D.F. and M.J. Miller 1972. The establishment of dominance relationships in the blue gourami, Trichogaster trichopterus. Behavior 42: 8-61.

Heiligenberg, W. 1973. Electrolocation by the electric fish, Eigenmannia virescens. J. Comp. Physiol. 87: 137-164.

Hockett, C.F. 1960. Logical considerations in the study of communication. In Lanyon,E. and W. Tavolga, Animal Sounds and Communication. Am. Inst. Biol. Sci. Washington, D.C. pp. 392-430.

Hopkins, C.D. 1972. Sex differences in the signalling of an electric fish. Science 176: 1035-1037.

_______ 1974. Electric communication: functions in the social behavior of Eigenmannia virescens. Behavior L: 270-305.

Knudsen, E.I. 1974. Behavioral thresholds to electrical signals in high frequency electric fish. J. Comp. Physiol. 91: 333-353.

Lissmann, H.W. 1958. On the function and evolution of electric organs in fish. J. Exp. Biol. 35: 156-191.

_______ 1961. Ecological studies on gymnotids. In C.Chagas and A. Paes-de Carvalho (Eds.) Bioelectrogenesis. Elsevier, Amsterdam. pp. 215-226.

_______ and H.O. Schwassman 1965. Activity rhythm of an electric fish, Gymnorhamphichthys hypostomus. Z. Vergl. Physiol. 51: 153-171.

Marler, P. 1959. Developments in the study of animal communication. In Bell, P.R. (Ed.) Darwin's Biological Work. Cambridge Univ. Press, London. pp. 150-206.

Scheich, H. 1974. Neuronal analysis of wave form in the time domain: Midbrain units in electric fish during social behavior. Science 185: 365

Sebeok, T. 1970. Animal Communication. Indiana Univ. Press, Bloomington

Smith, W.J. 1965. Message, meaning and context in ethology. Am. Nat. 99: 405-410.

Steinbach, A.B. 1970. Diurnal movements and discharge characteristics of electric gymnotid fishes in the Rio Negro, Brazil. Biol. Bull. 138: 200-210.

Valone, J.A. 1962. Electric emissions in Gymnotus carapo and their relation to social behavior. Behavior 37: 1-14.

Watanabe, A. and K. Takeda 1966. The change of discharge frequency by a.c. stimulus in a weak electric fish. J. Exp. Biol. 40: 57-66.