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OLFACTORY CUES AND MOVEMENT: STIMULI MEDIATING INTRASPECIFIC AGGRESSION IN THE WILD NORWAY RAT[1]

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Male sibling pairs of wild rats were established in enclosures and their aggressive, amicable, and sexual behavior observed following the introduction of conspecifics. It was found that: (*a*) Intact male rats behaved amicably toward familiar male conspecifics, both aggressively and sexually towards unfamiliar anestrous and estrous female conspecifics, and aggressively toward unfamiliar male conspecifics; (*b*) anosmic males exhibited amicable and sexual behavior toward unfamiliar males, but did not initiate aggression toward them; (*c*) the storing of a member of a resident pair in a cage with or without wood shavings, urine, and feces from a foreign colony did not affect behavior toward him by his cage mate; (*d*) the storing of a foreign male in the wood shavings, urine, and feces of a colony did not affect behavior of that colony toward him; (*e*) cessation of movement on the part of an intruder of either sex inhibited attack; (*f*) immobile anesthetized male intruders elicited aggression; (*g*) when presented simultaneously with moving and anesthetized intruders, resident rats attacked only the former.

The social interactions to be observed within a colony of wild rats (*Rattus norvegicus*) are typically peaceful, the members engaging in a variety of stereotyped amicable behaviors involving cutaneous contact. With the exception of recently parturient females, who defend their nest sites against intrusion, overt fighting is rarely observed among members of an established colony (Barnett, 1963; Eibl-Eibesfeldt, 1961; Galef, 1970; Lorenz, 1966). Wild rats resident to an area will, however, readily attack unfamiliar conspecifics intruding into the vicinity of their nest sites (Barnett, 1958, 1963; Eibl-Eibesfeldt, 1961; Galef, 1970; Lorenz, 1966; Telle, 1966).

The fact that wild rats behave amicably toward fellow colony members while behaving aggressively toward unfamiliar intruders indicates that they are able to discriminate members of their own colony from strangers. There is, however, little information available concerning the cues enabling wild rats to distinguish friend from foe. The present series of studies was designed, first, to determine the stimuli necessary for wild rats to discriminate familiar from unfamiliar conspecifics, and second, to investigate the way in which these stimuli function in the maintenance of colonial integrity.

EXPERIMENT 1

In the present experiment a variety of intruders were introduced into the home cages of pairs of male wild rat siblings. The experiment was performed to define the range of intruders eliciting aggressive behavior from resident males and to establish the adequacy of our apparatus and procedures for the investigation of the aggressive behavior of wild rats.

Method

Subjects

Subjects in all the experiments reported below were second, third, and fourth generation lab-

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oratory-bred male wild rats (*R. norvegicus*), direct descendants of feral animals captured on the wharves of Philadelphia and on a farm in eastern Maine. Hooded rats of the Long-Evans strain were obtained from the Canadian Breeding Farms.

Apparatus

All observations were carried out via closed-circuit television monitored in rooms separate from experimental animals.

Experiments were conducted in cages, to be referred to below as home cages (3 × 3 × 3 ft.), constructed of ¾-in. plywood. The galvanized sheet-metal floor of each enclosure was covered to a depth of 2 in. with wood shavings, half of which were replaced every 3 wk. so as to maintain colony-specific odors within each cage. A single 12 × 12 × 5 in. nest box, which opened onto the home cage via a 3 × 3 in. door was attached to each cage.

Procedure

Residents. Twelve pairs of wild male siblings were weighed, marked by shaving so as to be distinguishable on closed-circuit television, and introduced (1 pair per enclosure) into the home cages described above. Each pair of resident rats was given 4–6 wk. to become established in its home cage and habituated to maintenance procedures. During this period the residents were fed powdered Purina Laboratory Chow for 3 hr/day. Overhead lights were illuminated for the duration of the feeding period (1:30–4:30 P.M.), providing regular periods for observation. Following 4–6 wk. of habituation, each pair of residents was observed for at least 4 3-hr. feeding periods prior to initiation of experimental manipulations. During these observation periods, base-line levels of inter-resident interaction were established. On the final day of each pair's habituation period, 1 male resident from each of 4 home cages was removed for 24 hr. to a holding cage. These animals were returned to their home cages at the beginning of the next feeding period, and interactions between members of reunited resident pairs were observed for the first ½ hr.

Intruders. Following habituation and establishment of base lines, a series of intruders were introduced into home cages during the first ½ hr. of daily feeding periods. A period of at least 1 wk. separated the introduction of any 2 intruders into a single home cage. Four types of intruders were employed: (*a*) *Unfamiliar male wild rats,* experimentally naive animals, born and reared in rooms separate from residents, were introduced individually into 4 home cages; (*b*) *unfamiliar male domesticated rats* (180–250 gm. male Long-Evans) were placed in 8 home cages for observation; (*c*) *unfamiliar anestrous domesticated female rats* were ovariectomized and allowed at least 2 wk. to recover from surgery prior to introduction into 6 home cages (½ hr. before introduction each was observed in the presence of an indicator domestic male—none elicited sexual response from the males); (*d*) *unfamiliar domesticated estrous females* were provided by subcutaneously injecting the ovariectomized females from the preceding group with .5 mg. of estradiol valerate (Delestrogen, Squibb) followed 42 hr. later (6 hr. prior to introduction) by injection of 1.0 mg. medroxyprogesterone acetate (Depo-Rovera, Upjohn). (Thirty min. prior to introduction into a home cage each female was observed in the presence of an indicator domestic male—all females in the present group elicited sexual behavior from the indicator male and responded with full lordosis; order of presentation of estrous and anestrous females was counterbalanced across home cages.)

Scoring. The experimenter observed home cages during ½-hr. periods of intruder presence via closed-circuit television and scored interactions on the basis of slow-motion analysis of videotapes.

The aggressive behavior patterns directed toward unfamiliar intruders by wild rats are similar to those described for the domesticated rat (Barnett, 1963; Grant, 1963; Grant & Mackintosh, 1963) but are performed with far greater vigor by individuals having wild genotypes (Barnett, 1963). Of the postures and activities commonly associated with aggression in rats (Barnett, 1958; Grant & Mackintosh, 1963), the "lateral" or "threat" posture, "boxing" or "upright" posture, and "attack" were initially selected for quantification.

Unfortunately, animals differed to such an extent in their fighting styles that ordinal scaling of the data proved impractical. Some animals would direct a single prolonged attack at an intruder while others would attack in a series of brief, discrete episodes. Lateral displays appeared and faded gradually, were interspersed with chases and attacks, and performed to different degrees of completeness on different occasions. As there appeared to be no way of measuring the relative intensity or amount of aggressive behavior in such variable behavior patterns, we did not attempt to do so. We have chosen instead to report only the presence or absence of classes of response elicited by various stimulus animals, as this procedure seems to give a less arbitrary picture of the interactions than any ordinal quantification scheme we could develop.

Amicable behaviors ("allogrooming," "crawling under," "walking over," and "huddling" [Barnett, 1963]) were similarly recorded, as was the presence or absence of feeding during the period of intruder presence. The scoring of male sexual behavior was confined to those aspects of resident behavior (mounting and thrusting) most readily observed via the system used. Intromissions and ejaculations were not recorded.

Results

Baseline Interaction of Resident Pairs

As can be seen in the left-hand portion of Figure 1, amicable behaviors were observed

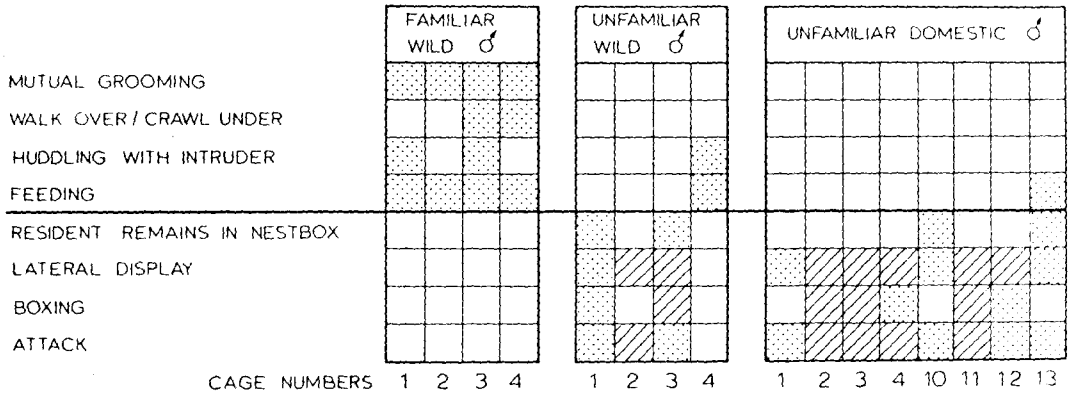

FIG. 1. Amicable and aggressive behaviors exhibited by residents in response to the introduction of male conspecifics. (Stippling indicates a behavior exhibited by a single resident, and cross-hatching a behavior exhibited by both members of a resident pair.)

in all resident pairs following the return of the resident removed for 24 hr. Feeding began within 5 min. of food presentation, and both residents spent most of the first ½ hr. of food availability at the feeding bowl. No aggressive interactions were observed within resident pairs following return of the temporarily removed resident nor were any observed during observations of undisturbed cage mates.

Responses to Unfamiliar Male Intruders

Figure 1 also depicts the behavioral events occurring during the ½-hr. introduction of unfamiliar wild and domesticated males. It is clear from examination of the figure that an introduced strange male interfered with feeding, did not elicit amicable behaviors, and did elicit considerable aggression.

During observation periods in which strange males were introduced into home cages, events followed a fairly regular sequence. When the experimenter entered a room for the purpose of introducing an intruding male into a home cage, both residents entered the next box. After a few minutes, one or both residents would approach the intruder cautiously in the stereotypic "stretched attention posture" (Grant & Mackintosh, 1963). The resident's approach usually culminated in vigorous sniffing directed particularly at the intruder's anogenital area. Overt aggressive displays usually followed this sniffing, the lateral display with accompanying piloerection developing gradually from a preliminary posture involving an arching of the back and mincing gate. Overt attack occurred suddenly; the duration and intensity of each element of such sequences varied considerably.

The presence of the intruder in a home cage occasionally led to a partial breakdown of interresident amicability. Interresident sniffing increased in frequency and brief instances of interresident aggressive behavior were observed in 2 of 12 home cages during situations of apparent confusion. For example, during aggressive bouts or chases directed at an intruder, residents would sometimes collide or come into close proximity and assume a boxing stance or lateral postures vis-à-vis one another. These confrontations, unlike displays directed toward intruders, were brief and ended peacefully after mutual sniffing by the residents.

The response of intruders to overt attack included fleeing, assuming submissive and boxing postures, or in the case of domestic males after particularly vicious attacks, a collapse best described as "cataleptic" (Grant & Mackintosh, 1963). In the case of all 6 intruders which responded to attack by becoming motionless, the residents' attack behavior immediately terminated and recurred only when the intruder resumed gross movement.

When intruders terminated attacks either by becoming motionless or by taking refuge

in the nest box and successfully defending it, residents frequently exhibited lateral displays and dug in the wood shavings near the intruder.

Responses to Unfamiliar Female Rats

As can be seen in Figure 2, the response of male residents to both estrous and anestrous intruding females was extremely variable. Both types of females elicited both sexual and aggressive behaviors on the part of males. The initial response of males to females in the 2 groups was indistinguishable (aggressive in the case of 4 estrous and 3 anestrous females and sexual in the case of 2 females in each group).

Throughout the observation period anestrous females vigorously resisted attempts to copulate, and the frequency of aggressive interactions with males remained constant. Estrous females did not resist those males who mounted, and in those cages where males responded sexually rather than aggressively to estrous females the frequency of aggressive actions decreased during the course of observation.

Discussion

The generality of the results described above to other situations is, of course, open to question. In the present study, resident pairs were all siblings, established colonies were of very small size, the areas in which they lived of limited extent, and intruders were placed in enclosures only during colony feeding periods. Variation in any of these parameters could have affected the frequency of occurrence of the behaviors observed.

The procedures used were selected on the basis of Telle's (1966) field observations of aggression directed toward intruders by feral rat colonies, so as to control variables of importance while maximizing the probability of aggressive encounters. Telle's studies indicate that (*a*) many feral rat colonies consist of family groups, (*b*) defense of the area immediately surrounding the nest site is most intense, (*c*) the attack of intruders is most frequently carried out by only 2 or 3 colony members, and (*d*) aggression to intruders is most frequently observed while members of small colonies are traveling to and from feeding sites. It is of relevance to note that the details of our observations of residents' reactions to intruders parallel Telle's observations of the behavior of small feral colonies very closely.

In general, our observations of resident response to the intrusion of foreign males

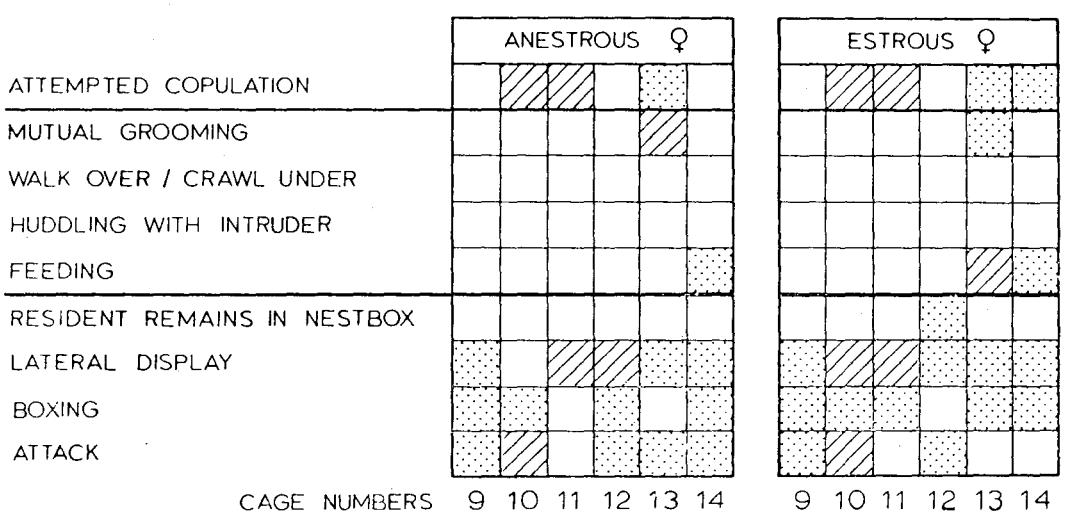

FIG. 2. Amicable, aggressive, and sexual behaviors exhibited by residents in response to the introduction of unfamiliar female conspecifics. (Stippling indicates a behavior exhibited by a single resident, and cross-hatching a behavior exhibited by both members of a resident pair [Cages 9 and 14 contained only a single resident].)

are in agreement with those of Barnett (1958), who emphasized the high probability of resident attack in such circumstances. Our observations of resident male response to female intruders show a much higher probability of attack directed toward strange females than Barnett (1958) reported and are in closer agreement with the field observations of Telle (1966), who introduced 47 male and 52 female marked wild rats into the territories of 25 wild rat colonies and observed no differences in rate of acceptance as a function of sex.

The data reported above demonstrate that in our experimental situation aggression can be reliably elicited by the introduction of foreign males and provide evidence that the present procedures are suitable for the investigation of aggressive behavior in wild rats.

The remainder of the present paper is concerned with an analysis of the cues eliciting aggression in wild rats.

Experiment 2

Virtually all observers of wild rat behavior have suggested that olfactory cues play an important role in the wild rat's discrimination of familiar from unfamiliar conspecifics. There are 2 pieces of evidence in support of this suggestion. First, fights between rats are almost always preceded by investigative sniffing (Barnett, 1958, 1963; Calhoun, 1962; Steiniger, 1950) and second, during periods of colony disturbance due to the intrusion of a stranger, there is an increase in what Barnett (1963) has labelled interresident "recognition sniffing."

The present experiment was designed (*a*) to directly investigate the importance of olfactory cues in eliciting attack directed toward unfamiliar conspecifics and, (*b*) to determine the way in which olfactory cues act to inhibit or elicit aggression. Two alternative but not mutually exclusive interpretations of the differential responding of male wild rats to familiar and unfamiliar conspecifics are available. It is possible that cues emanating from familiar conspecifics may serve to inhibit aggressive behavior, or alternatively, that cues emanating from unfamiliar conspecifics may serve to elicit aggression. The results of the present experiment provide data bearing on these interpretations.

Method

Subjects

Resident pairs of wild rats from 8 home cages and 8 male hooded rats served as subjects in the present experiment.

Procedure

The member of each of 4 resident pairs which had exhibited the least aggressive behavior during Experiment 1 was removed from its home cage and placed in an individual holding cage. The more aggressive cage mates of these animals were captured, anesthetized with ether, and rendered anosmic by bathing the olfactory mucosa with 10% zinc sulphate solution using the method of Alberts and Galef (1971). Anosmic animals were returned to their home cages immediately following treatment, and testing was initiated during the subsequent feeding period 24 hr. later. During this feeding period anosmic residents were observed for ½ hr. following the introduction of an unfamiliar domestic rat into their home cage. Following removal of this intruder, the familiar resident was returned to its cage mate, and interactions between the pair were observed for a further ½ hr. Ten days following zinc sulphate treatment this testing procedure (removal of the less aggressive resident, followed by introduction of a male hooded intruder, followed by return of the less aggressive resident) was repeated.

Results

As can be seen in Figure 3, the most striking consequence of rendering the more aggressive member of each resident pair anosmic was the disappearance of aggressive behaviors directed toward unfamiliar conspecifics and their replacement in 12 of the 16 observed interactions by stereotyped amicable behavior patterns. Returned residents continued to be treated amicably.

Unexpectedly, the loss of olfactory sensitivity resulted in some of the anosmic residents attempting copulation with both familiar and unfamiliar introduced animals. In all cases but one in which anosmic residents exhibited aggressive behavior, the aggression was initiated by the introduced animal during the anosmic animal's attempts at copulation. These attacks initiated by the introduced animal resulted either in counteraggression or the assuming of a

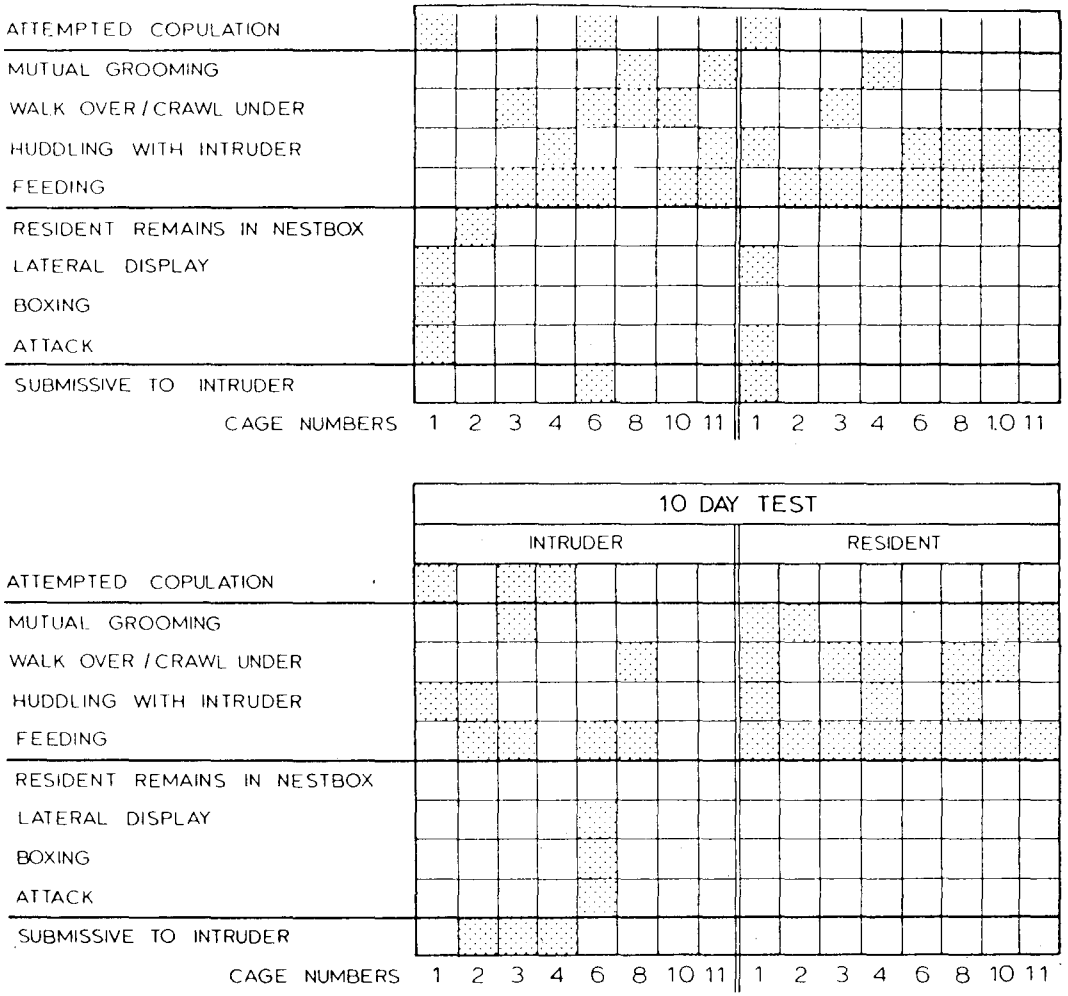

FIG. 3. Amicable, aggressive, and sexual behavior exhibited by zinc sulphate treated (anosmic) residents in response to the introduction of familiar and unfamiliar male conspecifics.

"submissive posture" (Grant & Mackintosh, 1963) by the anosmic resident. The assuming of a submissive posture by an intact wild rat during an aggressive interaction with a domesticated conspecific is very rarely seen.

Discussion

The data indicate that normal olfactory function is a necessary condition for wild rats to discriminate effectively between familiar and unfamiliar conspecifics. Loss of olfactory sensitivity did not appear to impair recognition of a fellow rat as a conspecific; both unfamiliar intruders and returning cage mates were responded to with stereotyped amicable and copulatory patterns normally elicited by familiar conspecifics; but anosmia does appear to preclude initiation of intraspecific aggression. The simplest description concordant with the data is that rats are capable of responding to conspecifics as such in the absence of olfactory cues, but will only initiate aggression

towards unfamiliar conspecifics if they are able to smell them. The extreme visual novelty of the unfamiliar intruders in the present experiment and their failure to elicit aggression emphasize the importance of olfactory cues in the initiation of aggressive behavior toward unfamiliar conspecifics.

A study in which unfamiliar anesthetized male domestic rats were presented to resident pairs while placed in either intact or perforated sealed plastic "Baggies", adds additional support to the present conclusion. All 4 resident pairs attacked the anesthetized intruders presented in perforated bags, while none of the 4 resident pairs attacked intruders in intact bags.

The fact that anosmia results in the loss of aggressive responses to unfamiliar conspecifics rather than in the acquisition of aggressive behavior towards familiar ones, indicates that it is the unfamiliar odor of strange rats which elicits aggressive behavior in wild rats. The data does not preclude the possibility that, in addition, the smell of a familiar rat may serve to inhibit aggression.

The observation of sexual behavior inappropriately directed toward male conspecifics by anosmic rats and the observation of sexual approaches by intact males to anestrous females in Experiment 1 suggest that male wild rats may not exhibit sexual behavior in response to a pheromone excreted by female conspecifics, but instead respond sexually to conspecifics which are not the source of inhibitory olfactory cues identifying them as males.

Barnett and Stoddart (1969) observed that intact sixth to ninth generation laboratory-bred wild rats mount intruding males, but they did not see similar behavior in either recently trapped or first to third generation laboratory-bred wild rats (Barnett, 1958). Male domesticated rats are commonly observed to mount one another. During the series of experiments reported here only anosmic male wild rats mounted other males. It is possible that continued breeding in captivity results in some olfactory impairment leading to the abnormal behaviors observed.

Experiment 3

The results of the preceding experiment indicate that wild rats identify intruders into their colony on the basis of aggression-eliciting olfactory cues which those intruders emit. Previous workers have suggested a number of possible sources of odoriferous substances which would allow members of a colony to respond differentially to one another and to intruding conspecifics. Lorenz (1966) has pointed to colony nesting material as the source of colony specific odors; Eibl-Eibesfeldt (1970) has suggested that male urine contains the important cues; and Steiniger (1950) has indicated that cutaneous contact with members of a strange colony is sufficient to make a rat a stranger to its original clan. The various sources of the suggested olfactory cues have in common the underlying assumption, made explicit in Eibl-Eibesfeldt's (1970) description of the wild rat colony as a "closed anonymous group," that colony members are reacted to as either possessing the "colony odor" or the odor of a foreign colony rather than as familiar or unfamiliar individuals. Since, according to this interpretation, the important cues for recognition of a rat would be externally imposed on the individual, they should be readily available for experimental manipulation.

In the present experiment, an attempt was made to alter the familiarity of both familiar and unfamiliar rats by manipulating olfactory cues previously suggested as important in allowing colony members to discriminate fellow members from strangers.

The present experiment is most easily described as 2 separate studies. In the first study, experimental manipulations were undertaken to produce acceptance of an unfamiliar rat by a resident pair, while the second study was designed to produce rejection of a member of a resident pair by its home-cage mate.

Method

Study 1

Eight adult male wild rats, unrelated and unfamiliar to the established resident pairs, were

anesthetized with Equi-thesin (intraperitoneal (ip) injection of .22 cc per 100 gm. body weight), scrubbed thoroughly with an emulsifying detergent soap solution (Phisohex), and rinsed with water and alcohol. Each washed rat was placed for 7 days in a plastic holding cage (12 × 17 × 8½ in.) containing urine and feces-impregnated shavings taken from one of the 8 home cages used in this study. Twenty-four hours before testing, the fur of each of these rats was moistened with approximately 15 cc of fresh urine collected from the members of the resident pair in whose shavings he was being kept, and fresh feces were deposited in his holding cage. Urine and feces were collected by placing both members of each resident pair overnight in a metabolism cage. Treated rats were assumed to carry odors representative of the colony in whose shavings they had been kept. Rats introduced into the same colony that had contributed the shavings are referred to below as "matched intruders", and rats introduced into a colony other than the one contributing their shavings as "unmatched intruders."

Matched and unmatched intruders were introduced in counterbalanced order into 8 home cages containing intact resident pairs, and their interactions observed for successive ½-hr. periods. One week later the less aggressive resident was removed from each of the 4 home cages 3 hr. before the feeding period, and the response of the more aggressive resident to matched and unmatched intruders and the returned resident observed during successive ½-hr. periods. In the following week the more aggressive member of each of these resident pairs was removed, and observations were made of the behavior of the less aggressive resident toward matched and unmatched intruders and toward its returned cage mate.

Study 2

In the present study an attempt was made to render the less aggressive member of 8 resident pairs "unfamiliar" by exposing them to the odor of foreign colonies. The procedure was identical to that of Study 1 of this experiment except that members of resident pairs were treated instead of foreign rats.

The less aggressive member of each of 4 resident pairs was removed from its home cage, washed, and placed in a plastic holding cage containing shavings from a home cage other than its own. Five to seven days after removal, and 24 hr. before being returned to their own home cages, these rats were bathed in the urine of the members of the resident pair in whose shavings they were being kept. They were returned to their own home cages, and their interaction with their more aggressive cage mate observed for ½ hr.

The less aggressive members of 4 additional resident pairs were removed from their home cages, washed, and placed for 7 days in 1 of 4 3 × 3 ft. holding cages, each containing 5 adult male Long-Evans rats which had been living in those cages for 2 wk. prior to the introduction of the wild rat. The usual ½-hr. observations of interresident interaction were made following the return of the treated resident to its original home cage.

Results and Discussion

The major results of Experiment 3 are reported in Figure 4. It is clear from examination of the figure that regardless of treatment procedure, unfamiliar rats were responded to aggressively, and returned members of resident pairs amicably. Data describing the behavior of single residents after the return of their unmanipulated cage mates are not presented in the figure, but was amicable in all 8 instances. The data indicate that the manipulations performed did not affect the ability of resi-

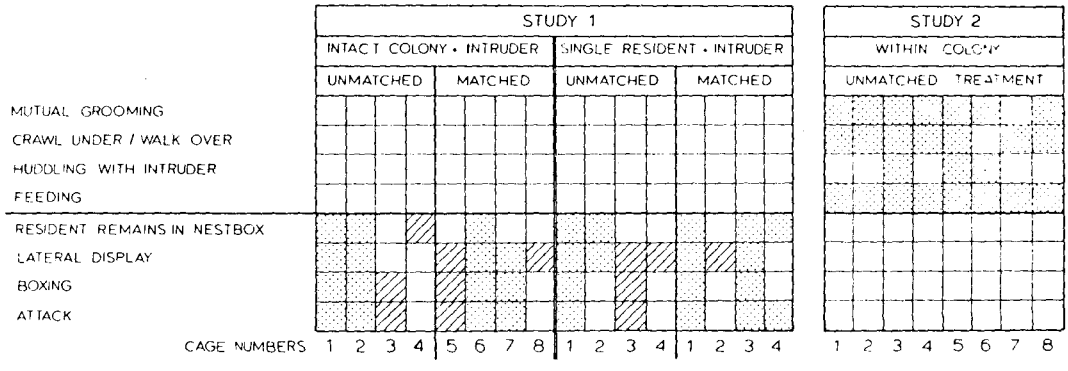

FIG. 4. Amicable and aggressive behaviors exhibited by individual residents and resident pairs in response to the introduction of matched and unmatched male conspecifics. (Stippling indicates a behavior exhibited by a single resident, and cross-hatching a behavior exhibited by both members of a resident pair.)

dents to discriminate fellow colony members from unfamiliar intruders.

These observations do not support previous descriptions of the wild rat colony as a closed anonymous group (Eibl-Eibesfeldt, 1970) in which membership is determined by the possession of a colony specific odor. Further, they are not consistent with hypotheses stating that acceptance into a colony is determined by an individual possessing olfactory cues acquired externally by contact with the urine or feces of fellow colony members or with other colony members. To the contrary, our data suggest that conspecifics are reacted to as familiar or unfamiliar on the basis of their individual scent.

Of course, the apparent primacy of individual odors in determining colony membership in the very small colonies used here does not preclude the possibility that such cues are less important and colony specific odors more important in determining the response of colony members to conspecifics in larger wild colonies. It is, however, relevant to note that Telle (1966) has interpreted the results of his exceptionally thorough field studies of *R. norvegicus* as indicating that members of large colonies of rats in the wild recognize one another as individuals and not as a result of their having a common colony scent. Telle's findings in the field are thus consistent with our laboratory results.

Unfortunately, our observations give no indication of the source of the olfactory stimuli which might serve to identify individuals, though the high frequency of anogenital sniffing prior to the occurrence of aggressive behavior suggests that secretion of glands concentrated in the anogenital area may be important.

Experiment 4

The results of Experiment 2 indicated that olfactory cues are of primary importance in eliciting aggression, while the results of Experiment 1 indicated that the behavior of residents towards an unfamiliar introduced conspecific was in some measure influenced by the behavior of the intruder itself. In particular, it was observed that immobility on the part of an unfamiliar conspecific appeared to inhibit aggressive behavior in residents. The present experiment was undertaken to examine the role of movement by an unfamiliar animal in eliciting and directing aggression.

Method

Eight male, five anestrous, and five estrous female Long-Evans hooded rats were anesthetized (ip injection of .25 mg. Equi-thesin per 1 kg. body weight) and introduced singly into the home cages of resident pairs.

One week later, 8 additional male Long-Evans rats were anesthetized, and each immobile rat and an untreated male Long-Evans rat simultaneously introduced into each of the 8 home cages used in the first part of the experiment. Observations were made in the usual fashion.

Results

Single Intruders

The responses elicited by immobile females were quite variable. Three of the five females in both estrous and anestrous states were attacked and bitten by members of resident pairs. However, some of these biting attacks appeared to lack effect, piloerection was absent, and the biting itself looked rather more like feeding behavior than the usual aggression. The lack of serious disruption following introduction of anesthetized females is further indicated by the the fact that 5 of 10 residents fed in the presence of unconscious female intruders.

In response to the introduction of a single immobilized unfamiliar male rat, 1 or both members of all resident pairs exhibited high levels of aggressive behavior. The unconscious rat was the recipient of vigorous lateral threat postures and vicious attacks. In addition, members of the 8 resident pairs spent considerable periods of time digging and pushing wood shavings in the vicinity of the immobile intruder, with the result that it was often half covered by wood shavings pushed around by piloerected residents.

Perhaps most important is the observation that during the ½ hr. that an immobile male intruder was present, members of 4 of the 8 resident pairs behaved aggressively toward one another. Interresident aggres-

sion was observed only in the immediate vicinity of the immobile intruder and was of brief duration, ending as soon as 1 of the residents assumed a submissive posture.

Pairs of Intruders

Behavior observed following simultaneous introduction of mobile and immobile intruders was consistent across the 8 resident pairs. Given 2 intruding rats differing only in mobility, motionless intruders were investigated but never attacked, while the moving intruder was the recipient of vigorous lateral approaches and attacks. No interresident aggression was observed in the presence of intruder pairs.

Discussion

The data indicate that both mobile and immobile unfamiliar male rats represent sufficient stimuli for the elicitation of aggressive behavior. However, it appears that a moving conspecific is a more adequate stimulus for the release of aggressive behavior than an immobile one. When both immobile and mobile intruders are present, it is the latter which is attacked; when only an immobile intruder is present, both "displacement digging" (Barnett, 1963) and "redirected aggression" (Bastock, Morris, & Moynihan, 1953) toward an inappropriate target occur. Current interpretations of both displacement and redirected behavior would indicate that the immobile intruder is not a totally adequate stimulus for the release and direction of aggression in the wild rat.

CONCLUSION

The results of the investigations reported above indicate that the response of wild Norway rats to conspecifics is determined by a multitude of stimuli perceived via several sensory modalities. Response to a conspecific as such (amicable and sexual behavior) can occur in the absence of olfactory inputs. On the other hand, the initiation of aggression would appear to be dependent on olfactory stimuli arising from an unfamiliar individual. Both the duration and direction of aggressive behavior is further modified by the behavior of target animals.

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