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Electric Organ Discharge Patterns during Dominance Related Behavioral Displays in *Gnathonemus petersii* (Mormyridae)

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Summary. 1. The electric organ discharge (EOD) patterns seen in pairs of mormyrid fishes (*Gnathonemus petersii*) during displays related to aggression and establishment of dominance are described.

2. A new method of reliably separating the discharges of the two fish was used. In this method a fine wire was attached to the tail of one animal (Fig. 1).

3. Discharge patterns were examined at different stages during the characteristic sequence of overt behavioral events which usually occurred after an intruder was put into a tank in which another fish of the same species had been resident for 1 hour or more. The resident attacked the intruder immediately, the intruder being initially unresponsive. After a few minutes, however, the two fish entered into intense, mutual, antiparallel displays (Fig. 2). The displays occurred repeatedly during a period of 0.5–30 min. This period ended suddenly with one of the fish clearly dominant as shown by one-sided attacks and avoiding behavior by the submissive fish.

4. All attacks were accompanied by a smooth acceleration to a high discharge rate which was usually terminated abruptly (Fig. 3). Anti-parallel behavior was accompanied by similar accelerations in both fish. Interdischarge intervals during these high rates changed discretely between those of about 15 msec and those of about 9 msec (Figs. 3–9). Initial attacks before the antiparallel period usually produced no effect or a brief acceleration in the discharges of the attacked animal. Similar attacks when dominance was well established caused a slowing of the discharge rate of the attacked fish.

5. The echo response in which one fish responds to the EOD of another with a discharge of its own at a latency between 11 and 14 msec was seen at all stages of the encounter. This latency corresponded rather exactly to the gap in the interval histogram between the shorter intervals around 9 msec and the longer ones around 15 (Figs. 11, 12). This correspondence led to a degree of avoidance of near synchronous discharges during those attacks which did not cause either slowing or accelerations in the attacked animal (Fig. 11). A degree of synchrony avoidance also occurred during the mutually high discharge rates of antiparallel behavior. This resulted from the phase locking of the two discharge trains which was often present at these times and which was probably due to the echo responses (Fig. 13).

6. Several features of the individual discharge trains and of their interaction were examined during the period of antiparallel activity. This was done in order

to see if some critical parameter could be detected which would allow one to predict the winner of the encounter and which might be used as a signal by the fish themselves. No single feature among those we examined was clearly and consistently related to the outcome of the encounter.

Introduction

Evidence for the use of electric organ discharges in communication among electric fish comes primarily from the effects which artificial electrical stimuli have on electric organ discharge patterns and overt behavior (Fessard and Szabo, 1961; Harder *et al.*, 1967; Bullock, 1970a; Moller, 1970). There have been only a few detailed studies of the actual discharge patterns seen when fish engage in socially significant behavior (Black-Cleworth, 1970; Bauer, 1972; Bullock, 1970a; Hopkins, 1972; Möhres, 1957), and only the brief reports of Bauer and Möhres are concerned with mormyrids. Studies of this type are necessary to know what signals are used by the animal and the behavioral circumstances under which they occur.

The lack of studies in this area has been partly due to the technical problem of reliably separating and recording the discharges of two fish which are free to swim about each other and interact socially. We have obtained at least a partial solution to the problem by attaching a fine wire to the body of one of the fish. The wire does not seem to interfere with the fish's behavior and makes possible laboratory study of discharge patterns during some social interactions.

For this study we sought a social behavior which could be readily elicited in the laboratory and which appeared important in the life of the animal. We found such social behavior in the characteristic sequence of events which frequently occurs in the species we have studied (*Gnathonemus petersii*) when an intruder is put into a tank in which another fish of the same species is already residing. This behavior sequence is probably related to establishment of dominance.

This study relies on point process statistics such as the interval histogram and cross-interval histograms to describe both the discharge patterns of single fish and the temporal relationships between the discharges of two behaviorally interacting fish. Such statistics are well suited to the brief all-or-none electric organ discharges of mormyrids with their highly variable inter-discharge intervals. These statistics allow one to determine the time course of the influence of one fish's discharges on those of a second fish. They thus reveal the presence of interactions like the echo response (Russell *et al.*, 1974), which could not be seen with other methods such as comparison of mean frequencies.

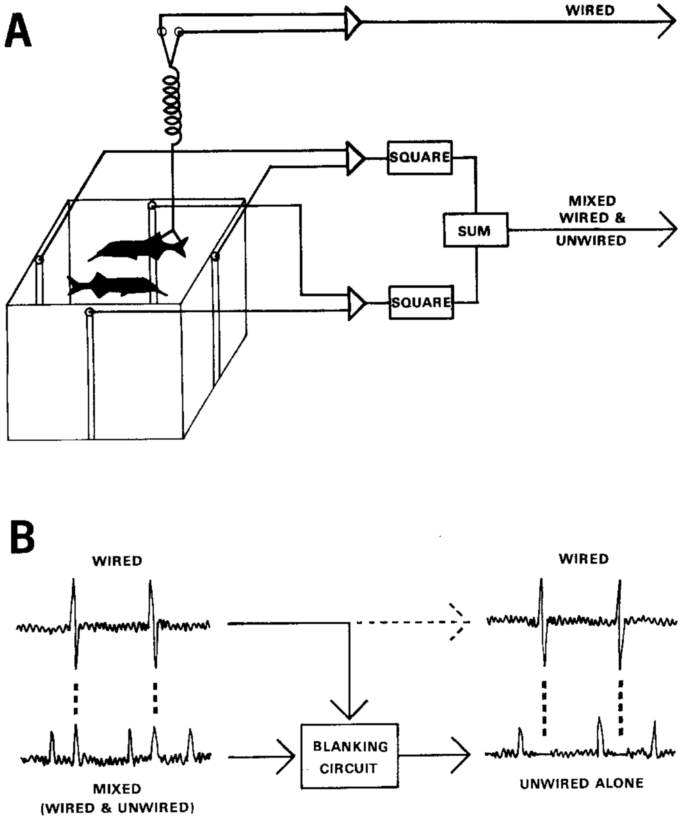

Fig. 1. A Methods of recording. B Method of removing wired fish's discharges from the mixed signal

Methods

Twenty-three different fish of the mormyrid species *Gnathonemus petersii* were used. All the fish were between 14 and 18 cm long as measured between mouth and tip of tail. Individuals were identified by making small notches on the dorsal and ventral fins. The home aquaria of the fish as well as the observation chamber were kept at temperatures between 25° C and 27° C.

The observation chamber was a cage made of plastic screen 40 × 25 × 30 cm, open at the top. It was supported in the middle of a large aquarium with the upper edge of the chamber protruding a few inches above the water surface. A tungsten wire electrode was placed just outside each of the four sides as shown in Fig. 1A.

To make our observations, single fish were taken from one of three home aquaria and anesthetized with MS-222 (ethyl m-aminobenzoate methane sulfonic acid), 1:10000. One wire of a double strand of fine, teflon-insulated, stainless steel wire (47 ga) was attached to the dorsal fin and the other wire to the tail fin. The fish were then placed in the observation chamber and allowed to recover from the anaesthetic. After an hour's wait, a second fish was introduced directly into the observation chamber from one of the home aquaria. Observations were made in a semi-darkened room. The pair remained in the chamber for a period of 15 to 45 min before the unwired animal was removed. Additional unwired fish were introduced in succession in the same way. As many as six different fish were run against the same wired animal.

The electric organ discharge of the wired fish was 1.5–3 V in amplitude as recorded with the fine wires. It was led directly to one channel of an FM tape recorder. A signal combining the discharges of both fish was recorded as shown in Fig. 1A. The potential differences across the longitudinal and transverse axes of the chamber were first squared and then summed together. This is a simplification of a method used by Black-Cleworth (1970) to minimize variations in amplitude as the fish swim about the chamber. The summed signal was recorded on a second channel of the tape recorder. Finally, a voice description of the ongoing behavior was recorded on a third channel.

Some observations were also made on three mormyrid fish whose species were unknown. Two of these lacked chin appendages and were from a group commonly referred to by tropical fish dealers as "round noses" or "baby whales". They were keyed to the genus *Marcusenius* using the key of Bennett (1971). The other fish had both jaws elongated and was probably of the genus *Gnathonemus*.

Analysis and Display

The discharges of the unwired fish were obtained in isolation by electronically removing the wired fish's discharges from the mixed signal (Fig. 1B). This was done by shunting the mixed signal to ground for 0.7 msec at the onset of the wired fish's discharge. All signals were removed during this 0.7 msec including any discharges of the unwired fish which might be occurring during that time. This resulted in a lack of near synchronous discharges in the two fish which is an artefact of our technique. Because of variations in trigger level the effect may extend between minus 0.5 msec and plus 1 msec with respect to zero delay.

We used electronically generated interval diagrams such as those in Fig. 3 to examine the data. These diagrams were made by initiating an ascending or descending ramp with an EOD (electric organ discharge) and brightening the oscilloscope beam just before the next EOD reset the ramp. The vertical distance of the brightened spot from the center is therefore determined by the duration of the interdischarge interval. We displayed the intervals of one fish in the upward direction and the intervals of the other fish in the downward direction with time on the abscissa (as in Figs. 3–8). In order to correlate discharge patterns with overt behavior such graphs were examined on a storage oscilloscope while listening to the voice record. The graphs were also photographed on moving film for more detailed analyses.

From selected sections of the recordings, the times of the EOD's were digitized and stored on digital magnetic tape for subsequent statistical analysis by the computer. These sections were between one and four minutes in duration and contained between 350 and 6000 discharges for each fish. Sections were taken from the different periods of the interaction sequence. More selective editing was done by playing the tape back at one-quarter the speed of the original recording and watching the interval diagram display on the storage oscilloscope. This made it possible to compute statistics for only those events occurring during particular discharge patterns, such as the accelerations of one fish or the mutual accelerations during agonistic displays.

Interval histograms were commonly used for examining the discharge trains of single fish and cross interval histograms for examining the temporal relationships between the discharges of two fish. The interval histogram is a plot of the distribution of interdischarge intervals of a single fish. The cross interval histogram is a plot of the times between each discharge of Fish A and the next following of Fish B, in the direction to the right of the reference point. In the other direction, to the left, it is a plot of the times between a discharge of Fish A and the *preceeding* discharge of Fish B. In this case the discharges of Fish A are termed the "reference" train, while those of Fish B are termed the "dependent" train. On occasion auto-correlograms were also used. The auto-correlogram estimates the probability of a single fish discharging as a function of time after one of its own discharges. The cross-correlogram estimates the probability of Fish B discharging as a function of time before or after Fish A. These statistics are described in detail elsewhere (Perkel *et al.*, I, II, 1967; Moore *et al.*, 1970).

Results

Overt Behavior Following Entry of a New Fish

We use the term "overt behavior" to refer to the visible, non-electric behavior of the fish. The following was the most common sequence of overt behavior; it was seen in 11 of the 21 pairs of *Gnathonemus petersii* studied. Upon introduction into the chamber with the resident fish, the intruder began swimming around the perimeter, probing the corners with its chin appendage. At the same time, the wired or resident fish focused its behavior toward the newcomer, following it about and attacking it every few seconds. By an "attack" is meant a suddenly initiated and rapid swim toward the body of the other fish, usually resulting in physical contact. On occasion, this was accompanied by biting as judged by lesions on the side of the attacked animal. After one-half to two minutes, the introduced fish began interacting with the resident fish either by entering into antiparallel displays or by initiating attacks, in which case antiparallel displays began slightly later. Antiparallel displays were a prominent component of the behavioral interactions observed under these conditions. During antiparallel displays, fish remained close together with the head of one near the tail of the other, often with the chin appendage curled over toward the other's tail, as in Fig. 2. The most striking feature was the rapid, vigorous, lateral movements of the head and tail, the two fish moving in an apparently coordinated manner.

In many cases the antiparallel bout was initiated by an attack directed toward the side of one fish. The attacked animal would then fold over against the side of the attacker so as to achieve the antiparallel position, and the mutual display followed. Another manner of initiating the display was seen in three of the most intense and long-lasting interactions. In these pairs the two fish swam around on opposite

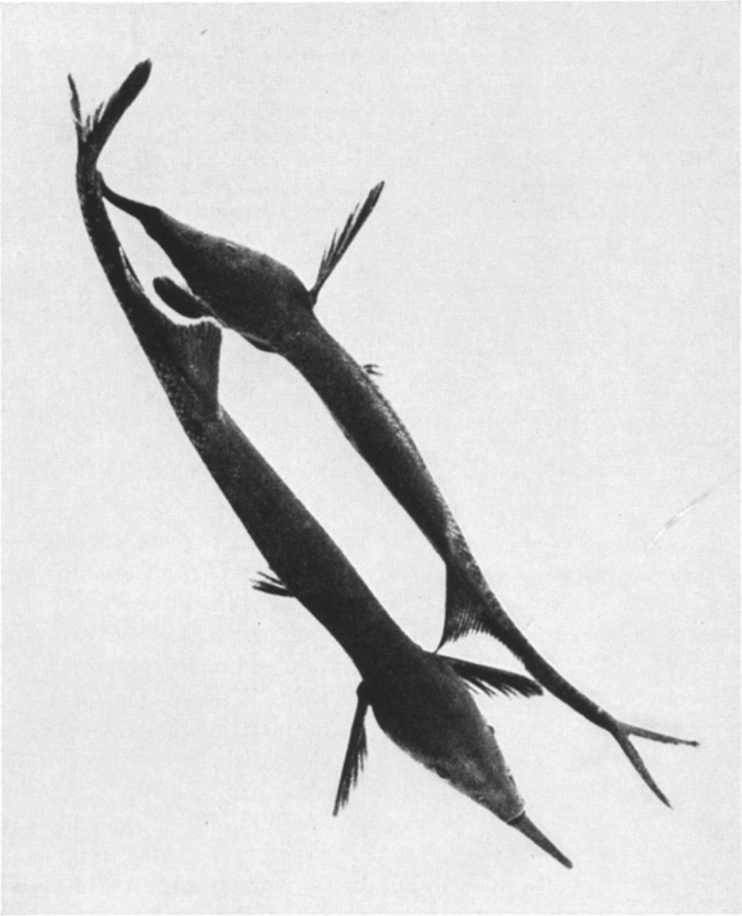

Fig. 2. Dorsal view of two fish engaged in antiparallel display

sides of a circle with a radius of about 20 cm. In doing this, each fish apparently avoided an attack from the rear. Every few seconds the fish interrupted the circling by swimming rapidly and directly toward each other. Sometimes they would slip immediately into antiparallel behavior, more commonly they would first engage briefly in repetitive head butting or apparent "fencing" with the chin appendage before sliding into the antiparallel display. In the fencing behavior the fish would repeatedly lock and unlock their chin appendages.

Attacks by both fish which did not lead into antiparallel displays occurred during the early part of the display period. The shortest period of antiparallel displays involved only 4 bouts in 15 sec, the longest contained more than 197 bouts in 25 min.

In every interaction, the period of antiparallel activity stopped abruptly. One of the fish continued to attack but the other no longer went into parallel behavior, and no longer attacked. If circling was present, it stopped at the same time. The first few attacks after the antiparallel period often elicited very little behavioral response from the attacked animal. Within a few minutes, however, the attacked fish showed signs of avoiding the other animal either by vigorous attempts to escape from the chamber or by repeatedly changing its position in the chamber so as to remain on the opposite side from its attacker. In 4 of the 11 pairs showing antiparallel behavior, the attacked fish ended up in a vertical posture on one corner, hanging with its tail down and its mouth at the surface of the water. At these times the attacking animal would frequently swim up parallel to it and butt against it with sideways thrusts of the head. The single direction of the attacks and the avoiding behavior following the antiparallel displays indicated to us that a dominance relation had been at least temporarily established, with one fish the winner and the other the loser.

The remainder of the 21 pairs showed no antiparallel displays. In three of these pairs the fish showed no clear behavioral interaction for 25–40 minutes, behaving almost independently of each other. The EOD patterns of these pairs were not analyzed further. In five of the pairs showing no antiparallel behavior the initial attacks by the resident fish continued for twenty or more minutes until the intruder was removed. During these encounters the attacked fish at first showed little reaction, but as the attacks continued it started to exhibit the avoiding behavior describe above. Finally, in two of the fish pairs showing no antiparallel behavior a much larger intruder immediately began attacking the resident and continued to do so until it was removed at the end of the session. The residents eventually showed avoiding behavior. In summary, there were three types of encounters: mutual struggles for dominance with antiparallel behavior (11/21), one sided routs with nearly all attacks by one fish without antiparallel behavior (7/21), and encounters showing minimal interaction (3/21). Table I summarizes some of the overt behavior information on the 18 pairs which showed intense interaction and which established dominance relationships.

Relative size seemed to be the most important determinant of the outcome of the encounter. The larger fish was the winner in 16 of the 18 pairs in which a clear dominance relationship was established by the end of the session. Prior residency in the chamber did not seem to be a factor since only one-half, 9/18, of the resident animals became dominant. That one-half of the resident or wired fish did become dominant

Table 1. Summary of fish pairs in which intense interaction occurred. The resident fish of each pair is placed first. The sequence in which different intruders were run against the same resident is as shown here. D indicates which fish was dominant. Only in pairs 13 and 17 did the smaller fish end up dominant

Pair	1		2		3		4		5		6	
Fish	1	2	1	3	1	4	5	6	5	7	8	9
Length (mm)	160	144	160	172	160	130	142	136	142	168	154	162
Antiparallel ?	No		Yes		No		Yes		No		Yes	
No. of ap bouts			29				63				12	
Dominance	D			D	D		D			D		D

Pair	7		8		9		10		11		12	
Fish	8	5	8	3	8	7	10	11	10	3	11	12
Length (mm)	154	142	154	172	154	168	148	137	148	172	137	145
Antiparallel ?	Yes		Yes		Yes		Yes		No		Yes	
No. of ap bouts	7		5		4		197				12	
Dominance	D			D		D	D			D		D

Pair	13		14		15		16		17		18	
Fish	13	14	13	15	13	16	13	12	13	17	13	18
Length (mm)	158	172	158	165	158	141	158	145	158	147	158	145
Antiparallel ?	No		Yes		No		Yes		Yes		No	
No. of ap bouts			10				4		54			
Dominance	D			D	D		D			D	D	

suggests that the wire did not markedly disturb the behavior. The importance of size and the lack of importance of prior residency in determining dominance has been established in another species of fish (Frey and Miller, 1972). Fish close together in size were more likely to engage in antiparallel behavior. The average difference in length between the two animals was smaller in the pairs which engaged in antiparallel displays than in those which did not (11 mm vs 20 mm). This difference was significant at the 0.001 level ($t(16)=4.24$). In our small sample there was not a clear relation between the number of bouts and the difference in length. Comparison of pairs 7 and 10, for example, shows a similar length difference in both but almost 30 times as many bouts in pair 10. An important factor which was not controlled in our studies was the sex of the animal. We know of no way to determine this in *G. petersii* without sacrificing the fish.

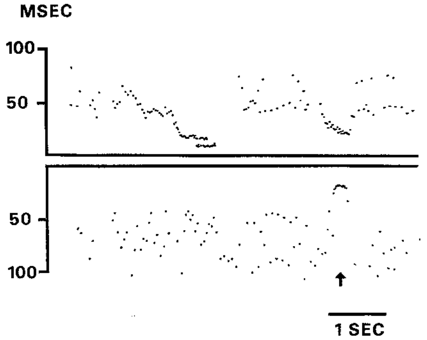

Fig. 3. Interval diagrams during two attacks in the period preceeding antiparallel activity. Interdischarge intervals of the attacking fish are shown above the center lines while those of the other fish are shown below. The first attack includes some intervals of 9 msec and has no obvious effect on the attacked animal's discharges. The second attack has no such intervals but evokes a brief acceleration (indicated by arrow). In this and the following pairs of interval diagrams, the point at which the first dot occurs should be taken as the start of the record. Long intervals which are off scale are not shown in these diagrams

Electric Organ Discharge Patterns during Different Stages of the Overt Behavioral Sequence

The resident fish stopped discharging for 2 to 6 sec immediately after the entry of the intruder. The attacks which followed and indeed all attacks at all stages of the behavior sequence were accompanied by an acceleration to a high discharge rate in the attacking fish (Fig. 3). Similar accelerations and high discharge rates occurred in both fish during antiparallel displays (Figs. 4, 5, 6). The high discharge rate during attacks lasted only 0.5–1.5 sec, whereas during antiparallel bouts it lasted longer, 1–4 sec. The quick movements of the head during the butting behavior described above were accompanied by brief (0.1–0.3 sec) pauses followed by rapid accelerations to the same high rate seen during attacks and antiparallel behavior. An example of such a brief pause followed by acceleration is indicated with an arrow in the lower half of Fig. 4. The episodes of chin appendage interlocking were also accompanied by similar brief pauses and re-accelerations.

The interdischarge intervals during attacks and antiparallel displays were very similar among different fish. A particularly striking feature was the discrete change in interval duration from intervals of about 15 msec to intervals of about 9 msec. Examples of these discrete changes can be seen in the interval diagrams of Figs. 3–6, 8, and 9. Interval histograms (Fig. 7) show the almost complete lack of overlap between these two interval sizes. Among different fish, modal values for the first

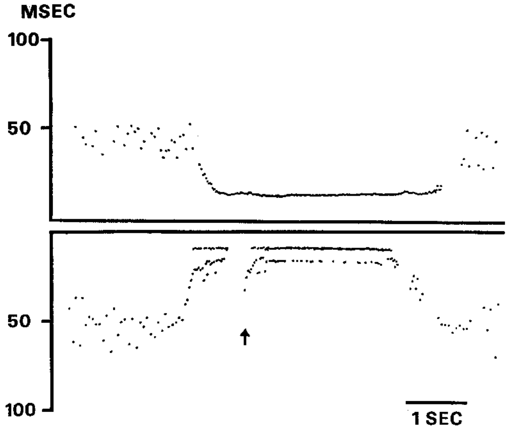

Fig. 4. Interval diagrams during an antiparallel bout. The fish whose intervals are plotted in the lower half shows both 9 and 16 msec intervals while the fish whose intervals are plotted in the upper half shows only 16 msec ones. The arrow points to a brief slowing, followed by a return to the same high frequency that preceeded slowing. A quick head butt directed toward the other animal accompanied this discharge pattern

peak were between 9 and 10 msec, for the second peak between 14 and 17 msec. The narrowness of the two peaks in the interval histograms shows the low variability in interval size within each of these classes. This is also seen in the interval diagrams when a fish discharges repeatedly at one interval or the other (Fig. 4).

The discrete changes in interdischarge interval were seen in ten of the fourteen fish which engaged in attacks or antiparallel behavior. Not all of these fish showed the same proportion of discharges at ~9 msec intervals. This was determined by comparing the amplitudes of the two early peaks. Some discharged at the shorter 9 msec interval only occasionally and only during antiparallel displays, others also did so during the attacks preceding and following the displays. In all cases the number of shorter intervals relative to the number of longer, 15 msec intervals, was greater during antiparallel displays than before or after. These features are illustrated in the series of interval histograms of Fig. 7. The interdischarge intervals of the resident member of an interacting pair are shown here at different stages of the behavioral sequence. The first histogram (A) is based on a recording taken before introducing the intruder. The second (B) is based on the period between introducing the intruder and the first antiparallel display. Accelerations during the attacks are reflected in the peaks at 9 and 15 msec. The next two histograms

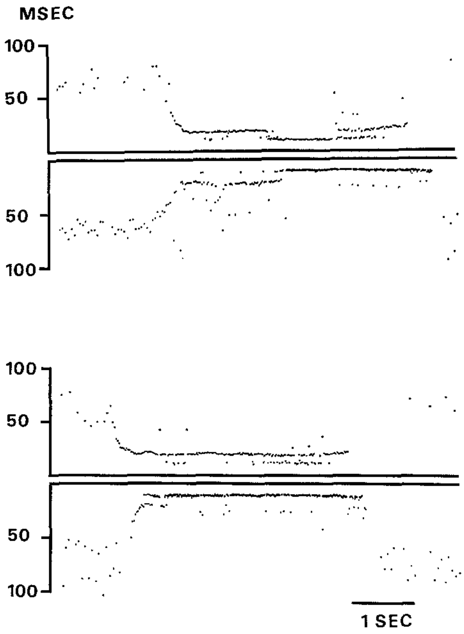

Fig. 5. Interval diagrams during two successive antiparallel bouts. The lower half is a continuation of the upper. 9 and 16 msec intervals are seen in both fish

(C and D) are from the period during antiparallel displays. The larger first peaks reflect the increased proportion of 9 msec intervals. Finally, the last histogram (E) is taken after the last display. The large peak at 15 msec and the small one at 9 reflect the continued presence of attacks but a decreased number of short intervals during these attacks.

Discrete changes in interval size were not seen in the remaining 4 fish out of the 14 that showed attack or antiparallel behavior; the discharges of one such fish are shown in the upper half of Fig. 4. Two of these fish participated in several encounters involving long periods of antiparallel displays with fish which did show the discrete changes in interval size. Each of the two fish was sometimes a winner and sometimes a loser. This suggests that the absence of short (9 msec) intervals was not a result of less intense behavioral interaction and also that the presence of such intervals in one fish did not guarantee its dominance.

High discharge rates and discrete changes in interval size during attacks and antiparallel behavior were also described by Bauer (1972) in a report on interactions between *Gnathonemus petersii* and *Mormyrus rume*. However, he emphasized such regular attack pattens as that shown

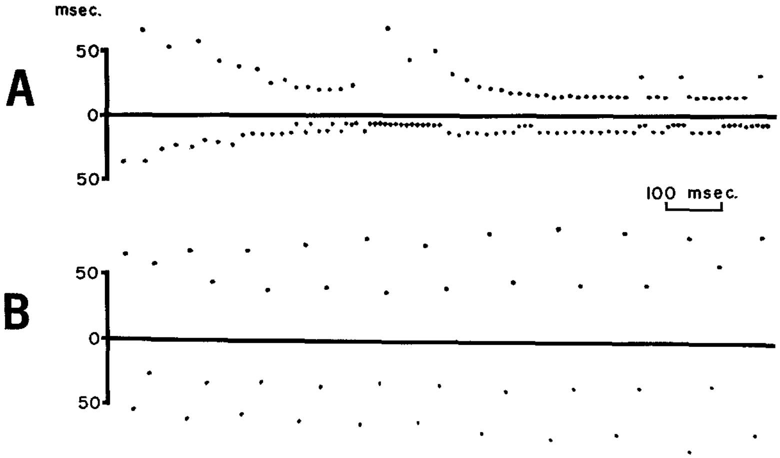

Fig. 6. Interval diagrams with an expanded time scale to show succession of intervals. A Initiation of antiparallel bout. The upper fish did not discharge at intervals shorter than 16 msec, while the lower one discharged at both 9 and 16 msec intervals. B Regular alternation of interval size and echoing. This graph is based on the same pair of fish as the upper half. It was taken immediately after the antiparallel bout initiated in A. The lower fish is discharging at intervals which alternate between those of about 30 and those of about 60 msec. Most of the lower fish's discharges are followed about 12 msec later by a discharge of the upper. The result is a reproduction of the lower fish's pattern. Regular alternation was common in one or both fish following antiparallel bouts but the amount of echoing seen here was rare

in Fig. 8, in which an initial regular alternation between intervals of about 9 and 15 msec is followed by a continuous sequence of intervals at 9 msec. Our results indicate such patterns may not be typical. While 2 fish occasionally showed patterns like that of Fig. 8, in most cases the discrete change in interval size occurred irregularly, and in 4 fish they did not occur at all.

The effect of an attack on the discharge pattern of the attacked animal was different at different stages of the behavior sequence. Pauses, brief accelerations and complete lack of effect were all seen. Pauses were most common during the last stage of the sequence when the attacked animal showed avoidance behavior. The pause or slowing in the discharge rate of the attacked animal occurred during or immediately after the attack. Examples of such pauses are seen in Figs. 8 and 9. Pauses were common at this stage in all 18 pairs in which dominance was established. It sometimes appeared as if the dominant fish's attacks were in response to brief accelerations by the submissive fish as in the last two attacks of Fig. 9A.

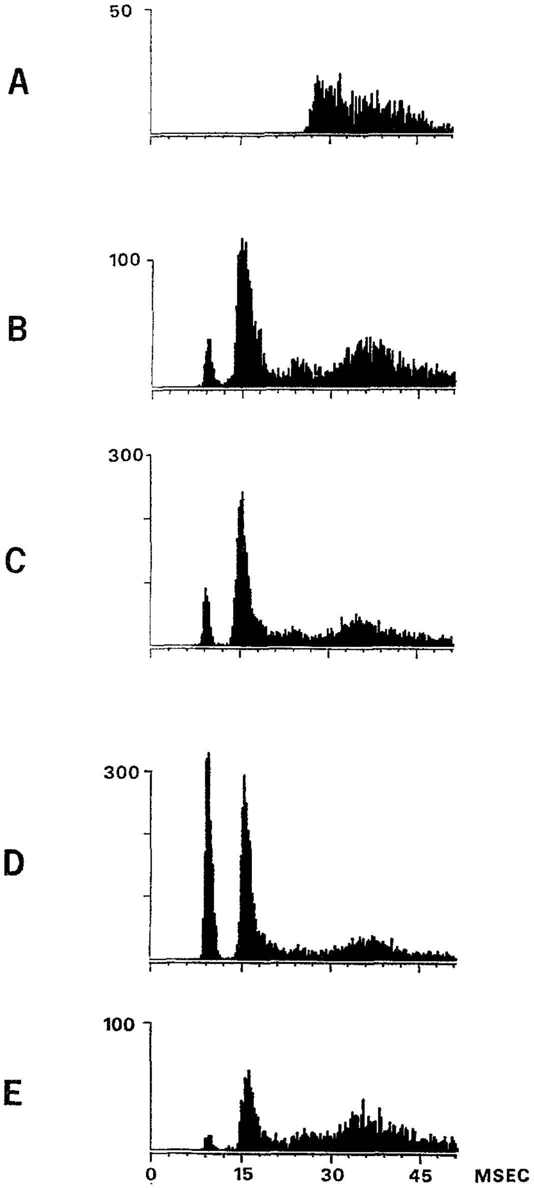

Fig. 7. Histograms of interdischarge intervals of one fish taken during different stages of the behavioral sequence. A Prior to entry of the intruder. N (total number of intervals) = 1094. B Between entry of intruder and first antiparallel bout. $N = 3677$. C Initial period of antiparallel activity. $N = 5633$. D Half-way through period of antiparallel bout. $N = 2422$. E Period immediately following last antiparallel bout. $N = 2442$. Bin width is 0.3 msec in these histograms. Scale of the ordinate indicates number of events per bin

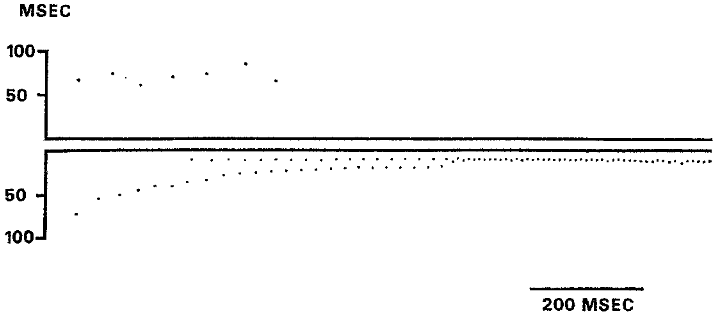

Fig. 8. Orderly discharge pattern in one fish during its attack (lower interval diagram). The attack evokes a pause in the discharges of the other fish (upper interval diagram). Regular alternation in interval size is followed by a steady discharge at 9 msec intervals (lower interval diagram)

The mean rate of the submissive fish was often very low during the period after the last antiparallel bout. This was also true in the later part of those encounters which did not include antiparallel behavior. The mean rate of the dominant fish during the last 1–2 minutes of recording was greater than that of the submissive fish in 15 out of the 18 pairs in which a dominance relation was established. The average of the mean rate in the 18 dominant fish was 21.8 (Range 14–32) while that of the submissive fish was 13.6 (Range 3–29).

Pauses in the attacked animal's discharge pattern were rare both during the first attacks by the resident following entry of the intruder and immediately after the antiparallel period. At these times, the attack had no effect on the discharge pattern. As described above, it was also at these times that the attacks had little influence on the overt behavior of the attacked animal. Finally, discharge accelerations by the attacker were sometimes met with brief accelerations by the attacked animal. This occurred both prior to and during the period of antiparallel displays. Such an acceleration is indicated by an arrow at the right of Fig. 3. Two encounters were described above in which larger intruders apparently became dominant almost immediately without any antiparallel behavior. In each of these pairs there were a few occasions early in the session when both fish accelerated to a high rate briefly and simultaneously. In all these cases the behavioral voice record simply referred to an attack by one of the fish and no antiparallel behavior was mentioned. Unfortunately, a voice record of behavior does not permit a re-examination of the overt behavior to see if hitherto unnoticed events were occurring during particular patterns of electric organ discharges.

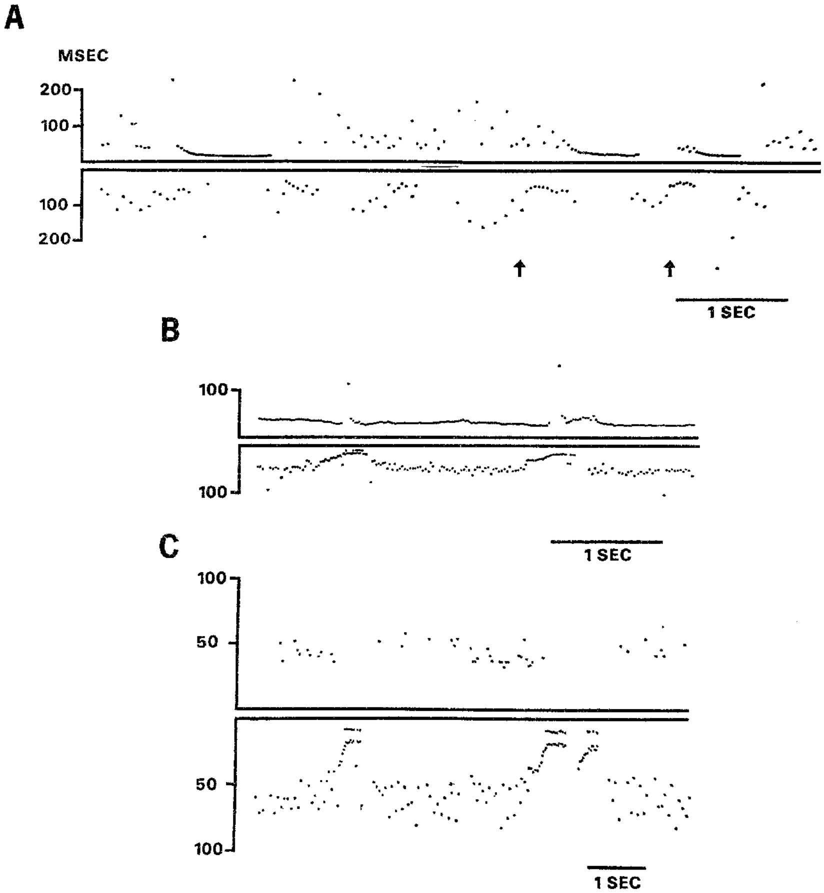

Fig. 9. Attack accelerations in one fish causing a slowing in the discharge rate of the other. A, B, and C were taken from 3 different pairs of fish during the period after antiparallel activity. At this time dominance has been established and all attacks are by the dominant fish. In each case the attack causes a pause or slowing in the submissive fish. In A there are three attacks by the dominant (upper) fish. The last two attacks are preceeded by slight accelerations (to about 30/sec) in the discharge rate of the submissive (lower) fish. These slight accelerations are indicated by arrows. In B there are two attacks by the dominant (lower) fish. In C there are three attacks by the dominant (lower) fish

Occurrence of the Echo Response at Different Stages of the Behavioral Sequence

"Echo response" is the term we have chosen to refer to the high probability with which the discharge of one fish follows that of another with a 10–14 msec delay. This response was the subject of our previous

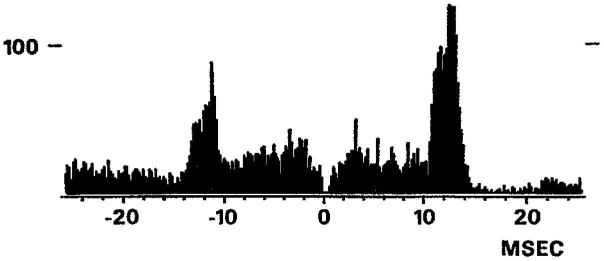

Fig. 10. Cross interval histogram between discharges of two fish. Taken from a period of antiparallel activity, includes events between bouts as well as those within them. Here and in subsequent cross interval histograms and cross-correlograms bins within + 1 msec and —0.5 msec of the zero delay point contains no events or a reduced number of events. This is an artefact of our method of separating the discharges of the two fish (see Methods). 0.2 msec bins, reference train 5254 events, dependent trains 3515

paper (Russell *et al.*, 1974). In the present study the echo reponse was seen at all stages of the behavioral sequence. On occasion its effect could be noticed in the interval diagrams as in Fig. 6B, where its occurrence causes the discharge pattern of one fish to duplicate, with a brief time delay, the regularly alternating discharge of the other. The echo response was seen most clearly, however, in cross interval histograms such as Fig. 10. In making the cross interval histograms the wired fish's discharges were usually used as the reference train. In such a case the peak to the right indicates echoing of the wired fish's discharge by the unwired fish; the peak to the left indicates echoing in the opposite direction. The peaks were often markedly different in size (Fig. 10), showing that one fish sometimes echoed more than the other. This asymmetry is discussed further below.

One would expect that the electrolocation system of a fish would be confused by synchronous or nearly synchronous discharges of other fish. It appears that under some circumstances this is avoided by a combination of the echo response and the limited values which inter-discharge intervals can assume. This is seen particularly clearly when one fish attacks another without causing an acceleration or a pause in the other fish. In two pairs this occurred over a sufficient period for analysis to be restricted to events occurring in both fish during the high discharge rate of an attacking animal. At these times a major proportion of the attacked fish's discharges were echo responses. The upper half of Fig. 11 A is an interval histogram which shows the two interval sizes of the attacking fish during the attack. It shows a gap at 11 to 14 msec between these two interval sizes. The lower half is a cross-correlogram from the

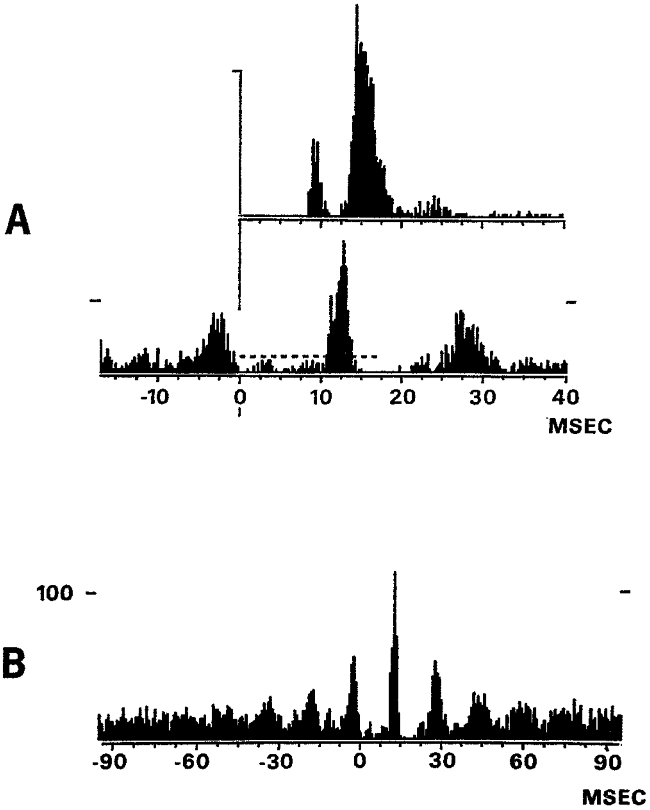

Fig. 11. Influence of discrete interval sizes and echo response on avoidance of synchrony. Selective analysis of events occurring during attacks of one fish prior to a period of antiparallel activity. A Comparison of the interval histogram of an attacking fish with the cross-correlogram from attacking to attacked animal, interval histogram above, cross interval histogram below. The dotted line indicates the number of events/bin which would be expected if the two trains were independent. This is computed with the algorithm $u_B \times \Delta\tau \times N_A$ where u_B = mean rate of dependent train, $\Delta\tau$ = bin width, and N_A = number of events in reference train (Perkel *et al.*, II, 1967). 0.25 msec bins. $N = 970$ for interval histograms and for reference train of cross interval histogram, $N = 376$ for dependent train of cross interval histogram. Scale mark on ordinate of interval histogram is 50 events/bin, that on the cross-correlogram is at 25. B Cross-correlogram based on the same trains as A, but with larger time bins. It shows the periodicity caused by the high frequency regular discharge of the attacking fish as well as the reduced number of events between 0 and 10 msec. Major peak at 12 msec is echo of attacked fish. Other prominent peaks are secondary and due to regularity of discharge in the attacker. Note lack of echo response in reverse direction, i.e. lack of echoing by the attacking animal. 0.75 msec bins

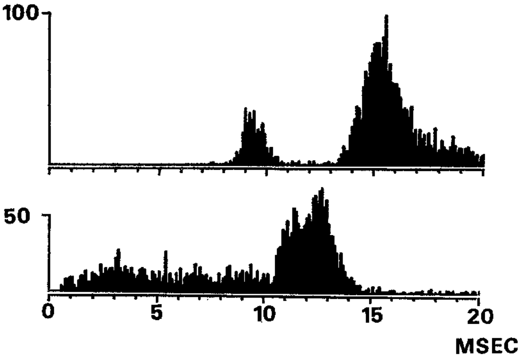

Fig. 12. Comparison of interval histogram of one fish (above) and cross interval histogram between this fish's discharges and the discharges of the other fish (below). Includes all events during a period of antiparallel activity, i.e. events both within and between antiparallel bouts. 0.1 msec bins. 5254 events in interval histogram and reference train of cross interval histograms, 3515 events in dependent train

discharges of the attacking fish to those of the attacked animal. It indicates a prominent echo response of the attacked animal between 11 and 14 msec. In fact, most discharges of the attacked fish occurred between 11 and 14 msec after a discharge of the attacking animal, while the attacker himself rarely discharged during this time. The result was partial avoidance of synchrony, suggesting a possible function for the echo and the lack of interdischarge intervals between 11 and 13 msec. A reduced number of nearly synchronous discharges is indicated in the cross-correlogram by the small number of events between 0 and 10 msec compared to the average, or expected counts/bin, shown by the dotted line. The peaks at —2 and + 28 are secondary effects due to the echo response at 13 msec delay in the attacked animal and the regular 15 msec intervals between discharges of the attacking fish (Moore *et al.*, 1970). The regularity of these secondary peaks is shown more clearly in the cross-correlogram with a compressed time scale in Fig. 11 B.

The temporal correspondence between the latency of the echo response and the gap in the interval histogram between the two sizes of short intervals is shown dramatically in Fig. 12. The figure is based on a large number of EOD's recorded during a period of antiparallel displays. The times between bouts as well as the bouts themselves were included in the analysis. Unlike Fig. 11, however, Fig. 12 is not directly relevent to the question of the avoidance of synchrony. In this case most of the echoing occurred at a different time (between antiparallel bouts) than did the short intervals and their discrete size changes (during antiparallel

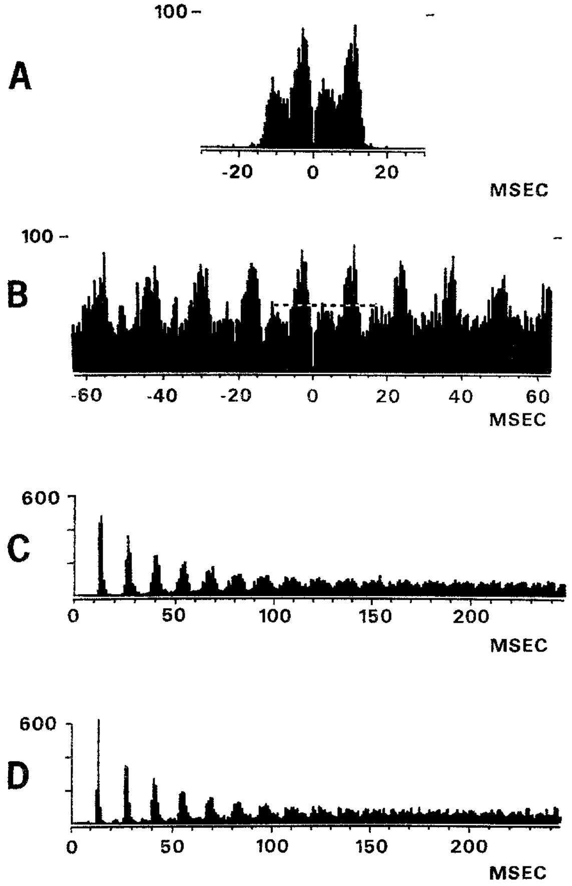

Fig. 13. Phase locking during antiparallel bouts. Only events occurring while both fish discharged at high rates (~70/sec) were included. A Cross interval histogram. B Cross correlogram. Dotted line indicates expected count/bin. C Auto-correlogram of reference train. D Auto-correlogram of dependent train. Bins in A, B: 0.5 msec; in C, D: 1 msec. N for reference train = 1476, for dependent = 1288

bouts). It does, however, suggest a relationship between the two phenomena.

Selective analysis showed that the echo response was much less prominent when *both* fish discharged at a high rate during antiparallel displays. The influence of the echo response could still be seen, however, in the relative timing of the two trains of discharges. This was clearest when both fish were discharging predominantly at the 14 msec interval with a minimum of 9 msec intervals (Fig. 13). Only those events occurring during the time when both fish were discharging at a high rate were included. The auto-correlograms show the high regularity with which both fish were discharging at 14 msec intervals (Fig. 13C and D). The two large peaks in the cross-interval histogram of Fig. 13A indicate that the discharges of one fish tended to occur about 3 msec before and 11 msec after discharges of the other. The phase locking is also seen in the cross-correlogram of Fig. 13B.

To make a finer analysis, individual antiparallel bouts were examined in one pair of fish with cross-correlograms made by hand from film. In some bouts there was no temporal correlation at all between the two discharge trains while in others the phase locking was clear. In some of the latter bouts the wired fish led the unwired by a few milliseconds, in other bouts the phase relation was reversed. The inclusion of a few bouts with a reversed phase relation explains the smaller peaks in Fig. 13A at −11 msec and +3 msec.

It is unlikely that the phase locking can be explained on the basis of two independent but highly regular trains of similar frequency. First, when the phase relationship was present it was always the same. During phase locking one fish tended to discharge from 5 to 2 msec before and from 9 to 12 msec after the discharge of the other. The phenomenon was seen in 9 of the 11 sections which were selectively analysed in 4 pairs of fish, each section based on 900 to 3000 discharges of each fish. Second, the autocorrelograms of Fig. 13C and D indicate that while the discharge patterns are highly regular, there is still too much variability for a consistent phase relationship to be maintained for a long time by chance alone. They indicate that after 10–15 discharges a particular phase relation would disappear if the trains were completely independent. It therefore appears necessary to postulate an influence of one fish's discharge on the time of discharge of the other during antiparallel bouts.

There is a problem of timing, however, in tracing this influence to the echo response. The 2nd peak to the right in the cross-interval histogram of Fig. 13A begins at about 8 msec. 8 msec is 2 msec earlier than the shortest latency at which an echo has been seen in other circumstances, i.e. with artificial electrical stimuli or when the two fish are discharging more slowly (Russell *et al.*, 1974). One possibility is that this peak does not represent an echo response by the fish whose discharges are the dependent train here; instead it may represent a longer latency echo response in the opposite direction, i.e. an echo response of the reference fish at a latency of 15 to 20 msec. Such long and variable latencies were noted in the previous paper when the artificial stimulus was given at the shortest possible delay with respect to the fish's own electric organ discharge. The shortest possible delay with which an echo could be evoked was found to depend critically on the existing discharge rate of the fish. Unfortunately, in the conditions of the artificial stimulation experiments isolated fish never discharged at 15 msec intervals spontaneously. Therefore, we could not test for an echo response to artificial stimuli in the presence of such high background rates. Nevertheless, it seems reasonable to suggest that the phase locking is caused by the influence on discharge probability corresponding to the echo response.

To the extent that echoing or phase locking was present, synchrony of discharges was, of course, avoided. The importance of this should not be exaggerated, however. Not all pairs showed phase locking, and it was not present in all the bouts of those which did. The relatively small effect on synchronous activity produced by the amount of phase locking which was present can be seen in Fig. 13B. Ignoring the bin with zero events, which is an artefact of our separation technique, one can see that the number of events in bins near the zero delay point is below the average count/bin (indicated by the dotted line), i.e. below what would be expected if the two trains were independent of each other.

Electric Organ Discharge Patterns and the Dominance Relationship

One can distinguish two phases of dominance relationships, a brief initial one of status determination and a longer period in which status is maintained (Frey and Miller, 1972). Both Frey and Miller's study on blue gouramis and ours on mormyrids were mainly concerned with the initial phase of determination. Frey and Miller examined the influence of size, prior residency and prior experience on the agonistic behaviors during dominance determination and on the final outcome of the encounter. They also examined the agonistic behaviors to see if some feature or combination of features of the behavior allowed them to predict the outcome, i.e. the winner. In our study we have examined in detail only the latter problem of predicting the outcome from behavior during the display and restricted ourselves further to electric organ discharge behavior. Our question was whether there were any features of the electric organ discharge pattern during antiparallel behavior which allowed one to predict the outcome of the encounter. We examined a variety of different aspects of the discharge pattern but the final result was negative. No single feature among those we studied allowed one to predict the outcome. The different analyses which we made are described briefly below.

The first analysis was based on interval diagrams of the entire period of antiparallel behavior for each pair (portions of which are shown in Figs. 4–6). We first counted the number of times each fish accelerated from its background rate of 20 to 30/sec down to the high rate of about 66/sec (15 msec intervals) or 110/sec (9 msec intervals). The behavior patterns corresponding to such accelerations include attacks, the initial part of an antiparallel bout, and head butting. In only 4 of the 11 pairs showing antiparallel behavior did the eventual winner accelerate more frequently than the eventual loser. The same result was obtained when we considered only those times when both fish were discharging at a high rate and tabulated which fish reached the high rate first, corresponding roughly to which fish initiated the mutual bout. Only clear instances, such as shown in Fig. 4, were included in the count. Again only 4/11 eventual winners initiated more bouts. In both of these measurements it was clear that residency was a more important factor than future dominance. In all 11 pairs the resident fish showed the largest number of accelerations and initiated more periods of mutually high discharge rates. Finally, we examined the number of times each fish terminated an antiparallel bout by being the first to return to its background discharge frequency. In 8/11 pairs the eventual winner terminated more bouts, in 3/11 the eventual loser terminated more. When the last bout was analysed separately we found that the eventual winner initiated 6 of them, the eventual loser 3, and on 2 occasions the initiating fish was not clear. On the other hand, the eventual winner and the eventual loser each terminated 5 of the last bouts while on one occasion the terminator was not clear.

The mean discharge rate and the degree to which each fish echoed the other were examined by computer from the digitized records taken from different stages of the behavioral sequence. In 8 of the 11 pairs showing antiparallel behavior, the period of antiparallel bouts was sufficiently long to digitize and analyse separately. In only five of the eight did the eventual winner discharge at a higher mean rate during the last one to two minutes of antiparallel activity.

The amount of echoing done by each fish during the last one or two minutes of antiparallel behavior also did not appear to be related to the eventual outcome of the encounter. This was examined by comparing the size of the two echo peaks in cross interval histograms such as Fig. 10. Since these peaks varied as much as 2 msec in both latency and width, it was difficult to measure their size in a uniform and quantitative manner. For this initial survey we simply divided the histograms from the last 1–2 min of antiparallel activity into those in which asymmetry in one direction or the other was clear, as in Fig. 10, and those in which a judgement was uncertain. Although the eventual winner did more echoing in 2 of the 8 pairs analysed by computer, the predominant direction of echoing was unclear in the remaining 6. The question of the relation between echoing and dominance is a difficult one for two reasons: 1) the problem of measuring the amount of echoing accurately; and 2) the critical importance of the discharge frequencies of both fish and of their relative spatial positions in determining the probability of one fish giving an echo response (Russell *et al.*, 1974). The latter factors would have to be experimentally controlled before postulating an independent role for the echo response in determination or maintenance of dominance.

During antiparallel bouts the relative spatial position and the discharge frequencies of the two fish are comparable. It therefore seemed reasonable to examine the "phase locking" which sometimes occurred during these bouts. We made cross correlograms from filmed records taking only those events occurring during the mutual acceleration. The last 2 or 3 bouts of all 11 pairs which engaged in these displays were analysed. There were between 70 and 160 events in the reference train in each such correlogram. In two pairs the eventiual winner showed a clear tendency to discharge between 8 and 13 msec after the eventual loser; in one pair this order was reversed with the eventual loser discharging at this delay with respect to the eventual winner. In 8 of the 11 pairs the cross correlogram was either flat or showed equal amounts of phase locking in both directions.

In summary, we tabulated the number of accelerations, the number of bout initiations and the number of bout terminations for both fish in every pair during the period of antiparallel activity. We looked in particular at the last antiparallel bout and noted which fish initiated it and which terminated it. We examined the mean rates and the predominant direction of echoing in the last few minutes of the same period. We looked at the phase relationships between discharges of the two fish during the last one or two antiparallel bouts. Finally, as described in an earlier section, we also noted the presence or absence of 9 msec intervals during the antiparallel period. None of these features of the discharge patterns were clearly and consistently related to the outcome of the encounter.

Once dominance was established, however, there were clear and consistent differences in the electric organ discharge pattern of the two fish. The exclusive acceleration to high rates by the dominant (attacking) fish, the pauses these usually evoked in the submissive fish, and the clear difference in mean discharge rates were already referred to. There was also some tendency for the dominant animal to echo more during the last one or two minutes of the interaction. This was judged, as above, by examining the relative sizes of the two peaks in the cross interval histogram. In 10 out of 18 pairs the dominant fish echoed more, in 2 pairs the submissive fish did so and in 6 pairs the predominant direction was unclear. This difference may have resulted from the relative spatial positions of the two fish. The dominant fish often chased the submissive animal or attacked it from the rear. At such times the head of the dominant fish would be receiving more intense electrical stimulation than the head of the submissive animal. The head region contains the largest number of electroreceptors and is thought to be the most sensitive to electrical currents (Harder *et al.*, 1967). We do not know how long these various differences in discharge patterns would be maintained. In all of our pairs the interaction was terminated within 15 min after the last antiparallel bout. Therefore, these results are not directly relevant to the problem of dominance maintenance.

Species Other than Gnathonemus petersii

Both the baby whales and the large double-lipped *Gnathonemus* attacked and were attacked by *Gnathonemus petersii*. They also engaged in antiparallel displays with *Gnathonemus petersii*. The attacks and antiparallel activity were always accompanied by accelerations in the discharge rates. Neither species, however, showed discrete step-like changes in interval size during these accelerations. The double-lipped *Gnathonemus* had a somewhat unusual pattern of discharge. It frequently alternated between intervals of long duration with a mode at 90 msec and one or two much shorter intervals of 15–18 msec. When it accelerated to a high rate during an attack or antiparallel display all its intervals were short, i.e. 15–18 msec. The baby whales echoed and were echoed by *Gnathonemus petersii*. Latencies of the echo response were similar in both directions. In the encounter with the large double-lipped *Gnathonemus* antiparallel behavior predominated and the only sign of the echo was phase-locking like that of Fig. 13A but with all 4 peaks of similar size.

Discussion

Many of the correlations noted here between electric organ discharge patterns and overt behavior in mormyrids have been seen in different contexts by other workers. Accelerations during attacks were noted by Szabo (in Lissman, 1961). Möhres (1958) saw a "tumultuous" and simultaneous increase in the discharge rate of both fish shortly after putting two *Gnathonemus petersii* together. Bauer (1972) noted the regular, high discharge rate during attacks and antiparallel behavior as well as the presence of discrete changes in interval size between those of about 9 msec and about 15 msec. A pause in electric organ activity following artificial electrical stimuli has been seen by Lissman (1958), Szabo (in Lissman, 1961), Harder *et al.* (1967), and Moller (1970). Using such stimuli Moller saw additional phenomena such as acceleration and regularization of discharge rate depending on the frequencies and intensities of stimulation. We have studied these phenomena while two conspecifics went through a behavioral sequence in which dominance was determined and have examined in particular detail the temporal relations between the discharges of the two animals.

The high rate and regular pattern of discharges seen during agonistic displays contrasts in part with the reputation of mormyrids for discharging slowly and irregularly. For example, intervals within the first peak of Fig. 7D had a coefficient of variation (standard deviation/mean) of 0.06. Intervals in the train whose autocorrelogram is shown in Fig. 13C had a coefficient of variation of 0.12. However, such regularity is still far below that of some gymnotids such as *Eigenmannia* or *Sternarchus* (Bullock, 1970a, b). The coefficient of variation in the interdischarge intervals of *Sternarchus* has the extraordinarily low value of 0.00012 (Bullock, 1970b).

The discrete changes in interval size during agonistic displays show two features which may be important in understanding the function of these changes. First, the relative number of discharges at the shorter 9 msec intervals was always highest during the period of antiparallel activity when behavioral interaction was most intense. This suggests that an increased discharge rate is one component of an increased intensity in the overall behavioral display. Some physiological mechanism prevents the increase in discharge rate from occurring in a continuous manner, however. The second feature is that this mechanism does not permit discharges to occur when the echo of another fish is most probable, i.e. at intervals between 11 and 14 msec. In some fish avoidance of these intervals was accomplished without stepping down, i.e. by keeping all interdischarge intervals greater than the upper limit of the echo response. In either case, if the echo probability was high, as in one-sided attacks which did not evoke pauses, the result was an avoidance of near synchrony in at least one direction (Fig. 11). When the echo probability was lower, as in the mutually high rates of antiparallel bouts, there was less synchrony avoidance. It is not clear, however, whether the small amount of synchrony avoidance attained is the primary function of the echo response and the discrete changes in interval size.

A fish's acceleration to a high discharge rate during attacks and the inititation of antiparallel behavior had markedly different effects on the second animal at different stages of the behavioral sequence. In the period before antiparallel displays it either had no effect or evoked a brief acceleration. In the period of antiparallel displays it led to a similar and prolonged acceleration with associated antiparallel behavior in the other animal. Finally, after dominance had been well established it usually caused a pause in the other fish's discharges. Thus it is clear that the past history or behavioral context of the animal determines how it will respond to the same signal. This should be considered in future work employing artificial electrical stimuli to study communication in these fish. The importance of context in determining the effect of a particular communication signal has been noted elsewhere (Smith, 1963).

Antiparallel displays very similar to those described here have also been seen in the behavior of other teleosts, both electric (Black-Cleworth, 1970) and non-electric (Barlow, 1962; Southwick and Ward, 1968; Frey and Miller, 1972). In all these studies it frequently occurred at times of dominance determination. Only in the paradise fish *Macropodus opercularis* as studied by Southwick and Ward, however, did it appear to be as prominent a component of the behavior as it did in our observations on *Gnathonemus petersii*. In the other species antiparallel displays were only one of a variety of displays and other types of interaction occurring at the time of dominance determination.

It should be emphasized that the experimental situation which our recording method imposed was unnatural and undoubtedly narrowed the range of possible behaviors. The fish were confined within a small space and therefore forced to interact to a degree to which they might only rarely do in their natural environment. Dominance determination might be infrequent under normal circumstances and once the bouts were over the loser would probably leave the area immediately rather than subject itself to repeated attacks. Unfortunately there are only a few observations on mormyrid behavior in their normal environment (Lissmann, 1958).

The basic question of what role the electric organ plays in establishing a dominance relationship between two fish is not answered by our study. There is also not enough information in the literature to resolve the question. On the one hand, observations on a number of species suggest that the electrical channel may be critical and possibly even sufficient in establishing the relationship between two electric fish. Westby and Box (1970) found that comparing the mean rates of two fish prior to putting them in the same space allowed one to predict the outcome of the encounter between two *Gymnotus carapo*, a weakly electric gymnotid. Möhres (1957) reported that a *Gnathonemus petersii* would immediately and vigorously attack a previously ignored non-electric fish as soon as electrical stimuli were introduced. He used the gauze-wrapped tail of a second *Gnathonemus* as the source of such stimuli. Black-Cleworth (1970) examined the ability of different fish models to elicit attacks from *Gymnotus carapo*. While the shape and motion of the model had some slight influence, the most important factor by far was the presence or absence of artificial electrical pulses. Mandriota (unpublished observations referred to in Moller, 1970; and personal communication) connected two separate aquaria electrically and placed a single mormyrid of the baby whale or "round nose" type in each. After a period of alternating pauses and bursts in both animals, one of the fish consistently responded with a pause to the accelerated discharge rates of the other. This could be interpreted to mean that a dominance relationship had been established. It suggests that the complex threats and information exchanged during dominance determination can be communicated over the electrical channel alone.

However, the results of our analysis of electric organ discharge patterns during a period which we took to be one of dominance determination were entirely negative. No single feature of the discharge patterns of individual fish or the temporal relationships between them could inform us (and presumably the fish) as to which animal was in the process of winning the encounter. Relative size was an important determinant of the outcome of the bout and the amplitude of the electric organ discharge is probably related to the absolute size of a fish (Hopkins, 1972). But if this were the only message being conveyed there would seem to be little reason for the long, intense electrical and behavioral interactions which we observed. It is also possible that some unmeasured feature of the discharge pattern or a vectorial combination of features (Frey and Miller, 1972) might lead to an accurate prediction. However, before proceeding with more subtle and detailed analyses it is necessary to establish that the relationship between two fish can indeed be determined by communication through the electrical modality alone.

Finally, recent observations of Moller (personal communication) indicate that much social interaction can occur among mormyrid fish in the absence of an electric organ. By cutting the spinal cord anterior to the motoneurons which drive the electric organ (for method see Belbenoit, 1970), he obtained fish which were electrically silent but were apparently unaffected in their overt behavior. These fish continued to interact with attacks and antiparallel behavior. Preliminary observations suggested the presence of a dominance hierarchy in these animals.

Further work confirming the preliminary observations of Mandriota and Moller would indicate that dominance can be established through either of at least two sensory modalities.

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