

Commonality among rats in production of reward and nonreward odors

PAUL J. ESLINGER and H. WAYNE LUDVIGSON
Chemistry of Behavior Program, Texas Christian University, Fort Worth, Texas 76129

Male and female test rats acquired a patterned response (fast on reward trials, slow on frustrative nonreward trials) in a runway based on differential odors excreted by donor rats during prior rewarded and unrewarded placements in the goalbox. Initially, donor-test rat pairs were identical: A randomly selected, same-sex donor preceded the same test subject on each trial. In subsequent phases of the study, donors were interchanged for test rats, both within and between gender categories. Response patterning changed negligibly when the donor-test pairs were altered, suggesting a high degree of commonality among rats in odor excretions following reward and frustrative nonreward treatments.

Behavioral evidence for differential odor production from rats experiencing reward (R) and frustrative nonreward (N) has consistently been reported (e.g., Eslinger & Ludvigson, in press; Ludvigson & Sytsma, 1967; Prytula & Davis, 1976; Seago, Ludvigson, & Remley, 1970), with the implication that one or both of these treatments result in a chemical excretion of potential value to the rat as a "communication" signal, either learned or unlearned. For a chemical excretion, as for any emitted stimulus, to serve as a communication signal, the excretion must be relatively similar from one organism to the other. In the case of "reward" or "nonreward" odors, few studies speak to the question of the extent to which either of these presumed odors is the same from one rat to another. Studies showing stereotyped "spontaneous" or preexperimental reactions (based on no known learning experiences) to these odors suggest a degree of similarity (Collerain & Ludvigson, 1972, 1977; McHose, 1973; Mellgren, Fouts, & Martin, 1973), although conceivably the simple differential locomoting responses measured could have been controlled by a wide range of odorants. Also suggesting similarity is the finding by Pratt (1970) that the partially learned reactions of rats to their own odors generated from latent extinction placements were not substantially different from their reactions to odors of conspecifics given latent extinction placements.

A learned reaction might be more sensitive to interanimal variations in odor production, but studies utilizing learned responses have not addressed this issue. Studies of a learned "response pattern" to R and N odors emitted by preceding subjects in a squad have generally used a procedure in which the order of sub-

jects remained fixed throughout the experiment (e.g., Ludvigson, 1969; Ludvigson & Sytsma, 1967; Prytula & Davis, 1976). It remains a matter of controversy, therefore, whether differential odors following R and N may be characteristic of a rat and might not readily control the behavior of a conspecific trained with a different donor. That this may be possible is suggested by data demonstrating individual odor differences in rats (Krames, 1970) and discriminations in mice based on the individual odors of other mice (Bowers & Alexander, 1967; Hahn & Simmel, 1968).

A closely related issue is the possible influence of gender in the production of and response to R and N odors. Means, Hardy, Gabriel, and Uphold (1971) found that gender of rats that were "pathmakers" in a T-maze had no effect on the performance of male "pathfinders." After forcing the pathmakers left or right toward reward in the maze, pathfinders were rewarded for following the odor trail to the appropriate goal area. However, there were no tests of odor trails from pathmakers receiving nonreward. McNeese and Ludvigson (Note 1) have reported that squads of gonadectomized and preputialectomized rats did not differ from sham-operated rats in their discrimination of R and N odors. These results suggested that discriminable R and N odors were emitted by all three groups and were not a function of androgen-dependent accessory reproductive glands. One might speculate from these reports that no sex variable is operating in the production of and response to R and N odors; however, no study has directly assessed this possibility using both male and female rats as odor donors and test subjects.

This study investigated whether there are functionally important (1) individual differences and (2) gender-related differences in R and N odors or in their discriminative use. This was accomplished by interchanging donors after test subjects established patterned responding with a particular donor.

P. J. Eslinger is now at the University of Iowa, Department of Neurology. The authors gratefully acknowledge the support of the Chemistry of Behavior Program and the Research Foundation of Texas Christian University.

METHOD

Subjects

Eight male and eight female albino rats purchased from the Holtzman Company were approximately 100 days old at the start of the experiment. They were individually housed in stainless steel cages in a constantly illuminated vivarium. Their daily food rations were adjusted to maintain body weights at 85% of preexperimental ad-lib weights for the duration of the experiment.

Apparatus

The apparatus was a 2.13-m alleyway, 8 cm wide and 9 cm high, divided into start, run, and goal sections measuring .3, 1.23, and .6 m in length, respectively. The runway was constructed of wood, painted white and covered with hinged Plexiglas. A microswitch activated by the raising of the startbox door, in conjunction with photocells located .15, .76, 1.37, and 1.68 m beyond the start door, permitted the recording of four traversal times from start, Run 1, Run 2, and goal sections. A goalbox door prevented retracing into the runway. The food cup was glass and present in the goalbox on each trial. On R trials, a pellet dispenser was used to deliver 45-mg Noyes pellets to the goal cup through a tube mounted in the end wall. White paper covered the alleyway floor. A vacuum cleaner attached to the end of the goalbox was used to exhaust air while vents in the startbox served as air entrance portals.

Procedure

Within 7 days after imposition of restricted food rations, all subjects had stabilized at 85% of their ad-lib body weights. Pellet and apparatus habituations were then begun, with four groups randomly established: male donors, male test subjects, female donors, and female test subjects. Pellet habituation consisted of 4 days in which 20 45-mg pellets were given in the home cage daily. Apparatus habituation, which occurred on the last 2 days of pellet habituation, comprised (1) 5 min of free exploration daily in the unbaited runway for the test subjects and (2) eight goalbox placements per day for donor subjects on an RRNNRRNN schedule.

During the acquisition phase of the experiment, all subjects were given a double-alternation schedule of R and N that was reversed every 2 days (RRNNRRNN to NNRRNNRR). All subjects were given Trial 1 before Trial 2, and so on. On a given trial, a donor was brought from a separate waiting room into the apparatus room, where it was placed directly into the goalbox to receive R, 30 sec of access to 12 dispensed pellets, or N, 30-sec retention in the goalbox without reward. Then the donor was removed to a third room. Next, the appropriate test subject was brought from the waiting room and allowed to traverse the alleyway to receive either R or N in the same manner as the donor. Pellets were dispensed for the test rat after it broke the last photobeam. Following each donor-test pair, odor excretions in the alleyway were cleaned out by changing the paper flooring and exhausting the air for 30 sec.

With this general procedure, the experiment was divided into three phases. In Phase 1 (12 days, 96 trials), all donor-test rat pairings were identical from trial to trial: A randomly selected, same-sex donor preceded the same test subject on each trial. The order of running of animal pairs was randomly determined each day and maintained throughout the eight trials of a day. In Phase 2 (4 days, 32 trials), the pairings of donor and test subjects, as well as running order, were randomly determined on each trial, with the restriction that the pairs be either male-male or female-female. Thus, each test subject could be paired with any of four donors of the same gender. In Phase 3 (4 days, 32 trials), the running order and the coupling of donor and test rats were randomly determined on each trial such that any test subject could be paired with any of the eight possible donors, regardless of gender.

RESULTS

Traversal times were converted to meters per second; daily means of these transformed scores are presented in Figure 1. Means of these data points over the 4 days of Phases 2 and 3 and the last 4 days of Phase 1 were subjected to a phases by goal events by gender analysis of variance with repeated measures on the first two factors. Data analysis revealed a highly significant difference between goalbox approach speeds on R and N trials [$F(1,6) = 133.84$, $p < .001$]. Test subjects demonstrated patterned responding (fast on R trials, slow on N trials) that did not significantly differ between gender groups or with changes in donor subjects in Phases 2 and 3 (see Figure 1).

Analysis of speeds in the Run 2 section of the alleyway revealed similar discriminative responding [$F(1,6) = 48.36$, $p < .01$] and a significant phase treatment effect [$F(2,12) = 6.90$, $p < .05$]. According to a Newman-Keuls analysis, the latter effect arose from faster speeds at the end of Phase 1 than in Phases 2 and 3, indicating a slower development of patterned responding than in the goal section. Importantly, however, there was no indication that discrimination differed between sexes or suffered with changes in donor subjects.

A significant goal event difference was found in the Run 1 speeds [$F(1,6) = 10.92$, $p < .05$], as well as a Goal Event by Phases interaction [$F(2,12) = 7.60$, $p < .05$]. Tests of simple main effects revealed that the interaction arose from significant differences between R and N speeds during Phases 2 and 3 [$F(1,6) = 7.65$ and 13.11 , respectively, $p < .05$], but no such difference in Phase 1.

Analysis of start speeds showed no differences for goal events, sex groups, or phases, indicating that the discriminative cues were restricted to the goal and run sections of the alleyway.

Although the above analyses revealed no disruption of mean discrimination (i.e., the R-N difference) across Phases 2 and 3, it was possible that highly transitory disruptions might have occurred on the first day of each new phase. However, there were no suggestions of change

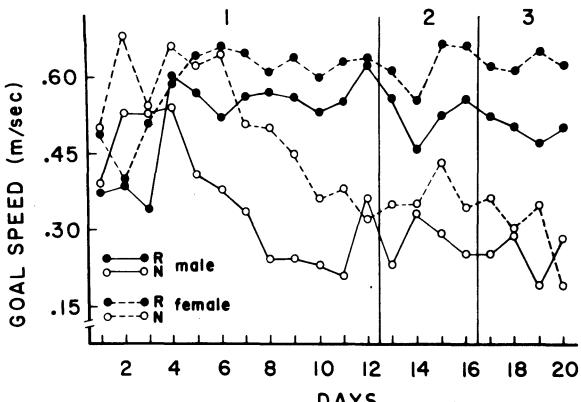


Figure 1. Daily mean goal speeds for groups of male and female test rats over the three phases of the study.

when the data were examined trial by trial on the first day of each new phase.

The random pairings of donor and test subjects in Phase 3 resulted in 51% of the pairings being sex-mixed (i.e., male-female or female-male). The goal speeds for each sex group in this phase were organized to permit analysis of speeds to male and female donors. No differences attributable to the gender of donor appeared for male or female test subjects, indicating that approach to R and N odors was not affected by the gender of subjects.

DISCUSSION

The results of this study are consistent with previous reports of a significant discrimination of odors excreted following R and N treatments (e.g., Morrison & Ludvigson, 1970; Prytula & Davis, 1976). It was demonstrated, further, that male and female test rats responded to donor rat odor cues in a similar manner regardless of gender factors, familiarity with the donor, or individual characteristics of donors. Thus, individual and sex differences in both the production of and discriminative use of R and N odors appear to be functionally unimportant.

This is not to argue with data suggesting odor differences among rats. For instance, studies by Bowers and Alexander (1967) and Hahn and Simmel (1968) with mice and by Krames (1970) with rats have demonstrated that individual scents can be discriminated by conspecifics. What the present data suggest is that any such individual odors must have been constant across both R and N trials, nondiscriminative with respect to the occurrence of reward, and thus irrelevant for the patterned responding. Given that, responding would not likely have been disrupted with the change in individual scent. The corollary to this inference is that odors that did provide the discriminative cues for patterned responding must have been rather similar from one donor to the next, so as to produce similar behavioral responses in conspecifics.

Assuming that, although constant and nondiscriminative, donors' individual scents were perceptible to the test animals of the present study, another inference is plausible. The individual scents would appear to have remained perceptually distinct and "ignorable" rather than to have fused with the discriminative odors; otherwise, odor Gestalten would have been formed on R and N trials. Such Gestalten would have been characteristic of the individual donor, and a change in donor should have disrupted performance because of the change in Gestalten.

It may be noted that, although the present data point to discriminative cues that are similar among rats, the question of whether the cues are different in a qualitative (different compounds) and/or a quantitative (different concentrations) sense cannot be resolved. Thus, if all donors had excreted on R and N trials more or less of some odor common to all of them, the present data could have resulted, as long as the quantitative variations were rather similar from donor to donor. In this regard, the possible role of subtle excretions of urine may warrant investigation.

The demonstration of interorganism similarity of R and N odors suggests that this experimental paradigm may be advantageous for chemical analysis of odor emissions with methods such as gas-liquid chromatography and mass spectrometry. One of the major limiting steps in the isolation and identification of chemical compounds influencing conspecific behavior is the extremely small concentration of excretions from any one organism. A fruitful approach to the chemical analysis of R and

N odors may be to collect odors from multiple donor rats and thereby enhance the concentration of the chemical compounds. Such efforts are currently underway.

In assessing the potential communicative value of R and N odor excretions for rats, the present data suggest that the prerequisite of interorganism similarity is satisfied. Therefore, continued study of the uses and limitations of these odors as signals (e.g., Eslinger & Ludvigson, in press) may aid the elucidation of the phenomenon of chemical communication and its possible role, as yet unknown in most cases, in common behavioral testing paradigms involving differential reward.

REFERENCE NOTE

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