

Positive Geotaxis in Infant Rats (*Rattus norvegicus*): A Natural Behavior and a Historical Correction

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Infant rats (*Rattus norvegicus*) placed on a shallow incline (2°, 4°, or 8°) oriented and moved downhill within 1 min; that is, they displayed positive geotaxis. Their downhill translocation increased with angle of inclination. A variety of possible behavioral elements (e.g., initial orientation, rotational movements, ambulatory velocities) were eliminated as explanations of the geotaxis. Wall contact was recognized as a determinative event: Pups on the inclines showed no orientation with respect to the geogravitational stimulus before contacting a wall. The event of wall contact, however, evoked reliable downhill orientation and more linear movements. Positive geotaxis was created by pups' orientation against walls and an associated increase in movement velocity. This is a distinct perspective on a behavioral response that replaces a traditionally misinterpreted phenomenon. The authors discuss the ecological validity and historical context of these findings.

It is commonly expected and asserted that an infant rat or mouse placed on an inclined surface will orient and move uphill. Such orientation and movement are termed *negative geotaxis* (e.g., Fraenkel & Gunn, 1961). The ability to exhibit negative geotaxis is believed to depend on (a) vestibular or proprioceptive receptor function sufficient to detect a geogravitational stimulus (the incline), (b) central organization sufficient to process differential inputs that reflect direction of the substrate angle in relation to the gravity vector, and (c) the motor competence to orient and move on the incline. For many, the phenomenon of negative geotaxis in infant rodents has been reified into a diagnostic milestone of early sensorimotor development (see Altman & Sudarshan, 1975; Fox, 1965).

The term *taxis* implies a kind of invariant, reflexlike automaticity of response that was, during the late 19th and early 20th centuries, the basis of a search for rules and laws of behavioral reactions to external forces (e.g., Loeb, 1912). Within this tradition, Crozier and Pincus produced an impressive series of 12 empirical reports presenting and detailing the phenomenon of negative geotaxis in rat pups (Crozier & Pincus, 1926, 1927, 1929a, 1929b, 1931a, 1931b, 1931c, 1931d, 1932a, 1932b, 1935, 1936).

There were, however, at least two contemporaries of Crozier who criticized his work and even challenged the very phenomenon of negative geotaxis in rats. Hunter (1927) was frustrated in his

attempts to replicate Crozier and Pincus's studies; he reported behavioral variability of rats on inclines of 25°–70° that violated the kinds of mathematical rules that they had used to describe the pups' responses. Hovey (1928) alleged that Crozier and Pincus (1926) were reporting data on selected subjects that had learned a response to maintain a foothold on steep inclines.

The fundamental conflicts among these earlier workers were unresolved and, it appears, were essentially overlooked or forgotten. Crozier and Pincus's numerous reports prevailed. Later, when Altman and Sudarshan (1975) included negative geotaxis in their inventory of locomotor milestones of rat development, this putative phenomenon became a standard measure of sensorimotor competence, used widely and with accepted validity (e.g., Adams et al., 1985; Alder & Zbinden, 1977).

More recently, in the twilight of the 20th century, Kreider and Blumberg (1999) reported a carefully conducted series of experiments in which 12- to 14-day-old rat pups were placed on a plane inclined at an angle of either 30°, 35°, 40°, or 45° and examined for reactions, especially negative geotaxis. These inclined planes had one of two types of surface. If the inclined surface was Dycem, a relatively smooth, high-friction material, the pups moved about on the plane but showed no evidence of geotaxis. Only if the surface was wire mesh were pups observed in a position with their heads toward the top. Was this negative geotaxis on the wire mesh surface? Kreider and Blumberg thought it was not. They noted that the head-up position on the incline resulted when a pup moved so that its hooked claws inserted into the spaces between the wires of the mesh, essentially allowing the pup's body to hang from these hooks, with its head necessarily toward the top of the incline. Thus, the pup's head-up orientation was not an active orienting reaction. They described additional observations that supported the general conclusion that young pups are posturally unstable on such steep inclines (their pups fell from the 45° inclines) and that reports of negative geotaxis appear to be descriptions of compensatory movements made to stabilize the body and prevent falling.

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We did not assume that steep inclines are needed to observe geotaxis, so we set out to examine infant rats on smooth surfaces at relatively shallow inclines, from 2° to 8° in the present study. Pilot data showed that infant rats are able to move about on smooth, low-friction inclines up to 10° without showing signs of instability, such as dorsoflexion of the tail (Kreider & Blumberg, 1999). Figure 1 illustrates these shallow angles and, for the sake of comparison, there are additional lines drawn at the much steeper angles than have been used previously for studies of negative geotaxis in rat pups. Figure 1 probably makes it clear that the modest angles used in the present experiment are not posturally challenging to a 10-day-old rat pup. On such shallow inclines, body direction and posture ought not to be the result of defensive or compensatory responses. If the pups' movements and orientation are lawful with respect to the gravity vector and we have eliminated or balanced all other stimuli that can change a pup's orientation or posture (e.g., ambient light, heat sources and thermal gradients of various kinds, numerous kinds of tactile cues), we should be able to observe and study geotaxis if it exists.

To us, it seemed that the shallow angles might also be more ecologically valid for behavioral testing of rat pups than are the extreme angles of inclination used previously. Norway rats and other rodents often live in underground burrows where, in general, the tunnels would contain more modest slopes. On the basis of data reported by Boice (1977), the average slope of a wild Norway rat's burrow is calculated to be 6.8° . Furthermore, Lore and Flannelly (1978) found that wild Norway rats in a landfill prefer to burrow into the slope of a mound or hillside (rather than into flat ground), achieving maximal depth without steep declines. It might be argued that an infant rodent's environment does contain steep inclines, such as those presented by the walls of a nest, but we then

must acknowledge that pups in such environments are not observed to reflexively climb up the walls as would be predicted if there were a negative geotaxis.

Method

Subjects

Thirty-two Sprague-Dawley rat pups (*Rattus norvegicus*) from five litters, born in the Indiana University colony from rats originally purchased from Taconic Farms (Germantown, NY), were used as subjects. Litters were culled to 8 pups each (4 males and 4 females) on postpartum Day 2 (day of birth = Day 0). Mothers and litters were housed in polypropylene tubs ($45 \times 25 \times 20$ cm) with stainless steel wire lids that presented commercial rat chow and water ad libitum. Subjects were 10 days old when tested, and equal numbers of males and females were used.

Apparatus

For the present study, we used a specially designed apparatus that provides control of illumination, air and surface temperatures, visibility, and chemical cues, all of which we have determined are essential for accurate and reliable studies of this type. Figure 2A illustrates the general structure of the apparatus. The entire apparatus was tilted to create the inclines used in the study.

Enclosure. The large housing (143×46 cm \times 56 cm high) shown in Figure 2A was constructed of clear Plexiglas and aluminum. Within this enclosure rested a rectangular platform, also seen in the figure, on which the animals were tested. Access to the interior chamber was through three round ports (15 cm diameter) located on the front surface of the housing. Each port was sealable to preserve ambient conditions within the enclosure. The front panel of the enclosure was hinged, which enabled more open access for cleaning and changing parts.

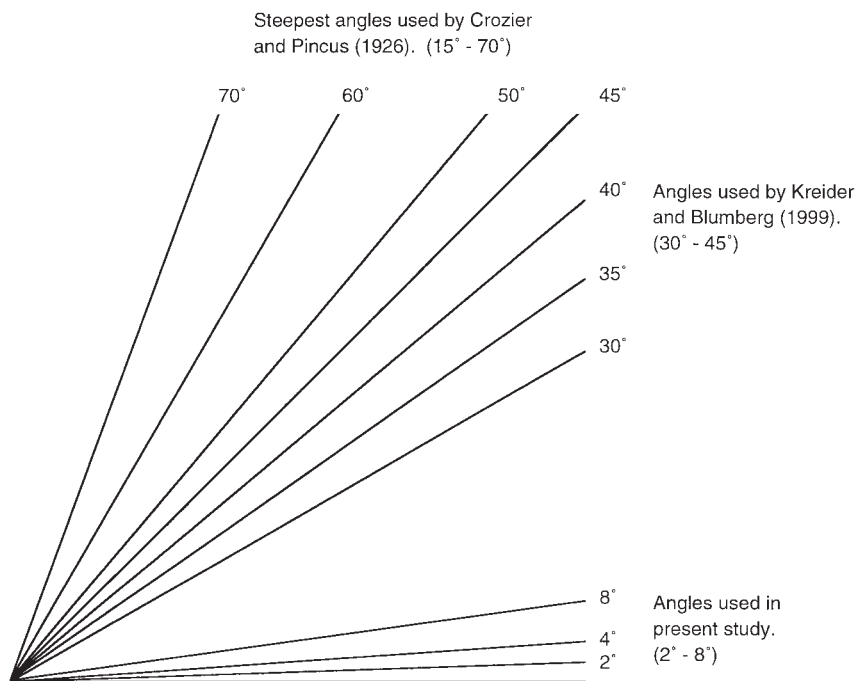


Figure 1. Visual depiction of angles used by Crozier and Pincus (1926), Kreider and Blumberg (1999), and in the present study.

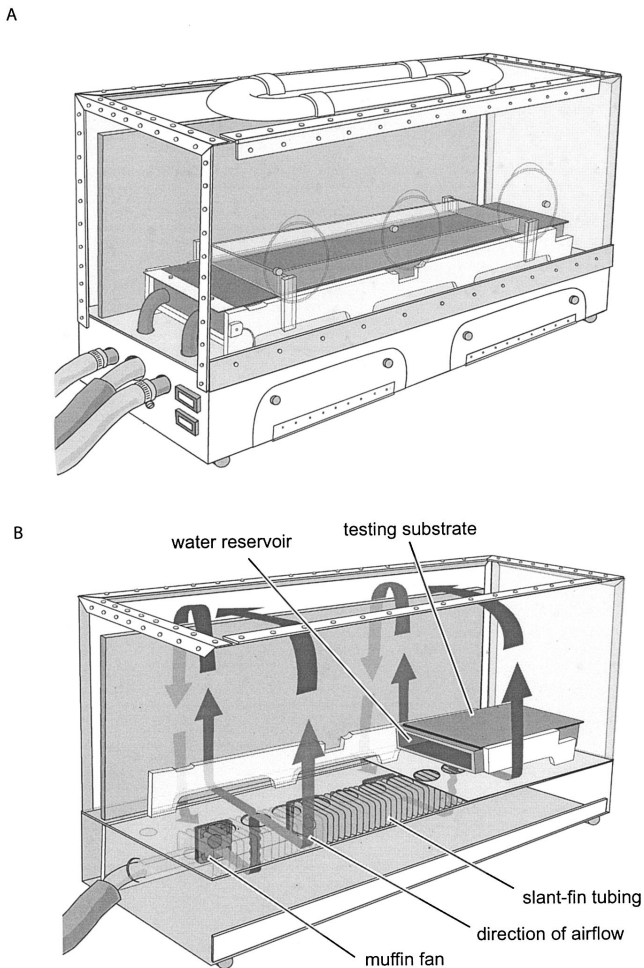


Figure 2. The apparatus used for studying geotaxis in rat pups. **A:** External view of the apparatus. The clear walls of the enclosure expose the raised, temperature-controlled surface on which the pups were tested. The low walls of the arena can be seen on the platform. Note also the three round ports that can be opened for access to the animals. On top of the enclosure is the housing of the lights that evenly illuminated the test area from above. **B:** Partial cutaway of the apparatus, revealing muffin fans, slant-fin tubing, the water reservoir below the animal's substrate, and the direction of airflow (arrows). Air was pushed continuously by the four muffin fans across the slant-fin tubing (for temperature conditioning) and through holes beneath the test platform. The arrows show how the airflow crossed the platform and returned to the fans via a route behind a baffle that served as a rear wall in the apparatus.

The entire apparatus was capable of being tilted to establish a geogravitational stimulus within the chamber. A set of pressed-wood blocks was created to be placed under either end of the apparatus. These blocks were designed to support the apparatus at various inclines up to 15° in increments of 0.1° .

Air temperature. Figure 2B is a partial cutaway view of the apparatus, showing that in the lower portion of the apparatus, beneath the Plexiglas chamber, there was mounted a strip containing commercial slant-fin tubing (122 cm long and 6 cm wide) that was plumbed to a separate, temperature-controlled recirculating water bath (ThermoElectron Isotemp 1016S, Waltham, MA) isolated from the enclosure. Temperature-conditioned distilled water was circulated continuously through this radiator system.

Figure 2A illustrates the hose to the radiator strip, flanked by hoses used to control the temperature of the platform, described below. The output from the radiator and its return to the water bath are not visible in the figure.

Four 5-cm muffin fans pushed air continuously past the slant-fins through 5-cm vents located beneath the platform. Airflow was thus established with conditioned air from beneath the test platform. One of the fans and some vents are depicted in Figure 2B. This air then moved to the upper zone of the enclosure and followed a path that ran behind a false wall (33 cm high) that extended the length of the enclosure. The arrows in Figure 2B illustrate the airflow pattern. Air temperature was thus maintained at 27.3°C , measured at opposite ends of the arena, 3 cm off the surface. Air currents created by this system were measured at the top of the false wall to be about 15 m/min. Note that airflow was perpendicular to the length of the apparatus, thus obviating thermal gradients that could confound the geogravitational stimulus.

Testing platform and arena. Figure 2A shows a long, rectangular platform within the enclosure. The surface of the platform was copper (3 mm thick), and it was the top of a water jacket equipped with the interior channels that directed the flow of liquid evenly and thoroughly beneath it. There were inlet and outlet ports (2 cm diameter) at one end of the platform, shown in Figure 2A. These ports were connected to a temperature-controlled recirculating water bath (ThermoElectron Isotemp 1016S, Waltham, MA) that pumped distilled water through the platform. The surface temperature of the platform was thus maintained at 32.5°C . This metal platform was set within a wooden frame that reduced conductive heat transfer to the metal surroundings and was easily cut along the base to create open channels for airflow. Clear acrylic (1 cm thick) was used to make a rectangular arena 91×20 cm that could be placed on the platform. The walls were 8 cm high, which was sufficient to contain the pups. The arena can be seen in Figure 2A.

Lighting. Overhead illumination of the arena was provided by a continuous ring of light-emitting diodes contained within flexible plastic tubing; this was a commercially available Rope-Light (Westek, Monsey, NY). We encased the lights in an opaque hood, created by cutting lengthwise a ring of polyvinyl chloride pipe (8 cm diameter). The lighting system rested on the clear top of the enclosure (see Figure 2A) and was dimmed (76%; 140 V) to provide about 80 lux across the entire arena ($M = 79.7$ lux; $SD = 1.9$). We incorporated this lighting system after discovering that point sources of light intended to wash the apparatus from about 1.5 m above influenced the direction of pups' movements. The homogeneity of illumination above the arena was important for these tests.

The entire apparatus was mounted on a sturdy workbench that was carefully leveled. From near the ceiling, an opaque black curtain was draped around the workbench so that the entire apparatus could be enclosed during trials, thus eliminating extraneous light cues.

Data recording. Approximately 1.5 m above the enclosure was positioned a CCD camera (Cohu, San Diego, CA) with an 8.5 mm lens that provided a view of the entire arena. Three types of recordings were obtained: (a) real-time video (29.97 National Television Standard Committee frames/s) for a continuous view of the pups' movements throughout the full 15-min test; (b) time-sampled video (1 frame/5 s) providing digital "snapshots" of location and orientation during the 15-min test; and (c) time-lapse video samples taken 3 frames/s for the 1st minute of the trial, providing a detailed, temporal microstructure of orientation and movement suitable for kinematic analysis.

Procedure

Individual subjects were separated from the litter 1 min prior to testing. They were then placed in a small, four-sided enclosure (8×8 cm \times 6 cm high) in the center of the testing arena and left undisturbed for 30 s. The enclosure's size prohibited a 10-day-old pup from extending its body to make pretrial responses to the incline. Trials began when the square enclosure was lifted. Pilot data showed that there was no preferred starting

orientation within the enclosure, so pups began the trial at different orientations relative to the incline. Each pup in a litter was randomly assigned to one of four experimental conditions: 0° (flat), 2°, 4°, or 8°. Two pups from each litter (male and female) were run at each incline. Trials lasted 15 min.

At the end of each trial, the pup was removed from the testing chamber, marked for identification, and returned to the home cage. Between each trial, the surface and walls of the arena were cleaned with a cationic surfactant, Roccal-D Plus (quaternary ammonium compound; Pharmacia & Upjohn, Peapack, NJ), and rinsed with 70% ethyl alcohol to eliminate any odor trails left by the previous subject.

Data Analysis

Video sequences were acquired and analyzed on a Macintosh G4 desktop computer using the public domain NIH-Image program (National Institutes of Health, n.d.). We developed macros for NIH-Image that allowed us—for each frame of every trial—to mark the x - y coordinates of a pup's nose and rump relative to the borders of the rectangular arena, accurate to 1.5 mm. From the x - y coordinates, we were able to compute for every frame the orientation of the pup relative to the geogravitational stimulus. For each frame it was also determined whether the pup was in contact with a wall or a corner of the arena.

The 1st-minute sequences (3 frames/s) were used to analyze the pup's initial reactions in greater detail than was possible with the 15-min (1 frame/5 s) snapshots. Using the higher frame rate, we were also able to compare the x - y coordinates of the pup's nose and rump between frames to compute turning velocity, linear velocity, and total linear movement. Together, these data provided the precise location, orientation, and tactile stimulation exhibited or experienced by the pup for 15 min in addition to the velocity and total distance ambulated at any point during the 1st minute.

Data were analyzed using both repeated-measures (for analyses over time) and single-factor analyses of variance (ANOVAs), with level of incline as the between-subjects variable. Using data acquired from the 15-min and 1st-minute analyses, repeated-measures blocks were established as follows: 1-min blocks for full 15 min and 15-s blocks for the 1st minute. Planned comparisons were drawn between incline conditions and 0° (flat) condition when significant effects on ANOVAs were found. Alpha level was set at .05.

Results and Discussion

The most stunning and unexpected result of the present study was that rat pups displayed positive geotaxis. This, of course, is a behavioral response directionally opposite to that of the traditionally touted negative geotaxis. We first describe the behavioral phenomenon and then dissect it by teasing apart different parameters of the pups' movements, analyzing which of these elements are central to the behavioral results. After such reporting and consideration of the immediate findings, we discuss the present study in its historical context.

Positive Geotaxis as a Function of Angle of Incline: The First 60 s

Figure 3 is a visual summary of the individual data for the first 60 s of the test. Each point in the figure represents the location of a subject's nose each 0.33 s of the 1st minute. Thus, there could be 180 points per rat, with each panel in the figure containing 1,440 samples. We did not include the first frame in each trial. In addition, we discarded the occasions when the pup's nose was positioned on the center line of the arena. Thus, the actual number of points in each panel ranges from 1,426 to 1,430. The rectangles

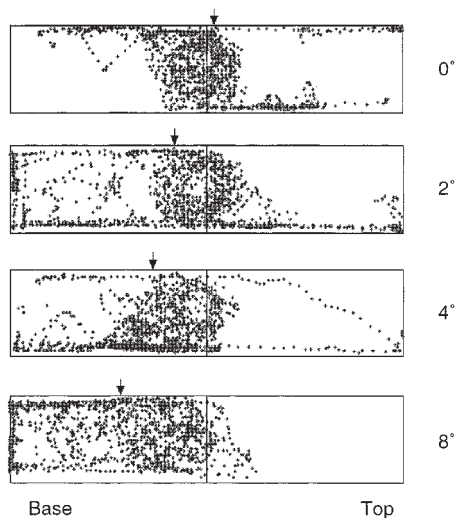


Figure 3. Location data during the 1st minute. Each point represents the location of a subject's nose every 0.33 s. Data points for all pups within each incline condition are combined. The rectangles are scaled representations of the testing arena. Arrows above each rectangle indicate the mean (x -axis) location in each condition. The right side of each rectangle corresponds to the raised end of the testing apparatus on incline conditions. The vertical line in the center of each rectangle indicates the midpoint.

in Figure 3 are scale drawings of the 91×20 cm test arena, and the points are the x - y coordinates as captured from the video samples when the arena was positioned at 0°, 2°, 4°, and 8°. (The narrowing of the field of points along the walls is an artifact of the angles between the overhead camera and the tilted testing surface in the various incline conditions.)

Viewing the distribution and density patterns in the panels in Figure 3, it can readily be seen that pups in the 0° (level) condition tended to remain centrally located in the arena. The overall distribution of points is essentially equal on the two sides of the midline: 695 points (48.7%) to the left of the midline and 731 points (51.3%) to the right (discounting the first point and any points in the exact center of the arena). The dense cloud of the data points in the central region of the field indicates that nearly all of the pups' movements were confined to about 22% of the total arena. The thin trails of points running along the long edges of panel are the movements of the rare individuals that left the mid-zone during the initial 60 s of the trial. When this occurred, they showed the characteristic thigmotactic style of rat behavior, moving along the wall.

With increasing angles there was a clear shift in the distribution of pup locations. In the 2° condition (second panel from the top), the data points are skewed to the left side, in the direction of the low end of the incline. Eight hundred eighty-four (61.9%) of the points are to the left of the midline (toward the lower end), and 544 points (38.1%) are on the higher half of the field. Evidence of thigmotactic movements along the length is also apparent. A more dramatic pattern is seen in the 4° condition, where 85.5% of the points are on the lower end. The bottom panel in Figure 3 shows 1,340 points (93.7%) in the lower half of the apparatus during the 60-s sample.

The arrows at the top of each panel in Figure 3 mark the location on the long axis of incline that is the numerical average of all

points for each incline condition. A repeated-measures ANOVA showed an overall difference between incline groups, $F(3, 28) = 4.782, p = .008$. Planned comparisons showed significant contrasts between the 0° and 4° ($p < .05$) and 0° and 8° ($p < .005$) conditions.

These results provide a compelling picture of positive geotaxis on shallow inclines. Pups on a flat surface moved around the central region of the apparatus, and their behavior was evenly distributed in the central zone. With increasing angles of incline, ranging from 2° to 8° , there was corresponding increase in the tendency to move downhill within the first 60 s of testing.

This is the first report of a positive geotaxis in rat pups and represents a major departure from conventional characterizations of an infant rodents' response to a geogravitational cue. Our methods also provided the ability to examine in much greater detail the behavior of individual pups, to which we now turn.

Initial Orientations

We can ask whether the regularity observed in the 1st minute of the test was related to a pattern of initial orientation within the start box. Each trial began 30 s after the experimenter placed a 10-day-old pup individually on the surface of the test arena within a small enclosure at a random orientation. As noted above, the start box was small: Although pups could move and reposition themselves within it, they selected orientations across the diagonal of the square, that is, with their snout oriented into one of the four corners. Present data show that there was no overall uphill or downhill preference for starting orientation when the enclosure

was lifted, $t(31) = 0.121, p = .905$, or preference between incline groups, $F(3, 28) = 1.021, p = .398$.

Pup Behavior During the Full 15-Min Trials

Surprisingly, perhaps, the results from the full 15-min trials were less clear and definitive than were those from the 1st minute of the test when the pups' average locations were regular and reliable (see Figure 3). During Minutes 2–15, behavioral variability increased and was sustained.

Figure 4 illustrates the behavioral variability that developed during the trial. Plotted in this figure are the standard deviations of distance (in centimeters) from the pups' average locations on the arena surface for all incline conditions. Data were taken from the 5 s/frame digital snapshots obtained. Note that the horizontal axis of Figure 4's left panel is scaled to 60 s, whereas the right-hand panel shows the subsequent 14 min (840 s). This provides a clearer view of the increase in variability that accrued during the 1st minute of the trials. Initially, as expected, the standard deviations were < 5 cm, about the length of the infant rat's body. Variability increased after 10 s or so, and by 30 s it had reached 20 cm around the mean.

Thus, we can see that after a brief period of regular movement, the pups engaged in more variable behavior, the sort that is typically labeled *general* or *exploratory* activity. Though there may be rules that can describe or account for the more variable movements of the pups as the trials progressed, these rules do not appear to involve geogravitational factors. We again note the absence of tail dorsoflexion and the unencumbered movements of

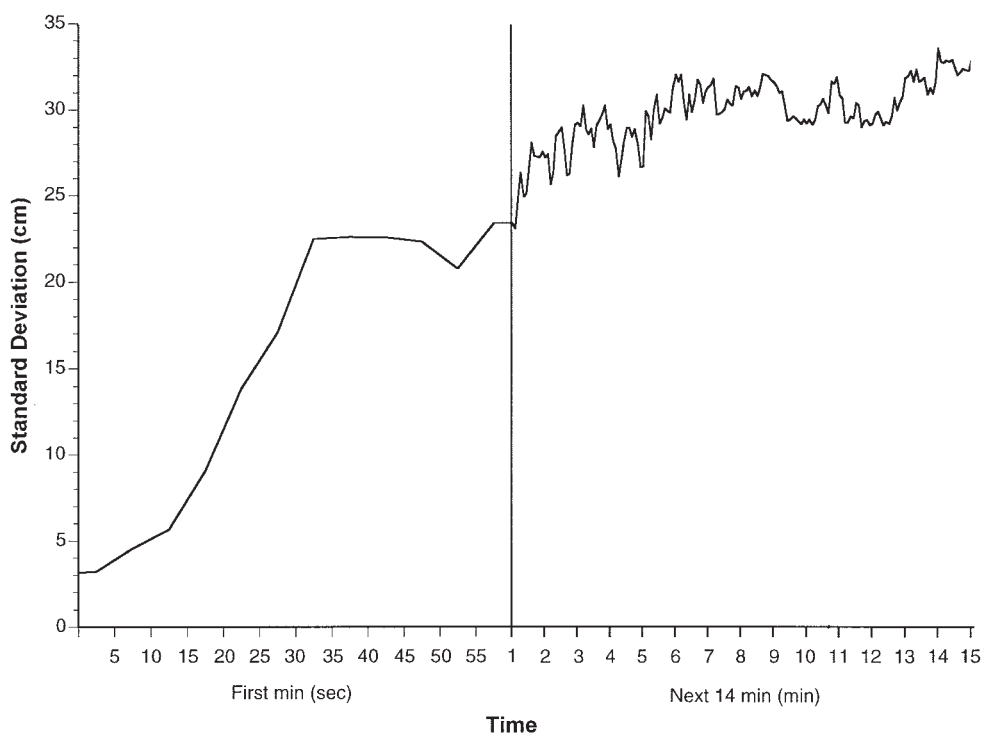


Figure 4. Standard deviation as a function of time throughout the 15-min trial (the 1st minute is expanded for a more detailed view). sec = seconds.

the pups as they traversed the substrate surface, orienting smoothly between head up and head down. There was no evidence of challenges to their postural stability during these tests. Therefore, we now examine events within the 1st minute of the test, for it is here that we can dissect and interpret the organization of their responses to the substrate angle.

Punting

When first released in an open field, pups 5–14 days of age display a distinct form of circumrotation in which the pup's body is propelled by extension of one forelimb while the hind limbs remain relatively inert. In effect, the one forepaw pushes (*punts*) the pup's body around a stationary rear. For purposes of the present analyses, punting was defined to occur when a point marking a pup's nose traversed a net angular distance of 360° within the initial 15 s of the trial. Punting was observed in 20 of the 32 trials (62%), with 4, 7, 6, and 5 pups displaying the behavior in the 0°, 2°, 4°, and 8° conditions, respectively. Of the 12 pups that did not meet the criteria, none displayed any marked rotational gestures.

Considering that (a) frequency of punting does not change systematically with increasing inclines and that (b) we observed downhill progression in the 8 subjects that did not display the behavior on inclines, we conclude that the positive geotaxis observed cannot be attributed to the pup's initial reactions. This finding represents another significant departure from the conventional view of an immediate, directed response. Thus, we must analyze in detail the parameters throughout the 1st minute that might skew the distribution seen in Figure 3.

Total Linear Movement

Distance traveled is a potentially important behavioral parameter in the present setting. If total movement increases with inclination, we must then consider carefully the manner in which such enhanced movement would combine with active orientation to produce a net directional translation of position.

NIH-Image was used to track the *x*-*y* coordinates of the pup at each time point sampled (every 0.33 s) during the 1st minute of the trial. At each interval we measured the coordinates of two points on the pup's body, snout and rump, and also calculated the midpoint between these locations, which generally corresponded to the mid-thoracic region and is dubbed "back" in Table 1.

The sums of the changes within each set of coordinates provided three measures of total distance traveled. Table 1 lists for the three points the average linear distances traveled in all groups and the ratio comparing the average snout and rump distances traversed. ANOVAs revealed no differences across conditions for any of the three measures or interactions between them. Hence, the present findings provide no basis for an explanation of the pups' movement down the incline on the basis of increased activity, either during their circling behavior (punting) or through some other form of enhanced linear movement.

It is instructive, however, to note two consistent patterns within the results in Table 1. First, total linear distances traversed by the pups' snouts were consistently greater than those traversed by points on the backs and rumps of the same subjects. This difference, which averaged about 120% more for the snout measures

Table 1
Total Linear Distance Traversed During 1st Minute as a Function of Incline

Incline	Location of measurement			Snout:rump ratio
	Snout	Back	Rump	
0°				
<i>M</i>	234.8	133.8	101.9	2.30
<i>SD</i>	61.7	28.1	25.8	
2°				
<i>M</i>	250.3	153.9	121.2	2.07
<i>SD</i>	34.5	25.1	27.8	
4°				
<i>M</i>	248.0	142.3	108.4	2.29
<i>SD</i>	29.5	14.4	23.8	
8°				
<i>M</i>	235.8	140.8	107.5	2.19
<i>SD</i>	46.4	23.9	20.3	

Note. The values represent the distance traveled in centimeters.

than rump measures, can be explained by the movements that accrued during scanning, sniffing, and punting, all of which involve movements of the pup's anterior end relative to points posterior. Second, the ratio of snout:rump mean distance traversed remains constant with increasing inclines. Hence, we emphasize our conjecture that the frequency of punting (or scanning) does not change with increasing incline.

Wall Contact Enables Geotaxis

One way or another, via punting or by more linear trajectories, the blind and meagerly ambulatory rat pups moved sufficiently to encounter one of the walls that formed the boundary of the arena. Within the 1st minute, 94% of the pups made contact with a wall. Among these subjects, latency to contact a wall averaged 24 s. Table 2 contains the latency data for all groups. There was no statistically discernible difference between pups that displayed punting and those that did not in the time to first contact with a wall, $F(1, 27) = 0.224$, $p = .639$. Pups invariably contacted the wall with the anterior end of their body, most likely with the aid of cues from their vibrissae.

The event of wall contact changed the pups' behavior. Figure 5 summarizes data for all pups during the 1st minute. For this analysis, orientation was measured on a scale with 0° representing an orientation with the body's longitudinal axis and rostrum (nose) pointed directly toward the base of an incline and 180° representing an orientation in line with the top point. Ninety degrees signifies orientation perpendicular to the incline vector. Measurements were made with NIH-Image, which enabled calculation of angle of orientation from a line connecting the nose-to-rump points. This line was compared with the (downhill) incline vector to measure the pups' orientation.

As can be seen by the four open bars in Figure 5, pups that were not in contact with a wall averaged almost exactly 90°, which reflected no bias for either uphill or downhill orientation. When against a wall, however, subjects on inclines were more likely to be oriented toward the base of the arena (values < 90°). An ANOVA showed that this tendency increased with increasing steepness of the incline $F(3, 53) = 4.860$, $p = .004$. Planned

Table 2
Latency to Wall Contact by Punting and Nonpunting Subjects

Incline	Punting	Nonpunting
0°		
<i>n</i>	4	3 ^a
<i>M</i>	31.0	22.2
<i>SD</i>	19.3	8.9
2°		
<i>n</i>	6 ^a	1
<i>M</i>	27.3	8.0
<i>SD</i>	11.4	
4°		
<i>n</i>	6	2
<i>M</i>	20.7	25.3
<i>SD</i>	11.1	24.5
8°		
<i>n</i>	4 ^a	3
<i>M</i>	21.8	24.4
<i>SD</i>	13.1	30.5

Note. The values represent the time at first wall contact in seconds.
^a One subject in these conditions did not contact a wall in the first 60 s.

comparisons revealed that in the 4° and 8° conditions, subjects' orientations while against a wall differed significantly from their orientations when not in contact with a wall ($p < .05$).

These behaviors are not simply artifacts of the angle at which the pup initially contacted the wall. We examined the visual records of each trial and confirmed that the orientation of the pup's body to the wall when contact was made was not related to subsequent orientation. Pups were in uphill orientation at point of wall contact in 13 of the 24 trials conducted on an inclined surface. In 9 of these 13 trials, they immediately reversed direction; in the other 4 trials, their positive geotaxis was delayed, but it occurred. In contrast, in the 0° trials, pups generally did not change directions after contacting a wall. In four of the seven 0° trials, pups were oriented in the direction that was uphill when the apparatus was tilted; these pups maintained the same direction of movement.

Wall Contact Also Activates Linear Movement

Having demonstrated that wall contact induces downhill orientation, we must now determine how ambulatory behavior changes to cause downhill movement; orienting reactions alone will not culminate in the distributions seen in Figure 3. Observations of a rat pup on an incline almost invariably included a view of it crawling or ambulating downhill, flank along the arena wall. Is this kind of linear movement distinguishable from other movements regularly displayed by the pups? Here we were reminded of *orthokinesis*, which, in Fraenkel and Gunn's (1961) system, is a class of stimulus-dependent movement that is relatively linear (as opposed to punting, or *klinokinesis*). We find that locomotion becomes more linear on wall contact, and on an incline, an ensuing thigmotactic progression toward the base occurs. To statistically demonstrate this transition, we focus our attention on the velocity of the pup's posterior immediately after the first wall contact. As previously noted, when a pup is scanning, pivoting, or punting in the open arena, the nose velocity is significantly faster than the rump velocity because the hindquarters remain anchored while the pup's head assumes an angular trajectory. In contrast, when a pup

is engaged in linear movement, ambulating in a straight line, the rump velocity is increased, and all parts of the body progress with the same velocity. We hope to demonstrate that following wall contact, pups' rumps move faster, thus indicating more linear movement.

A matched-pairs analysis was used. Within each incline condition (0°, 2°, 4°, 8°) each of the 4 pups that contacted a wall soonest (short latencies) was matched to another pup that had contacted the wall at least 10 s afterward (long latencies). For the pups that contacted walls soonest, we measured linear velocity of the point on the pup's rump for the 8 s following first wall contact (3 samples/s). This rump velocity was compared with that of its matched subject, which (by definition) had not yet contacted a wall. Thus, we were able to analyze the linear velocities within incline conditions at the same time in the trial, where the only difference was that 1 subject had contacted the wall. Rat pups can show time-related changes in activity levels under similar test conditions (e.g., Schank & Alberts, 1997), indicating the potential value of including time-based control factors.

Rump velocity in the 8 s (24 frames) following wall contact was faster than during the identical time frame for pups that were still in the open arena, not yet having contacted a wall (see Figure 6). This pattern is verified by a repeated-measures ANOVA: $F(1, 30) = 14.494, p = .0006$. There was no significant change in nose velocity, suggesting that the increased velocity is not merely an effect of heightened activity state. Rather, this serves as a reliable indication that a subject's locomotor pattern becomes more linear on wall contact.

It appears, then, that the vertical surface of the wall enables the pup's behavior to reform and, in so doing, respond to the relatively subtle, omnipresent geogravitational cues presented by inclines of 8° or less. Once wall contact is established, the pup's behavior creates a reliable geopositive orientation, and the linear ambulatory movements that follow move the pups' body downhill. The outcome is called positive geotaxis.

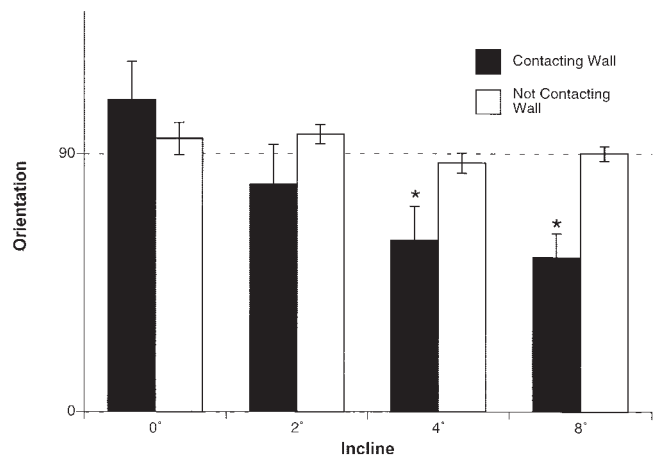


Figure 5. Relative orientation to incline during wall contact. An orientation of 0° represents orientation toward the base, and 180° represents orientation toward the top. Error bars indicate 1 standard error. * $p < .05$ (significant difference from 0° condition).

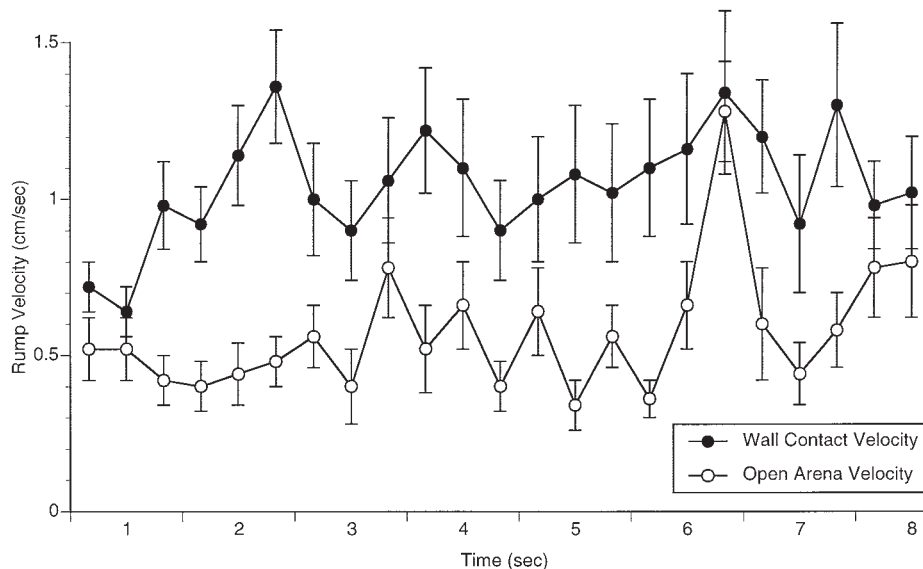


Figure 6. Rump velocity during 8 s following wall contact. Pups that have contacted a wall are compared with pups that have not yet contacted a wall during that same time interval. Error bars indicate 1 standard error. sec = seconds.

General Discussion

Geotaxis: Description Versus Explanation

We retained the term *taxis* for our discussion of the pups' behavior on these shallow inclines. We emphasize, however, that this is a matter of description of behavioral outcomes and definitely not explanation of behavioral mechanism. That is, we use the term *taxis*, in part, to honor a piece of intellectual history, and also because it helps us to quickly describe the existence of a naturally occurring behavior evinced by infant rats. Our initial analyses suggest that many of the sensorimotor behaviors we call *taxes* or *kineses* may be the result of more complex mechanical interactions of sensory input, the size and structure of bodies, and the structure of the environment.

The history of the concept of *taxis*, and the closely related ideas of *kinesis* as well as *tropism*, relate primarily though not exclusively to studies of relatively simple organisms such as bacteria, plants, and invertebrates (see Fraenkel & Gunn, 1961). Conceptually, these terms were used by researchers who were exploring how adaptive, organismal behavior could be explained by identifying movement reactions to external forces. Though such analyses may be valid and pertinent for explaining the movements of some bacteria, plants, and even certain actions of invertebrate organisms, it is not obvious that *taxes* and *kineses*, in their purest forms, are similarly applicable to explaining vertebrate behavior. Yet, in the context of describing response patterns of infant mammals, there may still be some general descriptive utility in identifying kinds of basic response patterns with terms such as *taxis*, *kinesis*, *reflex*, *automatic*, and *unlearned*—so long as we continue to understand that these are terms of convenience and general description; they are themselves not intended to explain the organization of the behavior.

We do not mean to imply that using *taxis* or *kinesis* constrains analysis to a superficial level of "mere description." On the con-

trary, we found power in the approach, because applying these constructs led us to identify relatively pure, unembellished elements of behavior that are amenable to operational definition and quantification. This kind of descriptor becomes a tool with which one can answer questions, test and reject hypotheses, and thus decipher organizational rules of behavior. In the present work, we were led to measure parameters such as turning frequencies and velocities, movement speeds, and spatial orientations and to consider contextual variables such as walls. We were able to reject a variety of explanations of the pups' behavior and identify behavioral elements that provide a parsimonious account of how a specific, lawful outcome emerged in a specific context. This kind of approach can be found in traditional comparative psychology (see, e.g., Maier & Schneirla, 1935).

We are not the first to probe into the organizational basis of geotaxis. While Crozier and his students were producing their corpus of reports on the young rats' negative geotaxis, Piéron (1928) was examining gravity responses of slugs (*Limax maximus*). Piéron worked within the mechanistic tradition, defining and quantifying behavioral elements while observing slugs on inclined surfaces with and without an aqueous surround. By manipulating specific parameters, he was able to dissociate between the slug's "reception" of gravitational cues and its "reaction" to them. We see the present study as a continuation of such a tradition, one that is central to comparative psychology.

The Rat Pups' Positive Geotaxis and Related Orientations

The results of the present study document the phenomenon of positive geotaxis in infant rats and identify specific behavioral components that account for the pups' downhill movement on the shallow inclines. We can summarize the findings of the present study with a set of terms that come from the intellectual tradition exemplified by Fraenkel and Gunn (1961).

We note that undirected activity by the individual pup was essential for the display of geotaxis in the simple, well-controlled environment used in the present study. Functionally, the role of undirected activity was to move the blind pup into contact with a wall. We recognized two categories of such activity, klinokinesis (punting) and orthokinesis (linear movement). Most pups (about 60%) displayed klinokinesis, but in the present testing environment, pups that displayed only orthokinesis had statistically equivalent latencies to encounter a wall (see Table 2). The kind of activity that the pups displayed did not affect the subsequent geotaxis.

It was with wall contact that orientation involving the geogravitational stimulus (geotaxis) was first expressed by the pups. Once in contact with a wall, pups on an incline were then likely to orient downhill (see Figure 5). The probability and extent of positive geotaxis in the presence of a vertical surface were increased by the angle of incline, which reinforces our interpretation that this is indeed a reaction to geogravitational cues. With a downhill orientation, locomotion shifted the pups' location downhill. Significantly, pups remained in contact with the wall and thus maintained a downhill orientation and, as a result, maintained downhill movement secondary to their orientation. The tendency to maintain contact with the vertical surface of the wall is, of course, traditionally termed *thigmotaxis* (Barnett, 1963; Fraenkel & Gunn, 1961) and is a well-recognized and oft-documented characteristic of Norway rats. It appears that thigmotaxis is an important, if not essential, element in the rat pups' expression of geotaxis.

A Historical Correction

Beginning with the reports of Crozier and Pincus (see introduction, above), negative geotaxis has been proffered as the basic, unlearned, automatic response to an inclined surface. For many, there has developed a belief that such an autonomic response can be used as an index of vestibular or proprioceptive function, reflected via a sensorimotor pathway that causes negative geotaxis (Adams et al., 1985). Significantly, Kreider and Blumberg (1999) challenged this assumption. They argued, with observations consistent with those of Hunter (1927) and Hovey (1928), that the behavior recognized as negative geotaxis was actually part of a rat pup's compensatory movements triggered by the postural instability created by placement on an extreme ($> 30^\circ$) incline. Kreider and Blumberg, whose methods were consistent with their predecessors', found no evidence of geotaxis in rat pups.

Our methods differed in several significant ways from those of all previous investigators. First, we used relatively shallow inclines (2° – 8°). We took exceptional care in the control of thermal, light, textural, and olfactory cues. Finally, because we used digital imaging software, our measures and analyses were probably more detailed and objective than those of others.

In accord with Kreider and Blumberg (1999), we believe that negative geotaxis, per se, does not exist in rat pups. Nevertheless, with our apparatus, methods, and procedures, we have identified a novel behavioral phenomenon that is directionally opposite the conventional view of geotaxis. On the basis of the present investigation, we are excited to report that rat pups do show a natural response to a geogravitational stimulus: positive geotaxis.

The results and interpretation of the present study do not necessarily diminish the utility of using pups' behavioral responses to

a robust incline (i.e., $> 30^\circ$) for behavioral screening or in schemes of developmental milestones. Such tests may continue to be useful predictors of teratological effects, for example, but our findings do not allow interpretation of a so-called negative geotaxis as a measure of vestibular or proprioceptive function in rat pups. Nor should positive geotaxis be construed as an index of vestibular or proprioceptive function, reflected via a sensorimotor pathway that causes downhill translocation. The explanation we propose for positive geotaxis does not solely reside in the organism but rather with the organism situated within a specifically structured environment. Thus, we must be careful in applying behavioral tests as indices of sensorimotor development without first understanding how even simple geometrical configurations of an environment can structure behavior.

To advance further the ideas and interpretations presented in this report, one might include precise identification of sensory mechanisms that are used to detect and discriminate the geogravitational stimulus. These might be vestibular, proprioceptive, or both. In addition, we now know that similar inputs that represent perception of the wall stimuli are also critical to understanding even this simple orientation and behavior. We believe the approaches used in the present study (e.g., subtle stimuli, precise control of the testing environment, and analyses of multiple parameters of separable behavioral elements) provide fresh perspectives on how behavior can be systematically analyzed and elucidated.

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