inefficient if used in such difficult but important problems as scene analysis. Furthermore, studies on such disparate topics as mammalian vision and human speech indicate that such an atomistic approach to classification provides an inadequate description of the recognition involved in such tasks. Recent work has opened up structural (or syntactic) approaches to these problems (*13*). Structural recognition begins with features too, but these are first classified into pattern primitives that are the basis of the recognition system. This limited set of basic patterns is then input into a hierarchically organized recognition system whose output is a significant message. However, unlike the inputs, which form a very limited set, the output messages can be essentially unlimited because the repetition of basic units also conveys information. The English language, for example, combines a set of about 45 phonemes into words, words into phrases and sentences, and sentences into larger structures of meaning. Thus, a relatively limited sensory basis can provide very complex signals for cuing behavior.

In understanding olfactory stimuli, specifically pheromones, as inputs, we need to consider their mode of action. The pheromones that have been the object of most recent investigations are of the type classified by Bossert and Wilson as releasers—reception triggers a characteristic, immediate, and overt behavioral response in the affected organism (*14*). Characterization and synthesis of such releasers, together with behavioral and electrophysiological studies of pheromones and related compounds, have shown a remarkable specificity in reception and action, often coupled with a large number of receptor sites for the active compound (*15*). The recognition system appears to be discriminant (rather than structural), with classification occuring at or near the receptor level as diagrammed in Fig. 1a. Recent work on multicomponent pheromones does not contradict this basic picture, although the requirement that the compounds be present in the proper ratio does require more feature processing capability than the monocomponent system that is shown in Fig. 1b.

While releaser pheromone systems certainly show specificity and tracking behavior requires at least some quantifiability, they lack the other two properties exhibited by the *D. pseudoobscura* rare male system—ability to deal with novel information and hierarchical structure. These two characteristics are specifically present in structural recognition systems. Other structural recognition systems, such as mammalian vision, are already well known in comparative psychology. The pattern primitives in the pheromone system could be individual substances or particular concentration patterns of substances. Chemical investigations in our laboratory so far indicate the latter, and such multicomponent systems can certainly carry more information with fewer substances than monocomponent ones (*16*). These pattern primitives are then hierarchically processed according to rules laid down by the limitations of the nervous system. This processing suppresses some information [such as the proportion of *or* males when there is a type (i) advantage] on the basis of other signals present, as schematized in Fig. 1c. The females' ability to respond to a broad range of olfactory stimuli, to process these stimuli in a hierarchical fashion, and to quantitate the population by these stimuli points toward a more complex processing of olfactory cues than had previously been suspected.

JACK E. LEONARD
Texas A&M University, College Station 77843
LEE EHRMAN
State University of New York, Purchase 10577

References and Notes

1. C. Darwin, in *Darwin*, P. Appleman, Ed. (Norton, New York, 1970), p. 126.
2. L. Ehrman, in *Sexual Selection and the Descent of Man*, B. Campbell, Ed. (Aldine, Chicago, 1972), p. 105; C. Petit, in *Genetics, Environment and Behavior*, L. Ehrman, A. S. Omenn, E. Caspari, Eds. (Academic Press, New York, 1972), p. 105; E. B. Spiess, in *Essays in Evolution and Genetics in Honor of Theodosius Dobzhansky*, M. K. Hecht and W. C. Steeve, Eds. (Appleton-Century-Crofts, New York, 1970), p. 315.
3. A. W. Ewing and A. Manning, *Annu. Rev. Entomol.* **12**, 471 (1967); J. Grossfield, in *Handbook of Genetics*, R. C. King, Ed. (Plenum, New York, 1976), vol. 3.
4. C. C. Tan, *Genetics* **31**, 558 (1946); L. Ehrman, in *The Genetics and Biology of Drosophila*, T. Wright and M. Ashburner, Eds. (Academic Press, London, in press), vol. 2.
5. J. E. Leonard, L. Ehrman, M. Schorsch, *Nature (London)* **250**, 261 (1974).
6. L. Ehrman, in *Animal Behavior in Laboratory and Field*, E. O. Price, Ed. (Freeman, San Francisco, ed. 2, 1975), p. 71.
7. This procedure is standard in our laboratory to guarantee the vitality of the stocks. No chamber in this study was rejected; in 42 chambers (1008 females) no female failed to mate within 3 hours of introduction into the chamber.
8. Correction for this disadvantage is made by the formula

$$m_{\exp,i} = \frac{Nf_i}{n_{AR}f_{AR} + n_{CH}f_{CH} + n_{or}f_{or}}$$

where $m_{\exp,i}$ is the expected matings involving the ith strain of males; N = total number of matings expected; n_i is the number of males of the ith strain present, and f_i = mating frequency of males of the ith strain, relative to AR males when i and AR are present in equal numbers ($f_{AR} = f_{CH} = 1.0; f_{or} = 0.5$). For example, for 144 matings and AR:CH:*or* = 1:1:1 (48 each type), the expected ratio is 57.6:57.6:28.8 (observed ratio was 55:51:38).
9. From current data we cannot demonstrate that *or* recognition is mediated by odor. However, if it is not, the recognition system—classification, quantitation, and identification—must be significantly more complex because it must integrate data from different sensory modalities.
10. J. M. Findlay and A. J. Daniell, *J. Theor. Biol.* **38**, 641 (1973); F. J. Fuller and W. K. Taylor, *ibid.* **41**, 97 (1973); C. A. Rosen, *Science* **156**, 38 (1967).
11. R. R. Sokal, *Science* **185**, 1115 (1967).
12. H. C. Andrews, *Introduction to Mathematical Techniques in Pattern Recognition* (Wiley-Interscience, New York, 1970); J. T. Tou and R. C. Gonzalez, *Pattern Recognition Principles* (Addison-Wesley, Reading, Mass., 1974).
13. K. S. Fu, *Syntactic Methods in Pattern Recognition* (Academic Press, New York, 1974).
14. W. H. Bossert and E. O. Wilson, *J. Theor. Biol.* **5**, 443 (1963).
15. D. Schneider, in *The Neurosciences: Second Study Program*, F. O. Schmitt, Ed. (Rockefeller Univ. Press, New York, 1970).
16. E. M. Barrows, W. J. Bell, C. D. Michener, *Proc. Natl. Acad. Sci. U.S.A.* **72**, 2824 (1975).

21 March 1975; revised 3 May 1976

Dufour's Gland: Source of Sex Pheromone in a Hymenopterous Parasitoid

Abstract. *Females of* Apanteles melanoscelus *and* Apanteles liparidis *produce a sex pheromone in Dufour's gland of their reproductive system. Males of both species exhibit premating behavior when in contact with filter paper smears of the gland of their respective females.*

Sex pheromones are known to occur in a number of hymenopterous parasitoids (*1*). However, the pheromone source has apparently not been found, although the general body surface (*2*), male pygidial glands (*3*), and thorax (*4*) have been implicated in different species. Dufour's gland, a prominent structure of the female reproductive system in Hymenoptera, is known to produce pheromones, but to my knowledge none of these has previously been identified as a sex pheromone (*5*).

I have found that Dufour's gland does produce sex pheromones in two hymenopterous parasitoids. The insect primarily investigated, *Apanteles melanoscelus*, is a small braconid wasp, which attacks larvae of the gypsy moth, *Lymantria dispar*, throughout the latter's range in North America and Europe. Both *A. melanoscelus* and *A. liparidis*, the other species used, were maintained in the laboratory on gypsy moth caterpillars.

Courtship in *A. melanoscelus* is as fol-

Table 1. Responses of *A. melanoscelus* males (one male = one replicate) to hexane extracts of vials in which females have been confined. Numbers in same column followed by same letter are not significantly different at $\alpha = .05$ by analysis of variance and selected treatment comparisons.

Female equivalents per filter paper (No.)	Replicates (No.)	Percentage of contacts (average) leading to	
		Examinations	Flutters
0.8	12	18.5a	1.6a
1.6	12	38.0a	3.8a
3.2	8	77.5b	31.4b

lows. Males do not respond to receptive females from a distance, but on coming within about 0.5 cm of a female they stop their forward motion, raise their wings, and begin fluttering them. This behavior occurs for several seconds and usually terminates in a vigorous flutter lasting less than 1 second. The male then immediately mounts and copulates with the female, who remains quiescent throughout (*6*).

To determine if the female releases a sex pheromone, three females 1 to 24 hours old (*7*) were placed without food in an inverted glass shell vial (1 cm in diameter and 3.5 cm high), as were three unmated males of similar age in a separate vial. After 4 hours males and females were removed and one fresh unmated male was placed in each vial as well as in a clean vial, which had not held parasitoids. The number of times each male fluttered its wings in a typical courtship response was recorded over 15 minutes. The test was replicated eight times. Males placed in "female" vials fluttered an average of 5.6 times each, but males placed in "male" or "blank" vials did not flutter at all. These results demonstrate that *A. melanoscelus* females produce at least one sex pheromone which releases fluttering behavior in males. Attempted copulation was not observed, indicating that other stimuli are necessary for the complete expression of mating behavior.

A concentration-response experiment, in which pheromone deposited in vials was extracted with varying amounts of *n*-hexane and exposed to males on 1-cm squares of filter paper, showed that males respond to increasing concentrations of the pheromone by increasing their wing flutters when they contact filter paper squares containing the pheromone (Table 1). They also examined such squares with their antennae (with or without subsequent fluttering) to a greater extent as pheromone concentration increased. Thus antennal examination as well as wing flutters can be used to bioassay for presence of sex pheromone.

The source of the pheromone was determined by testing responses of males to different parts of the female. Unmated females were immersed briefly and successively in *n*-hexane, 95 percent ethanol, and distilled water. The hexane wash was essential as preliminary experiments showed that all parts of the female are normally contaminated with pheromone. The female reproductive system and hindgut were removed by grasping the ovipositor with forceps and gently pulling it and the reproductive system out of the body. Parts of the reproductive system (Fig. 1) and hindgut were separated with insect pins in a small drop of distilled water. The different body parts to be tested were smeared on separate 0.5-cm-square pieces of filter paper and any cuticular fragments removed. The squares were then anchored with small drops of honey to the bottom of a glass petri dish 10 cm in diameter in a circular array (*8*). One unmated male was released in the dish and the number of contacts, antennal examinations, and wing flutters on each square was recorded for 15 minutes or until ten contacts per square had occurred. The parts of the female bioassayed in three different tests and the male responses are given in Table 2. Males examined and fluttered most often at squares smeared with female abdomens, reproductive systems, and Dufour's gland in tests 1 to 3, respectively.

These results show that Dufour's gland is the source of the female sex pheromone in *A. melanoscelus*. Test 3 was repeated with *A. liparidis*. Of the contacts which males of *A. liparidis* made with smears of *A. liparidis* Dufour's gland, 19.5 percent led to examinations and 13.6 percent to flutters. No examinations or flutters occurred on any other part of the female's reproductive system (11 replicates, results statistically significant at $\alpha = .05$). Dufour's gland thus appears to produce the sex pheromone in this *Apanteles* species as well. *Apanteles glomeratus* males responded most to the last segment of the female's abdomen (*9*). It is likely that here also Dufour's gland is the pheromone source. Indeed, it is probable that Dufour's gland produces the sex pheromone in all *Apanteles* species and possibly in other parasitoids as well.

Table 2. Responses of *A. melanoscelus* males to different parts of the female. Numbers in same column and same test followed by same letter are not significantly different at $\alpha = .05$ by analysis of variance and selected treatment contrasts.

Female part tested	Replicates (No.)	Percentage of contacts (average) leading to	
		Examinations	Flutters
	Test 1		
Head	8	8.0a	0 a
Thorax		62.5b	12.9a
Abdomen		91.5c	76.0b
	Test 2		
Alimentary canal except hindgut	6	13.9a	0 a
Reproductive system plus hindgut		72.4b	48.7b
Rest of abdomen		7.0a	0 a
	Test 3		
Ovary	6	3.8a	1.3a
Hindgut		3.2a	2.1a
Poison reservoir		2.6a	0 a
Poison gland		0 a	0 a
Dufour's gland		50.5b	18.8b

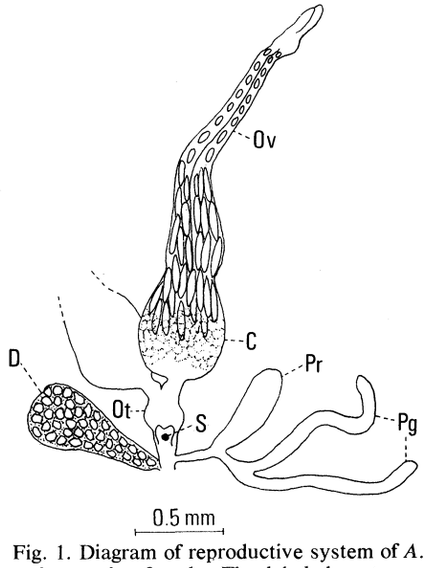

Fig. 1. Diagram of reproductive system of *A. melanoscelus* female. The labeled parts are the ovariole (*Ov*) and calyx (*C*), which together constitute the ovary; the poison reservoir (*Pr*); poison gland (*Pg*); spermatheca (*S*); oviduct (*Ot*); and Dufour's gland (*D*).

RONALD M. WESELOH
Department of Entomology, Connecticut Agricultural Experiment Station, New Haven 06504

References and Notes

1. J. van den Assem, *Neth. J. Zool.* **20**, 329 (1970); _____ and G. D. E. Povel, *ibid.* **23**, 465 (1973); G. M. Bousch and R. A. Baerwald, *Ann. Entomol. Soc. Am.* **60**, 865 (1967); L. R. Cole, *Anim. Behav.* **18**, 184 (1970); D. E. Fink, *J. Agric. Res.* **32**, 1121 (1926); P. Genieys, *Ann. Entomol. Soc. Am.* **18**, 143 (1925); S. Khasimuddin and P. DeBach, *ibid.* **68**, 893 (1975); W. J. Lewis, J. W. Snow, R. L. Jones, *J. Econ. Entomol.* **64**, 1417 (1971); A. Schwartz and D. Gerling, *Entomophaga* **19**, 483 (1975).
2. S. B. Vinson, *Environ. Entomol.* **1**, 409 (1972).
3. K. S. Hagen, *Proc. Hawaii. Entomol. Soc.* **15**, 115 (1953).
4. S. V. Rao and P. DeBach, *Hilgardia* **39**, 515 (1969).

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.

3 May 1976; revised 21 June 1976

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

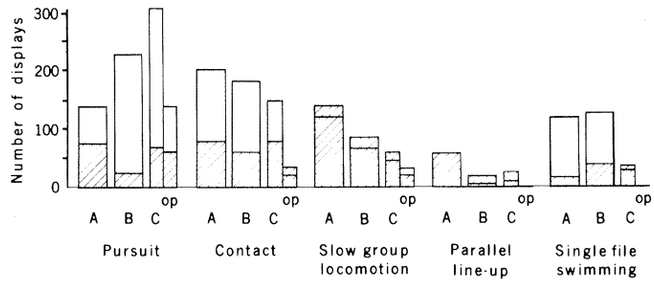

Fig. 1. Frequencies of five social interactions among individuals of three groups of intact *M. cyprinoides* (weakly electric fish) and one operated, electrically silent group (*C op*). Behavior was observed before (open bars) and after (hatched bars) overnight adaptation to an observation tank. Successive 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.