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Review article

The validity and utility of geotaxis in young rodents

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Abstract

Negative geotaxis, an automatic, reliable, stimulus-bound, orientation and movement directionally against gravitational cues, is often used for behavioral assessments of infant rodents. We summarize historical and contemporary analyses and conclude that negative geotaxis does not exist in infant rats. Infant rodents placed on inclined surfaces (ranging from 15° to 70° in most tests) are posturally unstable and their compensatory responses have been misinterpreted as negative geotaxis. In fact, recent findings suggest that if infant rats display a geotaxis, they show positive geotaxis on shallow angles of inclination (e.g., 4° and 8°). There may be utility in assessing postures and motoric responses of infant rats on relatively robust angles of inclination, but these are not tests of negative geotaxis.

Keywords: Geotaxis; Teratology; Posture; Orientation behavior; Test battery

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Behavioral assays are important in toxicology, teratology, phenotype screening, and in other applications that require animals' functional status to be measured. When assessment involves infant animals, it can be especially challenging because an immature animal is often more fragile, prone to fatigue, has limited sensory and motor capabilities, and may be differentially responsive to standard challenges such as water or food deprivation. Moreover, tests that involve training are often inapplicable with young organisms because the training itself can require days or weeks that conflict with timely developmental assessment. Thus, evaluating infant animals places a premium on tests that incorporate natural, unlearned, reliably expressed, even 'reflexive' responses. *Negative geotaxis* is commonly considered to meet such criteria, and is part of the Functional Observational Battery [14,13] and other popular assessment batteries (e.g., Cincinnati Psychoteratogenicity Screening Test Battery [17]; Collaborative Behavioral Teratology Study Battery [1]; SHIRPA [16]).

Negative geotaxis refers to an orienting response and movement expressed in opposition to cues of a gravitational vector [8]. An infant rodent placed on an inclined plane and observed for several minutes is said to have displayed negative geotaxis if it turns toward the high end of the plane

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and moves uphill. As an unlearned response to gravitational cues, negative geotaxis is considered diagnostic of vestibular and/or proprioceptive function.

Early ontogenetic testing for the presence of geotaxis has particular appeal because one "rule" of sensory development posited for all vertebrate species is that onset of vestibular function is either the first or a close second in the developmental sequence of sensory function; indeed, onset of vestibular function occurs before birth or hatching in all birds and mammals [9,2]. Thus, negative geotaxis has a privileged place among behavioral indices of sensory function.

We feel it appropriate to use this commentary to assert that, contrary to conventional wisdom, infant rats do not display negative geotaxis. We believe that at least 75 years ago negative geotaxis was misidentified and, despite protests and attempted corrections around that time, this putative phenomenon acquired undeserved reality status. Not until recently was the phenomenon challenged again and, more recently yet, an opposite phenomenon (positive geotaxis) has been identified.

To appreciate the basis of a decades-long misunderstanding and to suggest a more accurate application and interpretation of gravity-oriented behavior by infant rodents, we review briefly: the history of geotaxis in rats, a recent reevaluation of the original phenomenon, and the new and contrasting phenomenon of positive geotaxis. We conclude with recommendations on interpretation and terminology.

1. A brief history

In the late the 19th and early 20th centuries there existed a general approach, often associated with Jacques Loeb, which sought to identify lawful accounts of behavior based on rule-driven actions. Investigators working within this framework saw organismal behavior as the sum of separable responses to stimuli or, in the vocabulary of the day, "...an unconditioned machine-like reaction of the organism to a field of force..." [10] These responses were thought to reflect corresponding physiological mechanisms that can be observed and quantified as movements or tropisms (from Greek *tropos*, a turn, change in manner). Later, tropistic behaviors were dissected into sub-types, including taxes and kineses [8]. Most of the research inspired by this approach focused on 'simple systems' such as bacteria, protozoa, and invertebrates.

William J. Crozier, working at Harvard University, sought to extend to vertebrate species the popular and powerful approach that Loeb had championed with invertebrate organisms. Between 1926 and 1936, Crozier and one of his associates, Gregory Pincus, published prodigiously on the geotropic behavior of rat pups. Their studies were conducted using a common methodology: They placed individual rat pups (13 and 14 days of age) on an inclined (15–70°) plane, the surface of which was wire mesh (1/8 in.). Initially, the pup's body axis was perpendicular to the slope (horizontal orientation). Then, when the pup was released and it assumed a steady, creeping trajectory, the angle (degrees from horizontal) of linear movement was recorded. Crozier and Pincus [5,7] reported in all trials their subjects promptly turned toward the high end of the incline and began creeping uphill. "Negative geotaxis" in rat pups was thus introduced.

Crozier and Pincus were not alone in these endeavors. Other investigators shared "personal predilections" to highly mechanistic and quantifiable analyses of behavior [11]. At Clark University, Walter S. Hunter began what was intended to be a broadly comparative program to establish and explore tropistic behavior in mammals. Hunter began his studies with young rats, in which he essentially repeated Crozier and Pincus' procedures. In contrast to his predecessors, however, Hunter reported that most pups on severe angles fell off the inclines. Soon there were a number of investigators whose hopes and plans were thwarted by similar findings. These disappointed and disillusioned researchers expressed skepticism if not outright rejection of Crozier and Pincus' analyses [10,11,15,18]. A common, but not the sole challenge to Crozier and Pincus' studies, was that a young rat is posturally unstable on the relatively severe inclines used in those studies. Steep slopes can be unmanageable to a preweanling rat still in the process of developing postural and motor control [4]. Evidently, the early investigators were aware of the pups' limited abilities on an inclined plane and they provided a substrate of wire mesh [10,5,11] or gauze-like material [7] to enhance the pups' performance. Hovey observed that with repeated experience some individual rat pups fell less frequently, and he suggested that Crozier and Pincus' subjects had learned to adjust their behavior to avoid falling, probably by inserting their claws into the mesh [10]. Indeed, pups are equipped with curved and beveled claws sufficiently rigid to act as hooks on which they can "hang" on the severe incline of a plane tilted 45° or more.

Crozier and Pincus' rebuttal was more dismissive (e.g., "We are quite sure that these criticisms originate from misconceptions which are in large part not unfairly characterized as inexcusable...") than reasoned or empirical [6]. They forged on. Between 1926 and 1936, Crozier and Pincus created a substantial corpus of work, at least 10 lengthy reports in the *Journal of General Physiology* alone.

How was it that Crozier and Pincus successfully published the large number of studies of a phenomenon that was so poignantly questioned by their peers? Perhaps the answer lies, in part, with Crozier's status from 1924 to 1955 as Editor of the *Journal of General Physiology*. We do not know the reviewing criteria used at that time; it may be that the papers were not subjected to the rigors of contemporary peer review. Crozier published a generous body of work and, perhaps by virtue of its shear volume, the range of analyses, its quantitative presentations, or Crozier's own prominence in the field, it maintained visibility and longevity in the literature [8].

Decades later, Joseph Altman and his associate, Kiran Sudarshan, assembled an extensive inventory of motor development in young rats. Negative geotaxis was reincarnated as a standardized measure [4]. It is noteworthy, however, that negative geotaxis, as operationalized by Altman and Sudarshan's measures, was a mere abstraction of the original, putative phenomenon. They placed infant rats 1 to 9 days of age facing downhill on plywood surface tilted to either 15° or 25° and observed them for 3 min. Pups that turned 180° from the initial, downward orientation were scored as "successful" in this negative geotaxis test. No level surface (0°) condition was included, so they were not able to describe the frequency with which pups in a control group might turn 180°. Rather, they used the age-related increases in successes as well as a corresponding decrease in latency to respond successfully as support for their assertion that negative geotaxis is a variation of the righting response as measure of vestibular function in a young rat. There was little discussion of the basis for such a belief. Moreover, they reported a nearly linear, age-related decrease in latency to turn from downhill to uphill. This pattern of results suggests the presence of significant task demands on the younger age groups, and that the results may have reflected the development of motor competence in addition to sensory function. Their analysis was exceedingly brief because this was but 1 of at least 27 discrete tests used. Nevertheless, the pups' turning was termed negative geotaxis and, in combination with the older, albeit controversial reports, the idea that infant rodents display a reliable, automatic, reflex-like orientation and movement was further reified in the literature.

2. The demise of negative geotaxis

Recently, Krieder and Blumberg revisited the phenomenon. They conducted a series of systematic observations and measurements of the reactions of 12- to 14-day-old rat pups placed on a plane inclined at an angle of either 30°, 35°, 40°, or 45°; inclinations commonly used by their predecessors [12]. As in previous studies, the testing surface (24 cm × 24 cm platform) was covered with wire mesh (brass wire screen with 1 mm × 2 mm grids). The 15-s trials began with pups placed in one of four orientations (facing up, down, left or right) and for each second, they measured posture, orientation and activity. In the first experiment of the series, Krieder and Blumberg found that pups in the 45° condition were more likely to orient head-up than were pups on a 30° incline. This result appeared to derive from the pups' instability, which was common on the 45° incline, and that "when contact was broken, the pup appeared to stabilize itself by orienting to a head-up position and clinging with its claws to the wire mesh." Like Hovey, Krieder, and Blumberg noted the relation of the pups' claw structure and its orientation on the wire mesh surface. The hooked shape of the claws may make some orientations, such as facing or moving downward, difficult for a pup to negotiate. Moreover, by virtue of their size and shape, the pups' claws can be inserted into the holes between the wires and act as hooks on which they can hang in an upward position. With such considerations in mind, Krieder and Blumberg tested pups on inclined planes covered with Dycem, a relatively smooth, high-friction material. Significantly, the pups maintained contact and moved about on the Dycem surface, but orientations and directionality were non-systematic in relation to either the extent or direction of the geogravitational cues of the plane. In other words, surface features but not angle of inclination affected the pups' orientation and behavior. Dorsoflexion of the tail, generalized leg extension responses, as well as high rates of falling, strongly suggest that the steep inclines are challenging and that the pups' responses are dominated by maneuvers to defend postural stability. Krieder and Blumberg, like some of their predecessors, concluded that rat pups do not display negative geotaxis on such inclined surfaces.

3. If there is geotaxis, it is positive geotaxis

More recently, Alberts and his colleagues examined the behavior of 10-day-old rat pups on surfaces at very modest angles of inclination (2°, 4°, and 8°) [3]. These tests were conducted in a custom-built apparatus with an especially well-controlled environment. Surface and air temperatures were regulated separately; lighting, and chemical cues were also well-controlled. The results were surprising and stunning: There was an overall, incline-related tendency for the pups to move downhill within one minute; that is, they displayed *positive geotaxis*!

How did the pups get downhill? These investigators used digital imaging software to track the $x-y$ coordinates of the pups' snout, back, and rump and create detailed (accurate to 1.5 mm) and fine scale (0.33 s intervals) kinematic accounts of the pups' movements on the various inclines. Initially, pups combined punting, scanning, and crawling to move about the surface. Their trajectories appeared undirected, and there were no inclination related differences in orientation, distance traveled or movement frequency. The critical event was contact with a wall. The pups' undirected movements brought them into contact with a wall, which was 10 cm away at the beginning of each trial. Wall contact was always made with the snout. Once contact was made, the pups' behavior changed.

To invoke the vocabulary of Loeb and his cohort, we might say that the pups' first discernible reaction upon contact with a wall was *thigmotaxis* and this enabled a *positive geotaxis* orientation, which was followed with an *orthokinesis* (increased linear movements) [8]. Whatever one calls the altered elements of behavior, there was an overall movement downhill, i.e., positive geotaxis.

Mechanistic accounts of behavior that rely on automatic, stereotyped orientation and movement reactions to external stimuli have been profitably applied to "simpler" organisms such as bacteria, plants, and insects. But even the stimulus-bound responses of mammals appear to be more variable and subject to modulation by other factors. Nevertheless, there is a tradition of retaining the terms taxis and kinesis for components of mammalian behavior, especially the reactions of infants. With careful qualification, we can see the utility in such terminology but we have emphasized that this is a matter of description, not explanation [3].

4. Is there validity for geotaxis in behavioral assessments?

In the historical pursuit of understanding fundamental mechanisms of behavior, geotaxis occupies a venerable position as a basic response to an omnipresent, global stimulus—gravity. Geotaxis has been a valid and valuable construct in the study of the growth and movements of plants, bacteria, as well some insects [8]. Having a clear, reliable, natural response to a specific stimulus allows researchers to identify sensory receptors and then trace efferent pathways from receptor to behavior. Hence, when behavior is disrupted–by a toxin, disease, or by another perturbation–there is a basis for identifying a corresponding disrupted in mechanism.

The existence of geotaxis or other tropistic responses to geogravitational stimuli has enabled the identification of statocysts and other kinds of graviceptors in a multitude of species. The situation for mammals, however, is complex. There are numerous internal cues, ranging from purely vestibular stimuli transduced by an otolith organ, which can combine with inputs from an inertial system in the canals, to even more global cues arising from proprioceptors located throughout the musculoskeletal system. Indeed, Crozier and Pincus hypothesized that the forces shaping geotaxis in rat pups arose, at least in part, from proprioceptors in the legs [5].

The fact that rat pups on severe inclines (>30°) do not reliably orient to or move in relation to an incline [10–12,3] eliminates the use of a negative geotaxis as a measure of sensory (vestibular or proprioceptor) function. On the other hand, the downhill movement of rat pups on modest inclines (2–8°) suggests that there may be a role for measuring sensory function by a positive geotaxis [3]. It must be noted, however, that the pups' downhill orientation and movements are secondary to wall contact [3]. Thus, at the present time, a primary geotaxis has not been identified in rat pups, though there is a behavioral measure that may be useful.

The behavior called negative geotaxis that is commonly measured in young rodents appears to be a form of compensatory response or even an emergency reaction to postural instability on an inclined surface. To orchestrate body, head and tail positions in combination with leg movements that afford hooking the claws into holes in wire and maintaining a more stable, head-up position may well be a practical composite measure of strength, stamina, and sensorimotor function. Indeed, it appears that investigators find utility in measuring frequency of remaining on an inclined surface. It is possible, even likely, that changes in successful performance in this demanding challenge of postural stability have utility for recognizing developmental perturbations. As such, it is a useful tool and can be applied productively, but it should be recognized for what it is and not be over-interpreted. We suggest that researchers use more operational terms such as "tilt table test," "stability on an inclined surface," or "mobility on an incline."

Strictly speaking, negative geotaxis has no basis in rat pups. Positive geotaxis may apply, but even this phenomenon is more complex than a pure taxis in the traditional sense [8]. The behaviors measured in these kinds of tests on severe and modest inclines are not purely vestibular and cannot be used accurately to assess sensory function in that system. They may, however, provide useful, quantitative measures of integrative, locally adaptive behavioral responses.

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Author's response to open peer comments

What's a word worth?

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Geotaxis denotes automatic, reliable orientation and movement in relation to a gravitational stimulus. It is, by definition, dependent on perception of gravitational cues or of stimuli that arise from gravitational forces, such as proprioceptive cues. Recent empirical re-examinations of negative geotaxis in infant rats, briefly reviewed in our commentary, indicate that the behavior of rats on an inclined plane is not geotaxis. Depending on factors such as the angle of incline or the substrate material, a rat pup may be observed to orient up, down, or in no particular direction. Absent is a robust, reliable and valid gravity-oriented response by infant rodents on inclined surfaces. There was no substantive disagreement expressed by the commentators on these points.

The discrepancy between the specificity of the term, geotaxis, and the general absence of an oriented response to gravitational cues bothers each of the commentators and us in different ways and to varying degrees. Despite these differences, it was gratifying that a common theme in each of the Open Peer Commentaries is a basic concern with the conduct of science.

Krieder and Blumberg drew a parallel between lack of terminological rigor and the absence of methodological standardization in testing infant rodents' performance on an inclined surface.

They see dual benefits to the use of standardized methods. First would be consistency, so that results from different laboratories could be compared legitimately. This is essentially impossible today, due to the wide variation of what is performed under the label of tests of negative geotaxis (see Kreider and Blumberg's Peer Commentary). We see many practitioners addressing this issue through the creation of formalized protocols, but these remain compromised by lack of rigor regarding gravity-determined responses. It is inefficient to base precise measures on imprecise behavioral constructs. Practical standardization would involve common implementation of precise measures, including those that would evolve through improved understanding. Krieder and Blumberg also called for concomitant standardization of parameters.

We endorse Krieder and Blumberg's extrapolations. Ambient temperature, light levels, acoustic background, substrate texture and odor, and gravity comprise a class of general, non-localized, omnipresent, "global cues" to which experimenters often attend less than to discrete stimuli that we carefully impose and withdraw in our tests. Some of the simpler rubrics of empirical methodology suggest that if we keep variables constant for different treatment groups, that the effects will be the same for each group and are thus not a matter of concern. But these global cues can exert significant physiological and behavioral consequences, so there is good reason to formalize our treatment of them. We recommend careful and systematic attention to contextual features such as temperature, odors, and substrate texture; when in doubt, opt for stimuli and values resembling those of the maternal nest.

Maurissen's comments highlight the problem of achieving validity in empirical analyses. He rightly recognizes the dual aspects of validity: "sensitivity" to measuring that which we intend to measure, and "specificity" to the focal variable and not measuring additional factors. Measuring behavior is a sophisticated and demanding enterprise, and the challenge of interpreting validity in our behavioral measures is great indeed. In fact, the analysis of behavior in terms of its organizational rules, its functional roles, and mediation by neural and physiological mechanisms, requires that we

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incorporate validation as a continual enterprise. Maurissen offers a succinct reminder that we are all part of a perpetual process of refinement and enhancement of knowledge. We can — we should — question and challenge even the most basic tenets of our knowledge base. It is through doubt and falsification and we break through barriers. It was flattering to have our approach associated with Claude Bernard's, and we thank Jacques Maurissen for his overview and insights.

Geotaxis testing in rodents lacks validity, but it may have utility. Virginia Moser champions a utilitarian perspective. Many experienced practitioners, she notes, consider the testing of young rodents on inclined surfaces useful. Moser accepts discriminant validity as a viable standard: It is possible that such testing on inclined planes can reveal differences in performance that involve integrated movements to maintain contact with the substrate (and prevent falling) or that enable pups to achieve a claw-hold and hang in place. That poorly understood, complex reactions would provide an efficient, sensitive measures seems to us improbable. We believe that there is practical knowledge to be gained from deeper understanding of emergent, integrated behavior. Even so, the question then becomes, what do measured differences validly measure? Only from a detailed understanding of the control parameters of the pups' responses in contexts of the relevant ontogenetic niche can the results of behavioral tests be interpreted fully. This, we think, is the likely next requirement of such methods and again the onus is on us all to refine our questions and to pursue them at multiple levels of analysis.

We are not sympathetic with Moser's concern that there might be "confusion" if a more accurate, operational term such as "incline test" were to be used. This would be progress, not confusion. (Speaking of accuracy: We acknowledge and thank V. Moser for correcting our misattribution of which batteries include geotaxis as a measure.) Our words must matter. Scientific knowledge is not static. It is acceptable, even desirable for knowledge to evolve and for our understanding to change. Terminology will change accordingly. Words are valuable and powerful. Our words guide our perceptions, our thinking, and our actions. They reflect our interpretation of the world. Accepting and using inaccurate classifications and terminology can only impede scientific process and progress. In an era like the present, with increasing interdisciplinary studies, it is especially critical that we communicate accurately and be prepared to be explicit about the bases of our ideas and words. We side with Maurissen and prefer an operational term such "incline test" for behavioral assays with infant rodents. And we endorse Krieder and Blumberg's call for standardization with careful attention to infant-appropriate parameters.

Our empirical study of geotaxis in rat pups began innocently. Like others before us, we intended to use a simple, robust and reliable behavior as a tool in other investigations. We were initially confused and disappointed by observations that contradicted our expectations, but we later were rewarded by the satisfaction of clarifying and achieving a new level of understanding. We would like to reserve "geotaxis" for orientation and movement that occurs automatically and reliably in relation to a gravitational stimulus. It's worth preserving. But its value will be a function of its validity, so we will do best by using it accurately.