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Technical Note: Earthworm Behavior in a Modified Running Wheel

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An apparatus which permits automated recording of earthworm wheel-turning response over many sessions is described. Data were obtained for three earthworms presented successively with five sessions of continuous darkness, five sessions of intermittent incandescent light, and five sessions of continuous darkness. Wheel-turning rates decreased during the first five sessions of darkness and remained at zero rates during the last five sessions of darkness. Furthermore, during intermittent incandescent light more responses were emitted during the dark phases than during light phases.

Automated test apparatus are currently in use for fruit flies (Platt, Holliday, & Druge, 1981), ants (Abramson, Collier, & Marcucella, 1977), house flies (Leeming & Little, 1977), and honey bees (Sigurdson, 1981a, 1981b). Parallel advances for annelids, however, have not kept pace. Classical, instrumental, and avoidance procedures for earthworms, though frequently used (Datta, 1962; Ratner, 1964, 1962), require the experimenter to manually initiate stimulus presentation and to manually record the data for each trial. Recently, an earthworm running wheel has been described (McManus & Wyres, 1978) which allows automatic detection of wheel-turning behavior. Currently, certain technical questions remain unresolved. For instance, can an earthworm survive repeated confinement in the device; what is the baseline wheel-turning rate over an extended time period; does the response habituate; and what is the effect of commonly used stimuli such as intermittent incandescent light. The purpose of this experiment was to answer these questions.

Method

Subjects

Three mature earthworms (L. terrestris) obtained from a local supplier were used (Subjects 2, 7, and 8). Each was maintained at 3 degrees C in individual glass containers (3.6cm x 2.9cm x 2.5cm) partially filled with soil.

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The mean weight of each subject at the start of the experiment was 5.1 gm with a standard deviation of 0.6.

Apparatus

A running wheel similar to one described by McManus and Wyres (1978) was constructed. The running wheel and base of the modified apparatus (Figure 1) were constructed from plexiglas. The wheel was made of two identical disks which were grooved along the outer rim. When the disks were fastened together a tunnel—the runway—was formed in which the earthworm was confined. The wheel weighed 97 grams with an inside radius of 7.56 cm at the deepest point in the grooved runway. The groove dimensions were 1.7 cm in width, 1.06 cm in height, and the length of the runway was 47.5 cm.

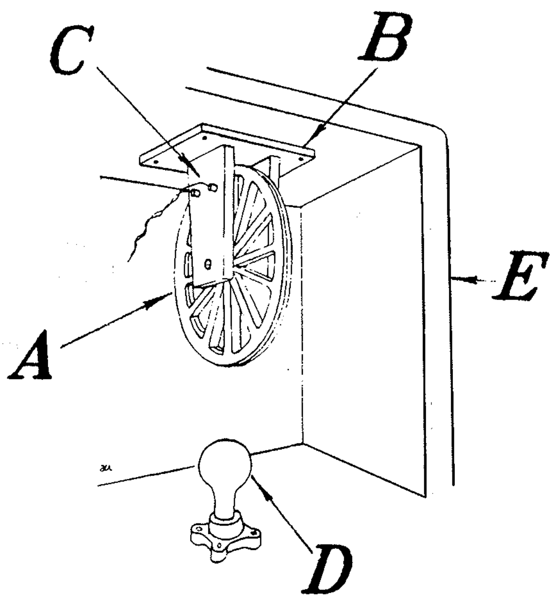

Figure 1: Modified running wheel for earthworm. A = Wheel, B = Base, C = Photocell placement (emitters not shown), D = Incandescent Light Bulb, and E = Enclosure. The spoke pattern sandwiched between the two halves of the wheel is not shown.

Two serious drawbacks of the McManus and Wyres wheel were resolved in the current design. First, turning rates of the McManus and Wyres wheel could be inaccurate. The photodetector which was used to measure wheel-turning responses could generate a rapid sequence of responses if a spoke of an oscillating wheel partially occluded the photocell beam. This was corrected in the current design. The base contained two photodetectors (GE L14g3) and two infrared emitters (GE Led55cf). One detector was connected to the set and the other detector was connected to the reset of a flip-flop and the output of the flip-flop defined a response. After a detector was tripped by a wheel spoke, further activity would not effect the state of the flip-flop until the other detector was activated. Second, accurate specification of light falling upon the worm was difficult with the McManus and Wyres wheel. The base obstructed light from the portion of the wheel in which the worm was most likely to reside. The wheel base of the current apparatus did not obstruct light. The base was fastened to the top of the chest with the light source placed on the floor of the chest directly under the wheel. The worm's weight within the wheel automatically centered the worm in an unobstructed position above the light source. In addition, the current design allowed the sensitivity of wheel-turning detection to be adjusted. The current design used a spoke pattern in order to break the photocell beam. The spoke pattern was xeroxed on a disk of celluloid and was sandwiched between the halves of the wheel. Twenty degree wheel turns were required for each response. Thus, on the average a worm crawled 2.38 cm along the circumferential runway to produce one wheel-turning response. Response sensitivity could be altered by xeroxing a different spoke pattern.

The apparatus was placed in a chest which was maintained at a room temperature of 28 degrees C. During the experiment a Sylvania 150 watt, 130 volt, incandescent light bulb served as the light source. The top of the bulb was five inches below the bottom edge of the wheel. Temperature within the wheel gradually increased during each session and ranged over sessions from 28 to 31 degrees C. Direct measurement of runway temperatures was made with an IN625 diode calibrated with a Tektronix DM501 Digital Multimeter and P6058 temperature probe. These measurements were made by enclosing the diode within the bottom of the wheel.

Procedure

Each earthworm was presented with five sessions of continuous darkness, five sessions of intermittent incandescent light, and five sessions of continuous darkness. Preceding each session, the subject was rinsed with water before being placed into the wheel. Each session was 53-min long and was made up of eight blocks of four-min durations—each block separated from the next by a three-min interval without illumination. During the three-min interval the data which had been stored in a microprocessor during the preceding four min was automatically transferred to a larger computer. Each block consisted of four periods of one-min duration and each one-min period was composed of a 30-sec light phase followed by a 30-sec dark phase.

During the light phase of the intermittent incandescent light condition the bulb was energized with 80 VAC and during the dark phase of the intermittent incandescent light condition the bulb was not energized. During both the light and dark phases of the continuous darkness conditions the light bulb was not energized.

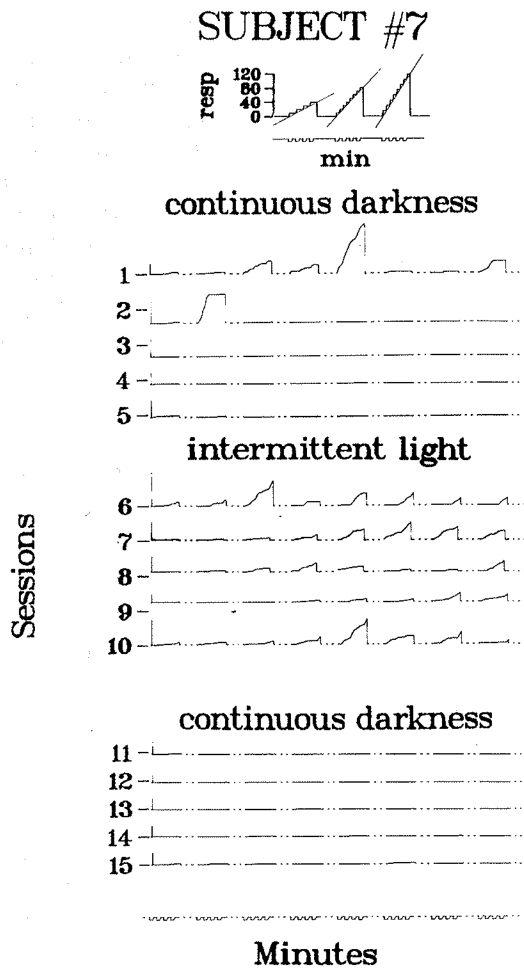

Figure 2: Cumulative records of wheel-turning response of Subject 7. Responses between blocks were not recorded as indicated by the dash lines connecting the cumulative records of successive blocks. The response rate per min during each block can be determined using the key located above the cumulative records.

Results

All subjects completed the experiment and remained active. Each subject responded with vigorous squirms to the water bath preceding each session as well as ten additional sessions not reported here. Subjects 7 and 8 demonstrated as much responding on the last day of intermittent incandescent light as on the first day of intermittent incandescent light. Estimated forward motion of the subjects determined from total responses per session compared favorably with other estimates in the literature. Minimal forward motion of subjects 7 and 8 was above 18 cm per min during sessions 1, 6, and 7. This is within the range of 14 to 30 cm per min reported by Gray and Lissmann (1938).

Response rate varied considerably from one block to the next within sessions. Figure 2 contains the cumulative record for subject 7. Cumulative records for the other subjects were similar. Responses between blocks were not recorded as indicated by the dash lines connecting the cumulative records of successive blocks. The response rate per min during each block can be determined using the key located above the cumulative records.

Response rate was greater during intermittent light. Figure 3 shows responses during both the light and dark phases. Each circle represents the number of responses during eight successive dark phases and each triangle represents the number of responses during eight successive light phases. Responding decreased during the first five sessions of continuous darkness and remained at a low rate during the second five sessions of continuous darkness. Response rate increased for all subjects when intermittent incandescent light was initially presented.

During intermittent incandescent light, all subjects emitted more responses during the dark phases than during the light phases while an equivalent number of responses were emitted during each phase during continuous darkness. Mean relative responding of the subjects in the dark phases during sessions 1 through 5 of continuous darkness was 0.47 with a standard deviation of 0.02 while mean relative responding of the subjects in the dark phases during sessions 6 through 10 of intermittent incandescent light was 0.69 with a standard deviation of 0.02. Assuming that the most probable relative response rate in the dark phase should be 0.5, mean difference scores were not significantly different from zero for sessions 1 through 5 of darkness ($t = 2.0$, alpha = 0.05) but were significantly different from zero for sessions 6 through 10 of intermittent incandescent light ($t = 15.2$, alpha = 0.05). Meaningful comparisons for sessions 11 through 15 were not possible because the response rates during most phases were zero.

Response decrement occurred over the first component of darkness and was retained in the second component of darkness. Response decrement did not occur for subjects 7 and 8 during intermittent light. Difference scores for

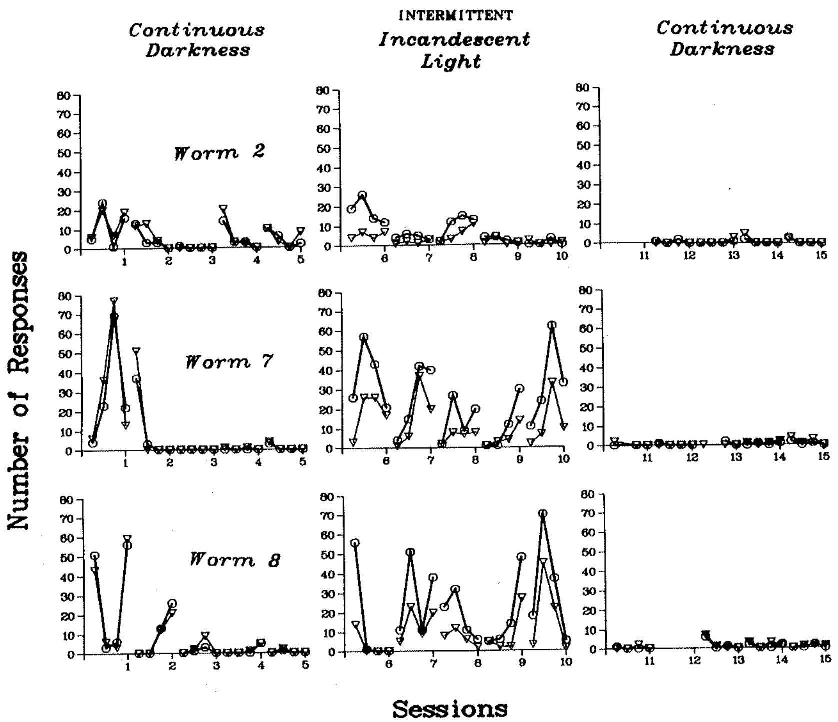

Figure 3: Number of responses in light and dark phases presented separately. Each circle represents the number of responses in eight successive dark phases and each triangle represents the number of responses in eight successive light phases. The data of session 11 of worm 2, the data of session 12 of worm 8, and a portion of the data of sessions 13 and 11 of worm 7 were lost.

session 1 compared with 5 were significantly different from zero ($t = 2.99$) but were not for session 6 compared to 10 ($t = .03$).

Discussion

The modified earthworm running wheel allowed investigation of earthworm wheel-turning response over many sessions. The subjects remained healthy throughout the experiment. The data were consistent with crawl rates observed outside of the running wheel (Gray & Lissmann, 1938). Response rate during darkness decreased over sessions; however, response rate during intermittent incandescent light remained stable. The data were consistent with previous reports on habituation of head movement in response to intermittent light (Ratner & Gardner, 1968, and Ratner & Stein, 1965). Ratner and Stein (1965) reported that the frequency of head movement did not significantly change during the session. In their experiment, earthworms were presented with one session of 60 trials, each consisting of a two-sec light pulse separated by 8-sec or 88-sec intervals of darkness. A 10-min period of darkness immediately preceded the presentation of the first light pulse. This is consistent with the current findings because the habituation to the wheel situation in the current data is not observed in the first session but only in comparison of the initial five sessions. Ratner and Gardner (1968) reported that frequency of head movement did not change over three sessions. In their session 30 min of continuous red-light preceded 40 presentations of two-sec light pulses separated by 58 sec. It is likely that the response decrement of the current data occurred during the 30-min interval preceding the start of their session.

In summary, the current findings demonstrate that the modified running wheel is a valuable tool for the investigation of earthworm behavior within a controlled and structured environment. Apparatus used in previous investigations were typically unautomated. They relied on the experimenter to detect responses and to administer stimuli. Unreliable data were often generated under these conditions. The running wheel described in this paper offers a reasonable solution for laboratory investigation of earthworms and supplies the investigator with a valuable addition to open field investigation.

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