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Geotaxis in 2-Week-Old Norway Rats (*Rattus norvegicus*): A Reevaluation

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ABSTRACT: In 1926, Crozier and Pincus first reported that 2-week-old rats placed head-down on an inclined plane orient in a head-up direction; this response is called negative geotaxis. In Experiment 1, we replicated this finding by testing 12- to 14-day-old rats on an inclined plane covered with wire mesh. Pups oriented in a head-up direction and avoided the head-down direction at inclines of 45° but not 30°. Because pups in Experiment 1 appeared to grasp the wire mesh with their claws, pups in Experiment 2 were now tested on a smooth but high-friction substrate. At inclines of 30°, 35°, and 40°, pups did not exhibit significant tendencies to orient in a head-up direction or avoid a head-down direction. Finally, in Experiment 3, the effect of substrate on geotaxis was tested further by comparing pups' behaviors at 40° with the inclined plane covered with either wire mesh or the high-friction substrate. Pups' orientation behaviors differed on the two substrates. Taken together, these data suggest that testing substrate affects the orientation behaviors of young rats and raise questions about the plausibility of applying the concept of geotaxis to young mammals, at least when tested on an inclined plane. © 1999 John Wiley & Sons, Inc. *Dev Psychobiol* 35: 35–42, 1999

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At the end of the last century, Loeb (1890) suggested that when acted upon by a physical stimulus, animals seek to equalize the incoming sensations by moving toward or away from the stimulus. Loeb's description of tropisms provided a new framework for studying behavior and influenced behavioral studies for many years (Fraenkel & Gunn, 1961). By the early 1900s, many orienting behaviors had been identified in animals including geotaxis, which is defined as the orientation response of an animal to a gravitational stimulus (Fraenkel & Gunn, 1961; Klopfer & Hailman, 1974).

In a series of studies beginning in the 1920s, Cro-

zier and Pincus (e.g., 1926, 1929) identified and described the development of geotactic behavior in young rats (*Rattus norvegicus*). In their experiments, 12- to 14-day-old rats were placed on an inclined plane covered with wire mesh in either a head-down or horizontal position. The animal's "angle of orientation" upon leaving its starting position was recorded. Crozier used nine different angles of inclination to test geotaxis, from 15° to 70°, and reported that as the angle of inclination increased, the animal was more likely to move vertically up the incline. These findings were supported and elaborated in subsequent publications (e.g., Crozier & Pincus, 1936). In addition, other associates in Crozier's laboratory reported similar findings in young guinea pigs (Elliot & Stavsky, 1933), mice (Crozier & Oxnard, 1927), and kittens (Stavsky, 1932, 1933).

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Outside of Crozier's laboratory, two other investigators attempted to replicate Crozier's findings, but without success. For example, contrary to the impression provided by Crozier's results, Hunter (1927a) found that many young rats changed direction and body orientation as often as 60 times in a single trial. In addition, Hunter found that at inclines greater than 45°, many animals fell from the incline within the first few seconds of a trial, thus making it difficult to assess their geotactic response (Hunter, 1927a, 1927b).

Hovey (1928) also took issue with Crozier's methods and conclusions. First, he questioned the small sample sizes used by Crozier and his colleagues (i.e., typically 2 to 4 animals per experiment). In addition, like Hunter, Hovey found that rat pups change body orientation frequently during a trial, thus making it difficult to accurately assess the pup's orientation at any single inclination. Furthermore, Hovey noted that the backward orientation of a rat's claws makes it difficult for a rat to move downward on an inclined plane, especially on wire mesh. Thus, in an article entitled "The nature of the apparent geotropism of young rats," Hovey wrote that it "seems reasonable to assume that the animal creeps upward because inhibitions are developed against downward and sidewise creeping as a result of purely physical and structural factors such as the arrangement of its claws and legs, shifting of the center of gravity within its body, etc., which tend to prevent it from moving in any direction other than upward" (Hovey, 1928, p. 560). Finally, that a pup's performance improved with practice further suggested that geotactic behavior was not reflexive, as Crozier argued, but learned. Thus, Hovey suggested that geotactic behavior is more accurately described as geokinesis, that is, a general arousal response to a gravitational stimulus that does not involve orientation of the body toward the stimulus (Klopfer & Hailman, 1974).

Despite Hunter and Hovey's reservations, Altman and Sudarshan (1975) used rat behavior on an inclined plane as a developmental indicator, thus further supporting geotaxis as an identifiable reflex in young rats. Currently, developmental studies in the field of teratology use behavior on inclined planes to assess geotaxis in young animals (Luthman, Oskarrson, Olson, & Hoffer, 1992; Norton, Terranova, Na, & Sancho-Tello, 1988; Paulson et al., 1994). Interestingly, however, the neural and physiological mechanisms underlying the expression of geotaxis have not been identified, nor has the functional relevance of geotaxis been addressed. In addition, methodological problems like those described above have not been confronted. Therefore, in Experiment 1, we repeat Crozier and Pincus' experiment using similar methods while also

considering the methodological concerns expressed by other investigators.

EXPERIMENT 1

Methods

Subjects. Sixty-four rat pups from eight litters were used. Equal numbers of males and females were used. All subjects were born to Harlan Sprague-Dawley females and were 12–14 days old on the day of testing. Subjects were raised in litters that were culled to 8 pups within 3 days after birth (day of birth = Day 0) and were housed in standard laboratory cages (48 × 20 × 26 cm) in which food and water were available ad libitum. All rats were maintained on a 12:12 hr light:dark schedule with lights on at 6 a.m.

Test Environment. The apparatus was made from a plywood base with a hinge mechanism that allowed the plane to be set at various angles of inclination. The inclined plane was constructed from Plexiglas and was 24 cm wide × 24 cm long. Its surface was covered with brass wire mesh (1 mm × 2 mm rectangular grids) and the central position of the plane was demarcated by a grid drawn on poster board that was visible beneath the wire mesh. All trials were conducted at room temperature.

Procedure. Approximately 5 min before testing, the dam was separated from the litter. Pups were randomly assigned to experimental conditions and were removed individually from the nest for testing. Each pup was placed on the inclined plane at one of two angles (30° or 45°) and in one of four starting positions (head-up, head-down, facing left, or facing right). After placement on the plane the pup was held gently in the starting position for 5 s before being released. Each trial was videotaped for at least 15 s, or until the pup fell or touched a side or bottom wall. After the trial, the pup was marked for identification and returned to the home cage. Before the next trial, the wire mesh was cleaned with ethyl alcohol to insure that odor trails from previous pups did not influence the behavior of subsequent animals. Each pup was tested once. When all pups in a litter had been tested, their sex and weight were determined and they were returned to the home cage.

Data Analysis. The data were scored by determining the orientation of the rat pup for every second of the trial. Orientation for each animal was measured by comparing the longitudinal body axis of the rat pup

(defined by the spinal column between the pectoral and pelvic girdles) to a clock face that was subdivided into 12 units. The top of the circle was defined as 12 o'clock and the bottom of the circle defined as 6 o'clock. For example, a rat pup in the 12 o'clock orientation was head-up on the plane with its tail at 6 o'clock. Quadrants of the clock were designated to identify four possible orientations. Thus, 11 to 1 o'clock was defined as the "up" orientation, 2 to 4 o'clock was defined as the "right" orientation, 5 to 7 o'clock was defined as the "down" orientation, and 8 to 10 o'clock was defined as the "left" orientation.

The data were analyzed using a Wilcoxon signed-ranks test to determine if animals, at each of the four starting positions and at each of the two angles of inclination, oriented in a head-up position or a head-down position more or less often than expected by chance. Specifically, the percentage of time that each pup oriented in a head-up position and the percentage of time that each pup oriented in a head-down position were compared to a chance level of 25%. Data were excluded from analysis if a pup fell from the apparatus or touched one of the sides of the apparatus within 5 s of release on the inclined plane. If, 5 s after release, the pup then fell or touched one side of the apparatus before the 15-s test was complete, the available data were analyzed. Alpha was set at 0.05 and the Bonferroni procedure was used to correct for multiple comparisons.

Results and Discussion

Only 1 pup fell from the apparatus within 5 s of release on the inclined plane and its data were excluded from further analysis. Of the remaining 63 pups tested, 8 pups either fell or touched one side of the apparatus before the 15-s test was complete (range = 6–13 s). The available data for these 8 pups were included in the analysis below.

The results for Experiment 1 are shown in Figure 1. At an angle of 30°, pups in the left starting position oriented significantly in the head-up direction, $z = 2.52$, $p < .01$, while pups in the other three starting positions (i.e., up, right, and down) did not, $.84 < z < 1.4$. Furthermore, pups in the left starting position also exhibited a significant avoidance of the head-down direction, $z = 2.5$, $p < .01$, while pups in the other three starting positions did not, $.28 < z < 1.9$. At an angle of 45°, pups in three of four starting positions oriented significantly in the head-up direction, $2.2 \leq z < 2.5$, $p < .01$, while pups in the left starting position did not, $z = 1.5$. Finally, while pups in the up, down, and left starting positions exhibited a significant avoidance of the head-down direction, $2.2 \leq$

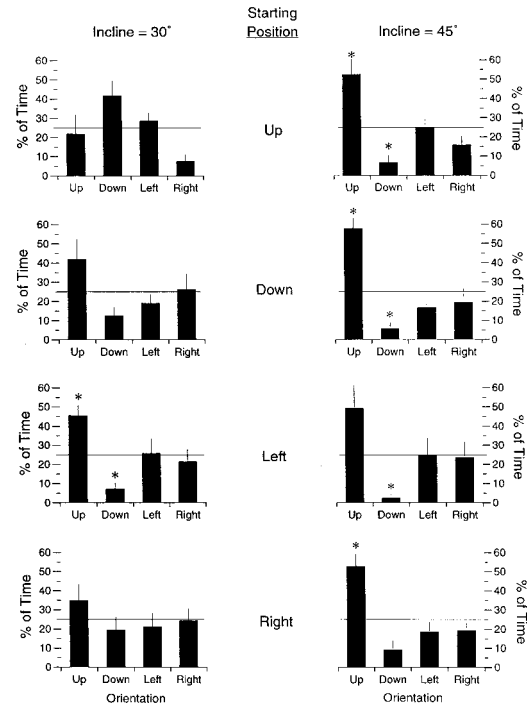


FIGURE 1 Percentage of time orientating in the up, down, left, or right direction as a function of angle of inclination and starting position in Experiment 1. For this experiment, the inclined plane was covered with wire mesh. * $p < 0.025$, head-up or head-down orientation significantly different from the chance level of 25% (horizontal mesh), Wilcoxon signed-ranks test. Mean + SEM.

$z \leq 2.5$, $p < .01$, pups in the right starting position did not, $z = 2.1$.

Slippage on the wire mesh was common at an angle of 45°. When contact with the surface was broken, the pup appeared to stabilize itself by orientating to a head-up position and clinging with its claws to the wire mesh. In contrast, at 30°, pups appeared more able to maintain stable contact with the surface and were also less likely to orient in a head-up position. Thus, these results suggest that the presence of a claw-hold affects the behavior of rat pups on an inclined plane, especially at steeper inclinations.

EXPERIMENT 2

In Experiment 1, the presence of holes in the wire mesh appeared to influence the behavior of young rats at an inclination of 45° by providing convenient insertion points for the pups' claws. Therefore, in Experiment 2, we replaced the wire mesh with a smooth, high-friction substrate. Pilot data indicated that pups were able to maintain contact with this substrate even

though they could not grip it as they did the wire mesh. We tested pups at four angles of inclination, from 30–45°.

Methods

Subjects. Forty-eight rat pups from eight litters, 12–14 days old on the day of testing, were used. All pups were housed and raised as in Experiment 1.

Test Environment. The apparatus described in Experiment 1 was used with one modification: The surface of the inclined plane was covered with a high-friction substrate (Dycem, Duro-Med Industries, Hackensack, NJ) instead of wire mesh.

Procedure. The procedure used was identical to that in Experiment 1 with two exceptions. First, only two starting positions were used (i.e., head-up and head-down) and second, pups were tested at one of four angles of inclination (i.e., 30, 35, 40, and 45°).

Data Analysis. The data were scored and analyzed as in Experiment 1.

Results and Discussion

As shown in Figure 2, 6 of 8 pups tested at an angle of 45° fell from the apparatus within the first 5 s of the test, regardless of whether they were first placed on the inclined plane in the head-up or head-down starting position. Analysis of the videotapes indicated that pups typically slid to the bottom of the apparatus either

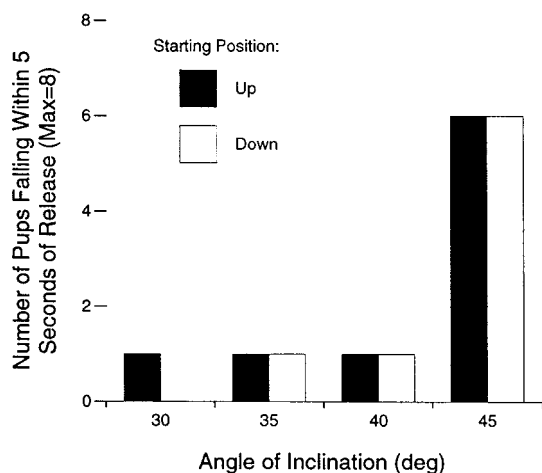


FIGURE 2 Number of rat pups falling within 5 s of release on the smooth, high-friction substrate (i.e., Dycem) at the various angles of inclination in Experiment 2. Pups were initially placed on the inclined plane in either the up or down position.

immediately after release or after the pup had turned to the left or right. In addition, pups sometimes resisted the hold of the experimenter on the inclined plane prior to release such that, after the experimenter's hands were removed, the pup was not able to maintain contact with the surface. Regardless of the cause of falling, however, the high falling rates at 45° precluded analysis of orientation behavior at that angle.

In contrast to 45°, rates of falling were very low at the other three angles of inclination. When pups did fall within 5 s, however, these data were excluded from analysis. In addition, 3 pups at 40° either fell or touched one side of the apparatus within 15 s (range = 10–11 s); the available data for these 3 pups were included in the analysis below.

The orientation data for inclination angles of 30, 35, and 40° are presented in Figure 3. At no angle and for neither starting position did pups orient in the head-up direction significantly more often than expected by chance, $z \leq 1.0$. Similarly, pups did not exhibit a significant tendency to avoid the head-down direction at any angle or at any starting position, $z \leq .3$.

It is possible that pups on the Dycem did not exhibit significant orientation in either the head-up or head-down direction because the surface inhibited the ability to move or turn. We do not believe this was the case for a number of reasons. First, Figure 3 shows that pups placed initially head-up or head-down were able to move to the head-left and head-right positions, indicating that at least some movement was possible. To further explore this issue, we examined the turning behavior of pups tested at the 40° angle of inclination. To do this, we determined the number of times in each test that a pup moved from a head-down to a head-up position or vice versa. Of the 7 pups started in the head-down position that did not fall within 5 s, all 7 exhibited at least one transition to the head-up position and 3 pups exhibited three transitions (i.e., head-down to head-up to head-down to head-up). Similarly, of the 7 pups started in the head-up position that did not fall within 5 s, 5 exhibited at least one transition to the head-down position and 3 pups exhibited at least two transitions. Therefore, even at the steep angle of 40°, it is apparent that the movements of pups on the Dycem were not inhibited.

EXPERIMENT 3

In Experiment 1, we showed that pups appear to exhibit geotactic behavior when tested on wire mesh at a 45° inclination angle, while in Experiment 2, geotactic behavior was not detected when pups were tested on a smooth but high-friction substrate at an

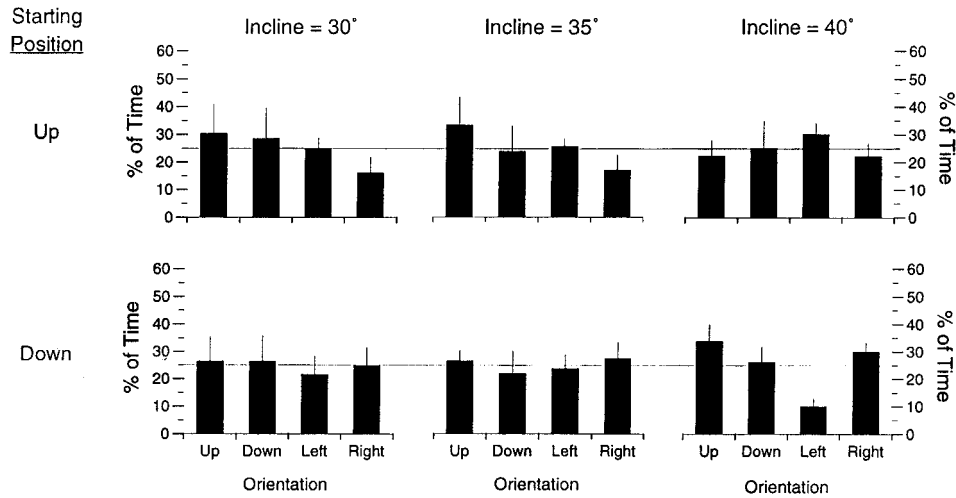


FIGURE 3 Percentage of time orientating in the up, down, left, or right direction as a function of angle of inclination and starting position in Experiment 2. For this experiment, the inclined plane was covered with a smooth, high-friction substrate (i.e., Dycem). No differences were statistically significant. Mean + SEM.

inclination angle as large as 40°. This failure to detect geotaxis on Dycem was apparently not due to an inhibition by this surface of the ability to move or turn. Although the results of Experiment 2 suggest that the testing substrate influences the expression of geotactic behavior, the inability of pups to maintain contact with the high-friction substrate at an angle of 45° precludes a clear conclusion. Therefore, in the present experiment, the effect of substrate on geotaxis is tested directly by examining the behavior of pups on the two substrates at the same angle of inclination (i.e., 40°).

Methods

Subjects. Twenty-four pups from eight litters, 12–14 days old on the day of testing, were used. All pups were housed and raised as in Experiment 1.

Test Environment. The apparatus described in Experiment 1 was used. The inclined plane was covered either with wire mesh or the high-friction substrate (i.e., Dycem).

Procedure. The testing procedure used was identical to that in Experiment 1. For this experiment, two designs were used—a between pup design and a within pup design. First, for the between pup design, 2 same-sex littermates were removed from the nest in succession and placed head-down on the inclined plane at an angle of 40°. One pup was tested on wire mesh and the other pup was tested on Dycem; test order was counterbalanced. Second, for the within pup design, a 3rd littermate was tested sequentially on both the wire

mesh and Dycem surfaces with a 5-min interval between tests; again, test order was counterbalanced.

On the few occasions when a pup either fell from the apparatus or touched one side of the apparatus before the 15-s test was complete, the test was terminated and a littermate was tested in its place.

Data Analysis. The data were scored and analyzed as in Experiment 1.

Results and Discussion

The results from Experiment 3 are presented in Figure 4. For the between pup design, the pups tested on wire mesh were significantly more likely to orient in the head-up direction than expected by chance, $z = 2.3$, $p < .01$, and were also less likely to orient in the head-down direction than expected by chance, $z = 2.5$, $p < .01$. As expected from Experiment 2, when tested on Dycem, pups did not orient significantly in the head-up direction, $z = 2.1$, nor did they significantly avoid the head-down direction, $z = .5$.

For the within pup design, pups tested on wire mesh oriented significantly more than expected by chance in the head-up direction, $z = 2.5$, $p < .01$, and were also less likely to orient in the head-down direction than expected by chance, $z = 2.3$, $p < .01$. In addition, although pups tested on Dycem oriented significantly in the head-up direction, $z = 2.2$, $p \leq .025$, they did not avoid the head-down direction, $z = .7$.

These results indicate that young rats, tested on wire mesh at an angle of inclination of 40°, exhibit strong tendencies to orient in the head-up direction and

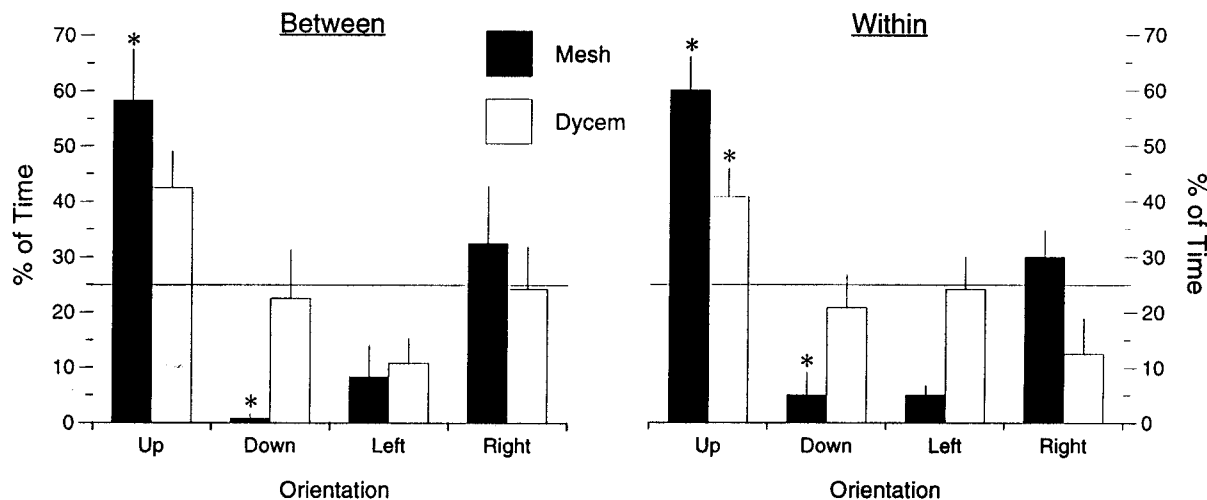


FIGURE 4 Percentage of time orientating in the up, down, left, or right direction when tested at an angle of inclination of 40° in Experiment 3. Pups were tested on wire mesh or Dycem using a between pup design or a within pup design. $*p < 0.025$, head-up or head-down orientation significantly different from the chance level of 25% (horizontal line), Wilcoxon signed-ranks test. Mean + SEM.

avoid the head-down direction. In contrast, testing on Dycem reduces these tendencies: Considering all the results of Experiments 2 and 3 for pups started in the head-down position and tested an angle of inclination of 40° , only one of six statistical tests was significant.

GENERAL DISCUSSION

Using similar methods to those first used by Crozier and Pincus (1926), Experiment 1 showed that 12- to 14-day-old rats, tested on an inclined plane at an angle of 45° covered with wire mesh, will orient in a head-up direction. Noting that pups were inserting their claws into the wire mesh, in Experiment 2 we replaced the wire mesh with Dycem, a smooth but high-friction substrate, and found no evidence of geotaxis at inclination angles of 30, 35, and 40° ; high rates of falling at 45° prevented an assessment of geotaxis at this angle. Thus, in Experiment 3, the two substrates were compared directly at an inclination angle of 40° . We found that pups exhibited a consistent tendency, on the wire mesh but not the Dycem, to orient in the head-up direction and avoid the head-down direction. Taken together, these results indicate that substrate influences the expression of geotaxis.

Regardless of the testing substrate, pups' initial behavior on the inclined plane appears to be a response to postural instability. This statement is supported by the following observation: In Experiments 2 and 3, when pups were placed in a head-down position on

either wire mesh or Dycem, we noted a marked dorsoflexion of the tail in nearly all pups that disappeared when pups moved to a head-up orientation. In contrast, pups placed on the inclined plane in a head-up orientation did not dorsoflex the tail, and this tail response was rarely seen when they then moved to a head-down orientation. This dorsoflexion of the tail may be a by-product of a generalized extensor response in the limbs when pups are most unstable, such as when they are initially placed on the inclined plane in a head-down position.

Postural instability and substrate also appear to influence adult rat behavior on an inclined plane. For example, haloperidol-treated adult rats tested in a head-down position on an inclined plane covered with a rubber mat often jump off the plane when stability is compromised rather than turning against gravity or exhibiting a "spread-eagle" posture as shown by undrugged animals (Morrissey, Pellis, Pellis, & Teitelbaum, 1989). This jumping behavior is inhibited, however, when the haloperidol-treated rats are tested on a wire grid. Such results, and those presented here, suggest that the behavior of rats on an inclined plane is a complex combination of multiple factors, including the maturity of locomotor (Westerga & Gramsbergen, 1990) and postural (Geisler, Westerga, & Gramsbergen, 1996) systems, body size and shape, the relative strength of forelimbs and hindlimbs, and the behaviors afforded by the testing substrate. Based on this perspective, behavior on an inclined plane may perhaps best be viewed as the product of multiple mechanisms

for defending postural stability (Morrissey et al., 1989; see also Fraenkel & Gunn, 1961 for a similar perspective).

In the field of behavioral teratology, investigators rely on simple reflexes and indicators of motor development to assess the damage that toxins or chemical agents have on developing animals. For example, water righting has been shown to provide meaningful information about the developing vestibular system of young rats (Pellis, Pellis & Teitelbaum, 1991). Like righting, geotaxis is also used as an index of development and it is assumed that geotactic behavior is indicative of a specific biobehavioral capacity. The neural or physiological capacity that geotaxis is thought to reflect, however, has not been identified in young mammals.

A review of the teratological literature reveals that at least three different surfaces are commonly used to test geotaxis in rats, including sandpaper (Luthman et al., 1992), wire mesh (Norton et al., 1988), and wood (Janicke & Coper, 1993). Although we can only speculate about the fundamental differences between these three surfaces, the present results comparing wire mesh and Dycem suggest that the testing surface influences the expression of geotactic behavior. Therefore, while teratologists interpret "failure" to orient in a head-up direction as an indication of a specific neural or motor deficit (e.g., Norton et al., 1988), the failure of pups tested on Dycem to orient in a head-up direction does not lead us to the same conclusion.

The original report of Crozier and Pincus (1926) established geotaxis as a functional characteristic of young animals despite the critical analyses of Hunter (1927a) and Hovey (1928). In retrospect, the most astute criticism was provided by Hovey (1928), who noted the relations between claw structure and orienting behavior of pups on wire mesh. Despite such observations, however, and despite the critical analysis of Fraenkel and Gunn (1961), current investigators continue to use geotaxis as a measure of motor development. But what is actually being measured? Certainly, it is odd that a task designed to unveil functional features of the nervous system should be so sensitive to the testing surface used. Therefore, the present findings provide further justification for questioning the utility of the concept of geotaxis in young mammals, at least when tested on an inclined plane.

NOTES

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