The effect of thigmotaxis on negative phototaxis in the earthworm

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Negative phototaxic (light avoidance) responses of earthworms were measured under two thigmotaxic (bodily contact) conditions: presence or absence of an alley. As predicted by Smith (1902), the presence of an alley greatly increased the time taken by Ss to move away from a light source. It was concluded that thigmotaxis is a powerful motivational variable in the earthworm.

Ratner & Gardner (1968) attempted to test a hypothesis by Smith (1902) that earthworms given an opportunity to maintain bodily contact with the environment (positive thigmotaxis) would reduce their avoidance response to light (negative phototaxis). In general, their experiment supported the hypothesis, but a number of comparisons were not in the expected direction, and others which were in the expected direction were not significant due to unreliable response frequencies. There are a number of probable sources of this unreliability. First, the light source was turned on for only 2 sec of every 60-sec period. Backward and forward responses during the light period and during the first 2 sec of the nonlight period were recorded. Part of the unreliability may stem from the fact that in response to bright light, earthworms in our laboratory typically move backward initially and then forward. Perhaps a better procedure would be to leave the light on continuously until the S made some specified response or set of responses and measure response time as an index of responsiveness. Second, to vary the amount of contact. Ss were run in alleys 3/16, 5/16, or 1/2 in. in width. In all three conditions, Ss were allowed contact with the floor and at least one wall. Perhaps a more reliable strategy would have been to have, in addition to an alley group, a no-alley group run on a flat surface with no available wall contact. Finally, repeated measures were taken on each S in each type of alley on separate sessions according to a counterbalanced design. In a separate experiment reported in the same paper, Ratner & Gardner (1968) reported some decrease in responding over sessions. This source of unreliability could be reduced by using an independent groups design using each S for only one session. The present experiment attempted to test the Smith (1902) hypothesis about the relationships between thigmotaxis and phototaxis, using the above suggested strategies.

METHOD

Twenty earthworms (L. terrestris) were haphazardly selected from a supply obtained from a local hatchery on the basis of size and apparent good health. Prior to selection, the worms were maintained in a $1 \times 2 \times 1$ ft wooden box containing moist sandy loam to which leaves and cornmeal were added for food. After selection, Ss were kept individually in 1-pint plastic cartons with lids to which a small amount of aged tap water was added to prevent desiccation. The apparatus consisted of a wooden surface marked with a 3-in.-diam circle and an 11-in.-diam circle sharing the same center. The surface was kept moist during the experiment with aged tap water. The bulb of a high-intensity lamp (Penetray No. 93) was located $6\frac{1}{2}$ in. above the center of the circles. Two $\frac{1}{2} \times \frac{1}{2} \times 12$ in. pieces of wood were placed 3/32 in. from a diameter of the circle in such a way as to form an alley $3/16 \ge 1/2 \ge 12$ in. over the center of the circles. The room was illuminated by a 25-W ruby red bulb.

The Ss were divided randomly into the four following groups of five each: an alley-light group (AL), a no-alley-light group (NAL), an alley-dark group (AD), and a no-alley-dark group (NAD). For Ss in the AL and AD groups the pieces of wood were placed to form an alley, and for the NAL and NAD Ss the pieces of wood were removed. For the NAL and NAD groups, each S was given one trial, which consisted of placing the S within the 3-in, circle and recording the time taken for the S to extend its first segment (prostomium) over the 11-in. circle. For the AL and AD groups, the procedure was the same, except that the S was placed in that portion of the alley marked off by the 3-in, circle to initiate the trial. An arbitrary upper limit of 15 min was set at which the trial was terminated if the S had not responded. For Ss in the AL and NAL groups, the high-intensity light was on throughout the trial. The Ss were run in blocks such that one S in each

group was run before a second S in any group. Within blocks, the order of running was random. No record was kept of the presence and amount of mucous secretions in the test area.

RESULTS

The median response times for the four groups were 500 sec for AL, 900 sec for AD, 220 sec for NAL, and 548 sec for NAD. None of the AD Ss responded within the 15-min upper limit. The following Mann-Whitney U comparisons were made: (1) To assess the effects of light, AL and NAL response times were compared with AD and NAD response times (U = 16.5, p < .01); (2) to assess the effects of the alley, AL and AD response times were compared with NAL and NAD response times (U = 11, p < .005); (3) to assess the effects of the alley under the lighted condition, AL response times were compared with NAL response times (U = 0, p < .005); and (4) to assess whether the light had a greater effect than the alley, AL response times were compared with NAD response times (U = 11, p < .05).

DISCUSSION

The results of this experiment strongly confirm the hypothesis of Smith (1902) and the main results of Ratner & Gardner (1968) that positive thig motaxis reduces negative phototaxis in earthworms. The results of the Mann-Whitney U comparisons indicate that both the presence of light (p < .01) and the absence of an alley (p < .005) caused the Ss to escape more quickly. The U comparison between the AL and NAL groups (p < .005) showed that the presence of an alley greatly diminished the effect of the light.

Although the significance probability for alley (p < .005) was less than the significance probability for light (p < .01), indicating a somewhat stronger alley influence than light influence, the U comparison between the AL and NAD groups (p > .05) indicated that the two influences were roughly equated in this experiment. This was an unexpected finding because phototaxis is frequently used as a motivational factor in earthworm learning experiments while thigmotaxis is not. Most of these experiments put the S in an alley allowing considerable contact with the substrate, presumably lowering, thereby, responsiveness to other stimuli. Perhaps earthworms would learn mazes more readily if the mazes were elevated, preventing contact with an alley.

In all cases when the alley was present, Ss maintained substantial contact with the intersection of one wall of the alley with the floor. Ss of the AL group were quite active but did not leave the 11-in. circle because they tended to keep their rear segments anchored to the substrate. Ss of the AD group displayed little activity, indicating perhaps that this condition included the essential components of an earthworm's home burrow.

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The developmental aspect of marking and nesting behaviors in Mongolian gerbils (Meriones unguiculatus)*

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The marking and nest-building behaviors of male and female gerbils were studied developmentally. Gerbils of both sexes began to mark at 5 weeks of age. though males did not mark more often than females until 16 weeks of age. Both males and females were able to use cotton to build nests at 5 weeks of age. No sex difference was found in cotton consumption at any age level. The marking and nesting activities were positive functions of age.

The purpose of the present study is to investigate the development of marking and nesting behaviors in male and female gerbils.

EXPERIMENT 1:

MARKING BEHAVIOR

Mongolian gerbils have been observed to mark prominent objects in their environment with the midventral sebaceous gland pads. This behavior has been studied extensively by Thiessen and his associates (Thiessen, 1968a, b; Thiessen, Friend, & Lindzey, 1968). Marking behavior is sex-dimorphic, androgen-dependent, and appears to relate to territoriality (Thiessen, 1968a). Lindzey, Thiessen, & Tucker (1968) reported that male gerbils began to mark at 70 days of age and showed a high degree of marking activity at about 100 days of age. Gerbils of both sexes were studied in the present experiment.

Subjects

Upon arrival, 10 males and 10

*This work was supported by National Science Foundation-University Science Development Program Grant GU-1598.

females, purchased from Tumblebrook Farm at 28 days of age, were housed singly in cages measuring 11¹/₂ x 7¹/₄ x 5 in. and maintained ad lib with water and Purina Lab Chow.

Apparatus

The Ss were housed in an air-conditioned room with a mean temperature of 76° F (74° to 78°). The laboratory had a 12-h light-dark cycle. Polypropylene cages and chrome-plated lids from Lab Cages, Inc., were used to house Ss. The testing apparatus was a black plastic box of 24 x 24 x 18 in. with a front transparent observation window. Six pegs $(1 \times 1/2 \times 1/8 \text{ in.})$ were arranged in two rows of three each, with equal spacing among pegs. The box was illuminated with a 15-W fluorescent light during testing.

Procedure

Ss at 4 weeks of age were tested in a random sequence once a week for 13 weeks. The S was placed in the center of the apparatus and observed for 5 min. The number of marks were recorded. The apparatus was cleaned with 50% Ethonal before and after testing of each S. At the end of the experiment, the sebaceous gland sizes of the Ss were measured.

Results and Discussion

Figure 1 presents the number of marks exhibited by the gerbils. The analysis of variance showed that there was a significant main day effect (F = 6.06, df = 12/216, p < .01), and both males and females indicated significant day effects (F = 4.06, 1.84, and p < .01, .05 for males and females, respectively; df = 12/117 in both cases). The positive correlation between marking scores and age is in agreement with findings of Lindzey et al (1968), and the number of marks exhibited by male gerbils at approximately 100 days of age observed in the present study are also similar to those reported by Lindzey et al. However, there are differences between these two studies in the time of onset of marking behavior. While Lindzey et al found that male gerbils did not mark until approximately 70 days of age, the present study showed that gerbils of both sexes began to mark as early as 35 days of age. The discrepancy may be due to differences in sampling or housing conditions.

Sex differences in the marking scores almost approached the significant level (F = 4.27, df = 1/18, p < .10). Daily sex comparisons revealed that males marked more frequently than females at 16 weeks of age but not at any other age level. The significant Sex by Day interaction further indicated that the increase of marking scores proceeded differentially in males and females along the age dimension (F = 2.72, df = 12/216, p < .01). Thiessen (1968a) also stated that adult males marked more frequently than adult females.

The Mann-Whitney test indicated that the mean gland size of males (L x W, 1.75 x 0.47 mm) was significantly larger than that of females $(0.26 \times 0.06 \text{ mm})$ (p < .01). The results are congruent with reports by Thiessen (1968a) and Lindzey et al (1968).

EXPERIMENT 2:

NEST-BUILDING BEHAVIOR

Gerbils have been reported to use leaves of buckwheat, Graminaceae and Cyperaceae to build round nests about 18-25 cm in diam (Schwentker, 1965), and to shred papers of various thickness to build nests (Glickman, Fried, & Morrison, 1967). Cotton was used as nesting material to investigate nesting activity in this study.

Subjects

The Ss were those used in Experiment 1; they were tested and maintained under the same conditions.