Extending the generality of the odor hypothesis: Double-alternation responding in the wood rat (*Neotoma floridana osagensis*)

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In an attempt to extend the generality of the odor hypothesis, two studies using wood rats (*Neotoma floridana osagensis*) as subjects were conducted. Experiment 1 demonstrated that this species was capable of establishing appropriate odor-based double-alternation patterning in the straight runway. The results of Experiment 2 indicated that albino rats were capable of using odor cues exuded by wood rats, and vice versa.

Since 1967, a rather large body of research data (e.g., Bloom & Phillips, 1973; Eslinger & Ludvigson, 1980; Ludvigson, 1969; Ludvigson & Sytsma, 1967; Prytula & Davis, 1974, 1976) has shown that rats exude different amounts or types of odors on occasions of reward (R) and nonreward (N), and that these odors can act as discriminative cues for the behavior of conspecifics. For example, such odor cues are used to learn appropriate double-alternation responding (i.e., fast to R and slow to N) in the straight runway (e.g., Davis, Burns, Howard, & Voorhees, 1982; Davis, Whiteside, Bramlett, & Petersen, 1981; Ludvigson & Sytsma, 1967; Prytula, Davis, & Fanning, 1981), choice behavior in the T-maze (Morrison & Ludvigson, 1970), and appropriate responding under a random daily schedule of R and N (Davis, Prytula, & Voorhees, 1979). Electrophysiological recordings of mitral cells in the rat's olfactory bulb have verified the existence of such proposed R and N odors (Voorhees & Remley, 1981).

Davis, Nash, Anderson, and Weaver (1985) have suggested the integration of this body of odor research within the context of optimal foraging theory (e.g., Charnov, 1976; Krebs, Houston, & Charnov, 1981; Mellgren, 1982; Mellgren, Misasi, & Brown, 1984). Certainly, it appears reasonable to suggest that such odors could be employed as cues to enhance effective and/or efficient foraging for food by rats in the natural environment. However, before such assays are made in a natural or even a simulated-natural environment, it would seem important to establish that these odors are produced by the animals that normally inhabit these environments. Since Boice (1984) has reported the successful comparison of two subspecies of wood rat in the study of an operant analogue of foraging behavior, the choice of the wild wood rat as a subject for the laboratory demonstration of odor-based runway responding seemed most appropriate. Posi-

tive results would provide an impetus for studying the use of odor cues in the foraging situation by this wild species.

EXPERIMENT 1

Experiment 1 was specifically designed to study the production and utilization of odor cues by the wood rat. To allow the use of previous data (e.g., Davis, Thomas, & Prytula, 1981; Ludvigson & Sytsma, 1967; Prytula & Davis, 1974, 1976; Prytula et al., 1981) as a reference point, the animals were trained under a daily eight-trial double-alternation schedule (i.e., RRNNRRNN). Because only six subjects were available, two groups for separate testing under odor-maximizing and odor-minimizing conditions were impractical, and a three-phase, within-subjects procedure was substituted. During the first phase, the subjects were trained in a fixed daily sequence under the double-alternation pattern. Comparisons of the initial (low odor accumulation) subjects with the terminal (high odor accumulation) subjects in the daily sequence should yield information regarding the utilization of odor cues. Furthermore, as the first subject in the sequence was always tested in a clean, odor-free apparatus and essentially served as an odor donor, it was predicted that this animal would not display double-alternation patterning. During Phase 2, the last animal in the running sequence was rotated to the initial (odor-donor) position. The odor hypothesis would predict an immediate cessation in patterning due to the lack of odor cues when the animal was rotated to this position in the running order. During Phase 3, the initial subject in the running sequence was rotated back to its original (Phase 1) final position in the squad with the attendant prediction that patterning would be reestablished immediately.

Method

Subjects. Two litters of wild wood rats (*Neotoma floridana osagensis*) served as subjects. The subjects (two males and four females) were born in the laboratory within 2 days of the capture of the mothers. At weaning, the pups were placed in individual cages

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in the vivarium and were maintained on ad-lib food and water until they were 90 days old.

Apparatus. A single, straight runway (11.4 cm wide $\times$ 12.7 cm high) with a gray startbox (28.1 cm), black run section (91.4 cm), and black goalbox (30.5 cm) served as the experimental apparatus. The startbox and goalbox were separated from the run section by Masonite guillotine doors. The activation of a microswitch on the start door and the interruption of a series of three photoelectric beams (15.2, 92.4, and 116.8 cm beyond the start door) provided start, run, and goal latencies on each trial. A plastic receptacle recessed into the end wall of the goalbox served as a goal cup. A thin sheet of transparent plastic covered the top of the apparatus to prevent odors from dissipating.

Procedure. Two weeks prior to the start of runway training (i.e., at 90 days of age), the subjects were placed on food deprivation and maintained at 85% of their free-feeding body weight. A 7-day pretraining period immediately preceded the start of Phase 1. On all pretraining days, the subjects received: (1) habituation to the 45-mg Noyes reward pellets in the home cage, and (2) a 5-min exploration period in the baited apparatus with doors raised and photoelectric equipment operative. The exploration period also involved acclimation to the hardware-cloth cone that was used to transport each subject to and from the experimental apparatus. At the start of pretraining, each subject was randomly assigned a permanent number (1-6) according to running order in Phase 1.

During all phases of the experiment, each subject was administered a daily eight-trial double-alternation schedule of reward-nonreward (i.e., RRNNRRNN). On all days, Trial 1 was administered to all six subjects before Trial 2 was administered, and so forth. An R trial always consisted of access to 12 45-mg pellets; an N trial was 30-sec confinement to the empty goalbox. The runway was swabbed twice with separate water-dampened sponges and allowed to air dry after the completion of each trial. Hence, Subject 1 was always tested in a clean, odor-free apparatus.

During Phase 1 (21 days, 168 trials), the daily order for running subjects was 1-6. Phase 2 (4 days, 32 trials) involved the rotation of Subject 6 to the initial position in the squad, that is, the subjects were run in a 6-1-2-3-4-5 order. Phase 3 (4 days, 32 trials) involved the rotation of Subject 6 back to its original position as the terminal subject in the running order, that is, the subjects were run in the 1-2-3-4-5-6 order.

Results and Discussion

Prior to analysis and graphing, all latencies were reciprocated and multiplied by the appropriate metric constant to yield speed scores in meters per second. Since preliminary analyses failed to yield differences between adjacent trials of the same type, they were combined in the following manner: the first two scores were averaged to yield a composite R_1 score, the next two scores were averaged to yield an N_1 composite score, and so forth, for each subject. Hence, the eight daily trials were reduced to four representative speeds, that is, R_1 , N_1 , R_2 , N_2 , which were used for graphing and analysis purposes.

Because only one group of animals was employed, it was felt that a comparison of the speeds of animals tested under low-odor-buildup conditions (i.e., Subjects 2 and 3) with the speeds of animals tested under high-odor-buildup conditions (i.e., Subjects 5 and 6) would provide a sensitive measure of the presence and operation of odors (see Prytula et al., 1981).¹ The Phase 1 goal-measure speeds of these low- and high-odor-buildup subjects are shown in Figure 1. Clearly, appropriate double-alternation patterning was established only by the subjects tested under the high-odor-buildup conditions (i.e., Subjects 5 and

Figure 1. Mean goal speeds (meters/second) for wood rat Subjects 2 and 3 (low odor buildup) and wood rat Subjects 5 and 6 (high odor buildup) during Phase 1 of Experiment 1.

6). Analysis of variance, incorporating odor buildup (low vs. high) as a between-subjects factor and type of trial (R_1 , N_1 , R_2 , and N_2) and days as within-subjects factors, was performed on the speeds from Days 13-21 (the point at which patterning had been strongly established by high-odor-buildup subjects). Start- and run-measure analyses failed to yield any significant effects. The goal-measure analysis yielded significance for the following effects: odor buildup [$F(1,2) = 339.90$, $p < .01$], type of trial [$F(3,6) = 46.11$, $p < .001$], days [$F(8,16) = 9.22$, $p < .001$], odor buildup $\times$ type of trial interaction [$F(3,6) = 67.5$, $p < .001$], and odor buildup $\times$ days interaction [$F(8,16) = 5.35$, $p < .01$]. The Newman-Keuls procedure was employed to probe the significant interaction. Of primary importance to the present study was the finding that both R speeds of the high-odor-buildup animals (Subjects 5 and 6) were significantly ($p < .01$) faster than both of their N speeds on Days 13-21. No such R-N differences were found for the low-odor-buildup animals (Subjects 2 and 3). Thus, the statistical analyses corroborate the graphical impression (see Figure 1) that appropriate double-alternation patterning was developed only by Subjects 5 and 6. These results are in agreement with the contention (e.g., Prytula et al., 1981) that odor cues accumulate and become more intense or potent as additional animals are run, and that several days of training are required for the subjects to associate the odor cues with the appropriate situation/behavior.

Figure 2 shows the performance of the rotated animal (Subject 6) during Phase 1 (as last subject in the running

EXPERIMENT 2

Figure 2. Goal speeds (meters/second) of wood rat Subject 6 when tested as the last subject in the running order (left panel, Phase 1), as the first subject in the running order (center panel, Phase 2), and once again as the last subject in the running order (right panel, Phase 3) in Experiment 1.

order), Phase 2 (as first subject), and Phase 3 (as last subject). As the odor interpretation would predict, strong patterning was shown when this animal was tested under maximum odor-buildup conditions (i.e., Phases 1 and 3), but was completely eliminated when this animal was rotated to occupy the first, odor-free position in the running order (Phase 2).

Figure 3 presents a more complete picture of Phase 2 and 3 responding and the performance of Subjects 2 and 3 and Subjects 5 and 6 during these phases. As in Phase 1, the display of patterned responding clearly was a function of position in the daily running-order sequence. As in Phase 1, odor-based patterning was shown only by the high-odor-buildup animals (Subjects 5 and 6). Furthermore, it should be emphasized that due to the subject-rotation procedure used in Phases 2 and 3, Subjects 2 and 3 and Subjects 5 and 6 graphed for Phase 2 were *not* the same rats as those graphed for Phase 3. Despite these subject differences, it can be seen from Figure 3 that the pattern of responding was quite consistent from Phase 2 to Phase 3. Statistical analyses yielding significant odor buildup [Phase 2, $F(1,2) = 161.77$, $p < .01$; Phase 3, $F(1,2) = 107.69$, $p < .01$] and odor buildup $\times$ type of trial interaction effects [Phase 2, $F(3,6) = 13.06$, $p < .01$; Phase 3, $F(3,6) = 17.24$, $p < .01$] were supportive of these graphical impressions. Newman-Keuls tests yielded significant ($p < .01$) R-N differences in both phases only for the high-odor-buildup animals (Subjects 5 and 6). Taken collectively, the results of Experiment 1 support extending the odor hypothesis to include the wild wood rat.

Since Experiment 1 had clearly demonstrated that wood rats were capable of producing and utilizing odor cues, Experiment 2 was designed to determine if odors produced by this species could be employed as discriminative stimuli by another species. In this regard, Davis, Crutchfield, Shaver, and Sullivan (1970) reported that albino rats were capable of establishing appropriate double-alternation responding on the basis of odors exuded by gerbils. Through the use of separate groups of albino rats and wood rats, Experiment 2 sought to address several specific issues pertaining to cross-species odor utilization. First, it would seem important to replicate the basic finding that one species is capable of producing an odor(s) that can be utilized by a different species (Davis et al., 1970). A second purpose was to examine the bidirectionality of this odor effect. More specifically, since the Davis et al. (1970) study demonstrated only that albino rats were capable of employing odors produced by another species, it would appear relevant also to establish that another species can effectively use odors produced by albino rats. Last, the robustness and generality of the odor hypothesis would appear to be strengthened via the demonstration of the bidirectionality of odor production and utilization by laboratory and wild rodent species.

Method

Subjects. Five naive male albino rats,² and the six wood rats employed in Experiment 1 were used as the subjects for Experiment

Figure 3. Mean goal speeds (meters/second) for wood rat Subjects 2 and 3 (low odor buildup) and wood rat Subjects 5 and 6 (high odor buildup) during Phases 2 and 3 of Experiment 1.

2. The albino rats were approximately 90 days old at the beginning of the experiment; the wood rats were 154 days old.

Apparatus. The straight runway employed in Experiment 1 was also used in Experiment 2.

Procedure. The albino rats were pretrained as were the wood rats in Experiment 1. At the end of pretraining, they were randomly assigned a permanent running-order number (1-5). To ensure adequate odor production by the wood rats, these subjects received 3 days of retraining immediately prior to the start of Phase 1.³

During all phases, the two sets of rats were run as one large squad; the apparatus was swabbed and aired after each trial for all animals. Experimental training was divided into four phases. Phase 1 (19 days, 96 trials) consisted of running the subgroup of six wood rats first, immediately followed by the subgroup of five albino rats, that is, the wood rats served as odor donors for the initial albino rats. Phase 2 and 3 were each 2 days (16 trials) in length. Each of these phases involved the rotation of the last animal in the subgroup of albino rats to the first position in the running order in that subgroup. During Phase 4 (4 days, 32 trials), the original 1-5 running order was reestablished for the albino rats and the ordering of the subgroups within the larger group was reversed, that is, the albino rats now preceded the wood rats.

Results and Discussion

The data-transformation and trial-averaging procedures employed in Experiment 1 were also used in Experiment 2. The speeds of the first two albino rats, last two albino rats, and last two wood rats during Phases 1-4 are shown in Figure 4. It is clear from this figure that appropriate double-alternation patterning was shown by

Figure 4. Mean goal speeds (meters/second) of the first two albino subjects, last two albino subjects, and last two wood rat subjects during Phases 1-4 in Experiment 2.

Figure 5. Goal speeds (meters/second) of the first albino subject and first wood rat subject during Phases 1-4 in Experiment 2.

these three pairs of animals during Phase 1. Analysis of variance supported this impression by yielding significance for the trials within days effect [$F(3,9) = 9.89$, $p < .01$]. Aside from a slight disruption in the R speeds of the last two albino rats during Phase 2, rotating the terminal albino animal to the first position in that squad during Phases 2 and 3 had very little effect. This result suggests that the initial albino animals were utilizing odor cues exuded by the wood rats that preceded them. As with Phase 1, analysis of variance yielded significant trials within days effects for Phase 2 [$F(3,6) = 21.24$, $p < .01$] and Phase 3 [$F(3,6) = 26.79$, $p < .01$]. Subsequent Newman-Keuls tests indicated that R speeds did not differ reliably from each other, but were significantly ($p < .01$) faster than both N speeds, which did not differ from each other.

The finding that the trials within days effect [$F(3,9) = 4.74$, $p < .05$] and the groups $\times$ trials within days interaction [$F(6,9) = 6.37$, $p < .01$] were significant supports the graphical impression (see Figure 4) that patterning of the initial albino rats was completely eliminated during Phase 4. In agreement, subsequent Newman-Keuls tests indicated that R speeds were significantly ($p < .01$) faster than N speeds only for the last two albino rats and the wood rats.

Figure 5 shows the speeds of the first animal in the albino and wood rat subgroups, respectively. Obviously, the behavior patterns shown by these animals are in accord with an odor interpretation. Namely, strong patterning was shown by the albino rat *only* when it followed the wood rats (i.e., Phases 1-3). Likewise, patterning was developed by the initial wood rat *only* when it followed the albino rats (Phase 4).

GENERAL DISCUSSION

Three major conclusions are prompted by the results of these two experiments. First, it is clear that wood rats produce and utilize characteristic R and N odors in the same manner as do the albino rats that have served as subjects in previous experiments. More specifically, odor-based double-alternation patterning was established by the wood rats in both experiments. That this patterning was displayed by animals tested under high-odor-buildup conditions is in agreement with odor-accumulation data reported by Prytula et al. (1981). The immediate elimination and reestablishment of patterning produced by rotating the terminal animal to the initial position in the running order and then back to the terminal position (i.e., Phase 2 and 3, respectively, of Experiment 1) would appear to rule out other cue sources, such as food odors that were not affected by the rotation, and strengthen the case for an R-N odor interpretation. Likewise, the maintenance of patterning by the high-odor-buildup subjects during Phases 2 and 3 of Experiment 1 suggests a commonality of odor cues among subjects of this species. This is suggested because the rotation procedure resulted in different animals' being tested under the high-odor-buildup condition during these two phases. Using similar rotation procedures with albino rats tested under different deprivation states, Weaver, Davis, and Moore (1984) also reported results consistent with a commonality viewpoint.

Second, the results of Experiment 2 demonstrate that odors produced by wood rats may be used by albino rats, and vice versa. Patterning was strongly established during Phases 1-3 by the first two and last two albino rats. However, the patterned responding of the first two albino rats was immediately eliminated on Day 1 of Phase 4 when the ordering of the albino and wood rat subgroups was reversed and these animals appeared in the initial (i.e., low odor accumulation) positions in the running order. Thus, it would appear that discriminable odor cues were present and utilized by the first two albino rats when they followed the wood rats during Phases 1-3, but not when they were run first during Phase 4. Likewise, the establishment of patterning by the first wood rat subject during Phase 4 suggests the presence of effective R-N odor cues (see Figure 5). As this subject had shown no evidence of patterning during Phases 1-3, the assumption that viable odor cues, exuded by the albino rats that now preceded this animal, were utilized during Phase 4 appears reasonable. Conversely, the elimination of patterned responding by the first albino rat on Day 1 of Phase 4 (see Figure 5) clearly reflects the effects of removing the wood rat odor cues that had served as discriminative stimuli during Phases 1-3. It is also worth noting that the rotation procedures employed in Phases 2 and 3 of Experiment 2 failed to produce any major disruption in double-alternation patterning. Thus, the rotated albino rats were capable of using odor cues exuded exclusively by wood rats as effectively as those odors that were present during Phase 1. In summary, Experiment 2 presents several

independent pieces of data that are supportive of the cross-species utilization of R and N odors.

Finally, the clear demonstration of odor-cue production and utilization by the wild wood rat suggests that such odors may also be present and utilized in the foraging situation. Obviously, further research is needed to substantiate this contention. However, the existence of data on taste preferences (Harriman, 1978), self-selection of diet (Harriman, 1974), and the geographic distribution and behavioral aspects (Poole, 1940) of several subspecies of wild wood rat will certainly facilitate this research.

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NOTES

1. Since Subject 1 was always tested in an odor-free apparatus and served as an odor-donor animal, its data were not included in the low-odor-buildup condition.
2. The death of one albino subject during pretraining precluded the use of same-sized groups in Experiment 2.
3. Two weeks elapsed between the end of Experiment 1 and the start of Experiment 2. Since the presence of a viable odor source was deemed important for the albino subjects, retraining was given to the wood rats.

(Manuscript received August 16, 1984;
revision accepted for publication December 12, 1984.)