5. E. O. Wilson [*The Insect Societies* (Belknap, Cambridge, Mass., 1971)] reports that Dufour's gland secretes alarm and trail pheromones in some ants. F. S. Guillot and S. B. Vinson [*Nature (London)* **235**, 169 (1972)] and S. B. Vinson and F. S. Guillot [*Entomophaga* **17**, 241 (1972)] showed that two braconid parasitoids produce a marking pheromone from Dufour's gland which when applied topically to hosts deterred other parasitoids from ovipositing. F. S. Guillot, R. L. Joiner, and S. B. Vinson [*Ann. Entomol. Soc. Am.* **67**, 720 (1974)] found the active material from the gland to consist of hydrocarbons.
6. In a cage uncontaminated with pheromone, fluttering was never exhibited except with reference to females and is a normal part of the courtship sequence.
7. Females are receptive to males during at least their first 11 days of adult life (R. M. Weseloh, in preparation).
8. Honey was used because it does not repel parasitoids and is easily cleaned from dishes.
9. M. Obara and H. Kitano, *Kontyu* **42**, 208 (1974).
10. I thank Elizabeth Wehrli and Arturo Giron for their valuable assistance in carrying out this study.

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# Electric Signals and Schooling Behavior in a Weakly Electric Fish, *Marcusenius cyprinoides* L. (Mormyriformes)

Abstract. *Field recordings of electric organ discharges and catches of* Marcusenius cyprinoides *showed that these electric fish form groups and move about in schools. The role of electric organ discharges in group cohesion was investigated by comparing interactions in groups of intact and operated, electrically silent fish. The absence of electric organ discharges reduced locomotor activity and resulted in the disappearance of two behaviors: parallel lineup and single file swimming. Electric signals are considered part of a schooling mechanism that aids the fish in maintaining group cohesion in their turbid environment and during migration at night.*

Electric organ discharges emitted by African mormyriform fishes and neotropical gymnotoids play a role in electrolocating and electrosignaling behavior (*1*). The present data demonstrate that these discharges are also used as a schooling mechanism in mormyrids.

Nighttime field recordings of the electric organ discharges and subsequent catches of the fish were made at Daga Weir on the El Beid River, an intermittent tributary connecting the large North Cameroon flooded plain (Yaéré) with Lake Chad (*2*). These observations showed that juvenile specimens of *Marcusenius cyprinoides* L. form groups and move about in schools (*3*) downstream toward the lake. During daytime smaller mormyrid species school in the shadow of partly submerged trees and bushes along the riverbanks. Vision is believed to be the major sensory modality in maintaining group structure among schooling fish (*4*). The African freshwater mormyrid fish are nocturnal and live in turbid water (*5*), which excludes vision as a schooling mechanism. A laboratory study was undertaken to assess the possible role of the electric signals in schooling of mormyrids by comparing group behavior of intact fish with that of fish made electrically silent by surgical intervention.

Freshly caught juvenile specimens of *M. cyprinoides* (length, 14.1 ± 1.2 cm) were transferred from Daga Weir into a concrete holding tank (*2*). On three different days, seven fish were removed from the holding tank to form three observation groups (A, B, and C), with the members of A having spent the shortest time in the holding tank and those of C the longest. Five typical group behaviors could be reliably identified: pursuit, physical contact, slow group movement, parallel lineup, and single file swimming. Pursuits were initiated by an individual fish following a second fish without actual physical contact. These pursuits terminated or resulted in resumed pursuits, physical contacts such as head-head and head-tail buttings or lateral attacks, and head-to-tail parallel displays with each fish butting the other's peduncle. Pursuit and contact occurred during fast locomotion. At times, groups composed of at least three individuals moved slowly by swimming close to and along the bottom of the tank. When such a group came to a halt, three or more fish often lined up in parallel in a head-down posture with interfish distances from 2 to 10 cm. In single file swimming one fish darted out of the more or less stationary group, immediately followed by two or more fish, all swimming one behind the other across the tank or circling within it, keeping the same order with interfish distances of 2 to 10 cm. This behavior differs from pursuits in that the termination of single file swimming was followed by regrouping and never resulted in contact behaviors.

The frequencies of these five behaviors depended in part on three variables: (i) the extent of the fish's adaptation, (ii) the number of fish present, and (iii) the observation tank's physical dimensions. To evaluate these variables, each group (A, B, and C) was observed in the following way. On day 1, seven fish were transferred, one at a time, from the holding tank into an observation tank (88 by 86 by 60 cm); water temperature ranged from 22.6° to 23.3°C; water conductivity was 300 ± 30 μmho/cm. Social interactions were recorded after addition of the second and each succeeding fish; subgroups of two to seven fish were thus observed. On day 2, after overnight adaptation of the seven fish to the observation tank, fish were removed one by one with observation sessions after each removal; successive subgroups of seven to two fish were thus studied. Each subgroup was observed for 15 minutes with a pause of 5 to 10 minutes between observations. After the three discharge-emitting groups were observed, the individuals of group C were made electrically silent by severing the spinal cord (which contains the motoneurons serving the electroplaques) just anterior to that part of the peduncle that contains the electric organ (*6*). The operated fish were kept in a separate 20-liter tank until they were subjected to the same observation procedure used for the intact fish. Observations were made between early morning and midday (except that on day 1, group

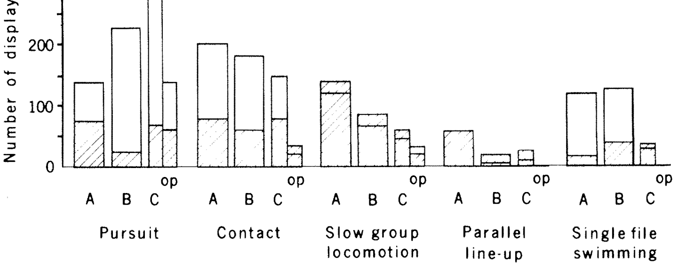

Fig. 1. Frequencies of five social interactions among individuals of three groups of intact *M. cyprinoides* (weakly electric fish) and one operated, electrically silent group (*C op*). Behavior was observed before (open bars) and after (hatched bars) overnight adaptation to an observation tank. Successive subgroups of two to seven fish were observed for 15 minutes each as fish were added to the tank on day 1; 15-minute observations were made of subgroups of seven to two fish as fish were removed from the tank. Fast locomotion behaviors (pursuit, contact, and single file swimming) decrease after overnight adaptation, parallel lineup increases, and slow group locomotion is not affected. The absence of electric organ discharges in the operated group is associated with a decrease in locomotor activity and the disappearance of parallel lineup and single file swimming.

B was observed between midday and midafternoon).

Five specimens of *M. cyprinoides* from groups A and B were sham-operated and tested under comparable conductivity and temperature conditions at a later date in my laboratory. The operation did not affect any of the social interactions under investigation.

Figure 1 summarizes the frequencies of the five social behaviors as combined from all subgroups for groups A, B, C preoperative, and C postoperative. Comparisons were made between behavior frequencies (i) before and after overnight adaptation and (ii) before and after elimination of the electric organ discharge activity (*7*). A comparison of the behavior frequencies in the intact groups before and after overnight adaptation shows a significant decrease ($P < .005$) in the fast locomotion behaviors (pursuit, contact, and single file swimming, except for single file swimming in group C), no significant change in slow group locomotion, and a significant increase in parallel lineup. Similarly, in the operated silent group, pursuits significantly decreased. No change in frequency was found for slow group locomotion and contact behavior. The absence of the electric organ discharge in the operated group was associated with reduced activity for pursuit, contact, and slow group locomotion as compared with fish before surgery. The decreases are significant for pursuit (day 1), contact (days 1 and 2), and slow group locomotion (day 2). Most apparent, however, is the absence of parallel lineup and single file swimming in the operated silent group (*8*).

Spacing and interactions among organisms are partly dependent on the available space. The effect of number of fish present in the observation tank, with and without electric organ discharges, on the frequencies of the five social behaviors is shown in Fig. 2. On day 1, when the fish were introduced into the tank one by one, the maximum activity for pursuit and contact occurred with three fish and then significantly decreased as each new fish was added. On day 2, after overnight adaptation, the most pursuits and contacts occurred with five fish. With less than four individuals present, these activities dropped to zero. The pursuit rate with six and seven silenced individuals present was significantly higher than that with the same number of intact fish (six fish on day 1, $P < .025$). Contact behavior was less frequent in the silenced group than in the intact groups, with most contacts occurring in groups of six and seven silenced fish on day 1 and in groups of five, six, and seven silenced fish on day 2. In the volume of water in the observation tank the presence of electric organ discharges thus inhibited pursuit and contact behavior in groups of six fish and more. No such inhibitory effect was noted for slow group locomotion, parallel lineup, or single file swimming. Here, the frequencies significantly increased with number of fish (single file swimming: day 2, $P < .05$). For the silenced fish, the increase of slow group locomotion with number of fish is significant only on day 1. Parallel lineup (data not shown) occurred with six and seven fish present, and then most frequently on day 2, after the fish had adapted to the tank.

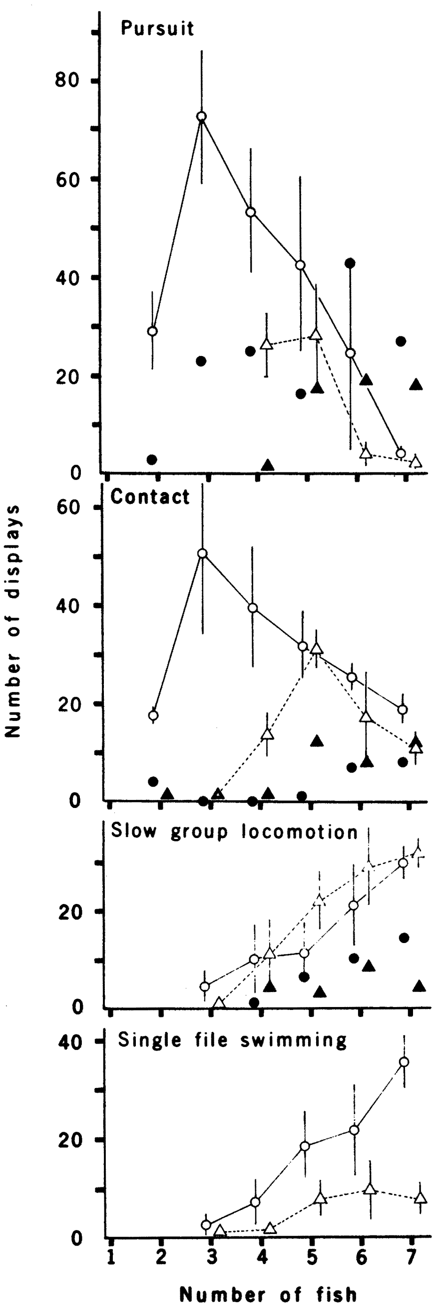

Fig. 2. Behavior frequencies (displays per 15 minutes) of four social interactions among individuals of *M. cyprinoides* as a function of the number of fish present in an observation tank. Means and standard errors are shown for three intact, electric organ discharge–emitting groups before (day 1, open circles) and after (day 2, open triangles) overnight adaptation to an observation tank. One group was subsequently made electrically silent by surgical intervention; behavior frequencies on day 1 (closed circles) and day 2 (closed triangles) are indicated. Electric organ discharges appear to inhibit pursuits and contacts when more than three fish (day 1) and five fish (day 2) are present in the observation tank. Slow group locomotion and single file swimming increase with the number of fish present. Single file swimming is absent in the silenced fish.

For the intact fish, a positive correlation was found between the distributions for pursuit and contact (Fig. 2). For the operated group, such a correlation could not be established (for instance, on day 1 there was almost no contact behavior in subgroups of three, four, and five operated fish). Pursuits in the operated fish, unlike those in the intact groups, seldom resulted in contact behavior; most frequently, the two fish swam away from each other. In the intact fish, resumed pursuits and contacts can be explained by active or passive electrolocation. The absence of this mechanism in the silenced fish may explain the frequent "loss" of the pursued fish which was electrically "invisible." With more fish in the observation tank, chances of two fish encountering each other increase; this is reflected in the increase of contacts in groups of six and seven silenced fish.

In summary, abolition of electric organ discharge is followed by (i) reduced locomotor activity, (ii) an increase in pursuits in groups of six and seven fish, (iii) a decrease in contact behavior, (iv) elimination of parallel lineup, and (v) elimination of single file swimming. The data suggest that the electric organ discharges, acting as an electrolocating or electrosignaling device, provide the basis for group cohesion by reducing the number of physical encounters and keeping individuals spaced within maximum and minimum limits.

Schooling behavior in fish has been defined as any grouping of individuals on the basis of "biosocial attraction" (*3*). Such biosocial stimuli presumably emanate from all participating individuals and were thought to be predominantly visual, with chemical, acoustical, and mechanical stimuli playing a less significant role. Such stimuli affect fish behavior in two ways: (i) individuals are attracted to each other and form nonpolarized groups, and (ii) individuals position themselves in characteristic polarized groups (such as with bodies parallel). In mormyrid fish the electric organ discharges provide an additional type of biosocial stimulation for achieving schooling behavior. The fish usually form nonpolarized groups and occasionally show polarization as in parallel lineup and single file swimming; thus they are "facultative schoolers" in Breder's terminology (*9*). The electric signals and the electrosensory system in mormyrid fish appear to function as part of another schooling mechanism that is adapted to aid group cohesion in the turbid water and during migration at night.

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### References and Notes

1. H. W. Lissmann, *J. Exp. Biol.* **35**, 156 (1958); P. Black-Cleworth, *Anim. Behav. Monogr.* **3**, 1 (1970); T. H. Bullock, *Am. Sci.* **61**, 316 (1973); T. Szabo, *Fortschr. Zool.* **21**, 190 (1973); P. Belbenoit, *Z. Vergl. Physiol.* **67**, 192 (1970); W. Harder, *Z. Tierpsychol.* **30**, 94 (1972); W. Heiligenberg, *J. Comp. Physiol.* **87**, 137 (1973), *ibid.* **91**, 223 (1974); *ibid.* **103**, 55 (1975); *ibid.*, p. 247; C. D. Hopkins, *Science* **176**, 1305 (1972); *Am. Sci.* **62**, 426 (1974); *Behaviour* **50**, 270 (1974); G. W. M. Westby, *J. Comp. Physiol.* **92**, 327 (1974); *ibid.* **96**, 307 (1975); R. Bauer and B. Kramer, *Experientia* **30**, 51 (1974); C. C. Bell, J. P. Myers, C. J. Russell, *J. Comp. Physiol.* **92**, 201 (1974); B. Kramer, *ibid.* **93**, 303 (1974); P. Moller and R. Bauer, *Anim. Behav.* **21**, 501 (1973); C. J. Russell, J. P. Myers, C. C. Bell, *J. Comp. Physiol.* **92**, 181 (1974).
2. The Office de la Recherche Scientifique et Technique Outre-Mer (ORSTOM) in N'Djamena, Chad, has been conducting a long-term project on fish populations of the El Beid River [J. R. Durand, *Cah. ORSTOM Ser. Hydrobiol.* **4**, 3 (1970); *ibid.* **5**, 147 (1971)]. The present laboratory data were collected by using the ORSTOM facilities in Chad.
3. The term schooling, as used here, denotes any grouping of fish that is the result of biosocial attraction; use of the term is in accordance with recommendations made at the 11th International Ethological Congress, Rennes, France (1969).
4. E. Shaw, in *Development and Evolution of Behavior*, L. R. Aronson, E. Tobach, D. S. Lehrman, J. S. Rosenblatt, Eds. (Freeman, San Francisco, 1970), pp. 452–476.
5. J. P. Gosse, *Ann. Mus. R. Afr. Cent. Zool.* **116**, 113 (1963); M. Poll, *Bull. Soc. Zool. Fr.* **84**, 259 (1959); P. Moller, field observations.
6. This operation does not interfere with the locomotion of the fish since the muscles controlling movement of the peduncle are located and innervated anterior to the lesion [V. Bruns, *Z. Zellforsch.* **122**, 538 (1971)]; M. V. L. Bennett, in *Fish Physiology*, W. S. Hoar and D. J. Randall, Eds. (Academic Press, New York, 1971), vol. 5, p. 347–491]. However, there probably was a loss of sensory input from cutaneous receptors in the skin surrounding the electric organ and the tail fin.
7. Behavior frequencies were compared by using the McNemar test for related samples. Correlation coefficients (Pearson product moment) were calculated to compare frequency distributions and to estimate frequency increases or decreases associated with the number of fish present in the observation tank. If not stated otherwise, the level of significance is $P < .005$.
8. The fish of group C had the longest time to adapt to the communal holding tank before being added to the observation tank. Part of the activity decrease could be accounted for by habituation; however, single file swimming and an increase in locomotor activity can be restored in an electrically silent group of fish by adding intact fish (L. Gordon, K. Johnson and P. Moller, in preparation).
9. C. M. Breder, Jr., *Zoologica* **52**, 25 (1967).
10. My stay in Central Africa was supported by grants from City University of New York (Faculty Research Award Program No. 10748E), the American Philosophical Society (Penrose Fund No. 7135), and the Explorers Club. Travel funds were provided by Hunter College. I thank T. Szabo for the invitation to join the *Chari* 1974–75 expedition; my friends and colleagues P. Belbenoit and J. Serrier for their help; A. DeFazio for transcribing the tape-recorded data; the director and staff of the ORSTOM laboratories at N'Djamena, Chad, for their hospitality and assistance; and L. R. Aronson, J. W. Atz, C. M. Breder, Jr., F. J. Mandriota, R. L. Thompson, and H. P. Zeigler for helpful comments on the manuscript.

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## Orientation Anisotropy: Incidence and Magnitude in Caucasian and Chinese Subjects

Abstract. *Cutoff spatial frequencies for sine-wave gratings were measured at four orientations for 100 Caucasian and 24 Chinese subjects, all of whom were raised in carpentered environments. For the Caucasian subjects, average acuity for horizontal and vertical gratings was superior to that for obliques by about one-quarter of an octave. However, about 10 percent of subjects failed to show the effect. The Chinese subjects showed an anisotropy of about one-eighth of an octave. The carpentered environment explanation of orientation anisotropy cannot, in its present form, account for the wide variety of response patterns obtained, nor the differences between Chinese and Caucasian subjects.*

Performance on a variety of visual tasks is better for stimuli oriented horizontally or vertically than for those oriented obliquely (*1*, *2*). Possibly, superior resolution for horizontal and vertical contours is the result of being raised in a "carpentered world" (*3*); that is, one in which such contours predominate. In support of an environmental hypothesis, Annis and Frost (*4*) report that a group of Cree Indians, raised in a relatively noncarpentered environment, failed to show a statistically significant anisotropy, while a group of Euro-Canadians, raised in typical North American homes, did show one. In the study described here, we provide evidence that the carpentered environment hypothesis of orientation anisotropy is inadequate in its present form.

We determined acuity for sine-wave gratings at four orientations: horizontal (0°), vertical (90°), oblique right (45°), and oblique left (135°) in 100 Caucasian and 24 Chinese subjects, all of whom had spent their early years in carpentered environments. Most of the Caucasian group had been raised in typical North American homes, and the majority of the Chinese sample had lived in apartments in Hong Kong during their early years.

Each subject was tested in a session lasting about 45 minutes. An extensive visual history was taken, followed by testing on a T-O vision tester (*5*) to obtain a measure of the individuals' current visual status. In those cases where it was appropriate, attempts were made to bring a subject's acuity into a normal range with lenses (*6*).

After the preliminary screening, subjects were seated with their heads positioned in a head rest. The distance from their eyes to the face of an oscilloscope was 344 cm. A circular target field, subtending a visual angle of 1.2°, was surrounded by a rectangular white mask, subtending 11° by 9°. The grating, generated on the screen by conventional methods, had a mean luminance of 48 $cd/m^2$ and a Michelson contrast of 0.50 (*7*). The surrounding field had a luminance of 10 $cd/m^2$.

Subjects turned a small knob controlling a ten-turn potentiometer to adjust the spatial frequency of the grating. They were required to begin at a point well below their ability to resolve the stripes and then to increase the width until they could just detect the orientation of the stripes. A number of practice trials were given, during which subjects were encouraged to refine their settings to achieve a threshold measurement. All testing was monocular. Trials were given in pairs, one for each eye, and the orientation of the grating was changed after every second trial. A total of 48 trials was given, six at each target orientation. The order of orientations was randomized, with the restriction that all four orientations were represented in every four pairs of trials, and the order of eyes was counterbalanced so that each eye received a given orientation first an an equal number of times.

Average threshold spatial frequencies were computed for each subject. These data, averaged for both eyes of all subjects within each group, are shown in