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Geotaxis and beyond: Commentary on Motz and Alberts (2005)

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Received 19 February 2005; accepted 18 March 2005

In its original conceptualization, geotaxis was defined as an automatic, stimulus-bound, reflexive response that results in a directional movement with or against the force of gravity [15]. When first described in invertebrates [4,13], geotactic responses were shown to serve critical adaptive orientating functions [15] that are mediated by identifiable receptors and organs [14,29]. In contrast, the notion that negative geotaxis is exhibited by infant rats [10] has been challenged by four different laboratories over the last 78 years [1,16,17,20]. With Motz and Alberts [24], we agree that in infant rats, “negative geotaxis” is not an automatic, stimulus-bound response, that its ecological validity is questionable, and that the neural substrates that might mediate this response are undefined [1,20].

Despite doubts concerning negative geotaxis in infant rodents, it remains a popular behavioral metric. In reviewing some of the work published over the past five years [3,8,9,11,19,21–23,25,28], we found that the methods used to assess negative geotaxis in infant rats and mice have not been standardized. Specifically, six different testing angles (20°, 25°, 30°, 40°, 45°, 90°) and many different ages (postnatal day 2–21) have been used. Most surprising is the method used in the SHIRPA [26] in which the animal is placed on a grid in the horizontal plane and the grid is then rotated 90°. This method comprises several features – including the use of a severe incline and the addition of rotational forces – that mark a significant departure from the methods of Crozier and Pincus [10], Fox [12], and Altman

and Sudarshan [2]. In addition, we found that at least six different testing substrates were used (wood, cloth, sand paper, glass paper, “rough surface”, grid surface) and ambient temperature was apparently uncontrolled (i.e., air temperature was not reported). Given these multiple methods for measuring negative geotaxis, generalizing across studies is difficult; yet, the popularity of such tests of geotaxis persists.

Like Motz and Alberts [24], we do not deny that motoric, postural, and vestibular processes underlie the ability of infant rodents to navigate on an inclined plane. But, in the face of multiple lines of evidence arguing against the existence and meaningfulness of this behavioral metric, and given other assessment tools like contact righting and cliff avoidance that are ecologically valid and that rely upon known neural substrates, it is indeed curious that negative geotaxis has achieved a preferred place in the methodological armamentarium of developmental researchers. Perhaps, as Motz and Alberts [24] suggest, Crozier [10] deserves much of the blame for this state of affairs. Regardless, given their findings [1] and ours [20], there is little basis for continuing to employ conventional tests of negative geotaxis in infant rodents for the purposes that are typically provided.

Published studies of motor behavior in infant rodents have interpretational problems that go beyond any single testing procedure. Specifically, as indicated above, the importance of ambient temperature as a modulating factor in infant behavior is typically ignored to the point that it is not even reported. Temperature, however, is perhaps the single most important modulator of infant behavior and one might think that developmental researchers interested in sensorimotor processes would take notice of any factor that exerts such powerful effects on muscle activity and neural function. This is not the case. For example, one of the most widely cited developmental studies of motor behavior in rats

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[2] tested rat pups from postnatal day 1 to postnatal day 21 at air temperatures ranging from 21 to 24.5 °C. Similarly, Fox's well-known and often-utilized neuro-developmental battery [12] also apparently tested mouse pups from postnatal day 2 to postnatal day 26 at room temperature (i.e., testing temperature was not reported).

Soon after birth, infant rats can produce heat endogenously using brown adipose tissue but the range of air temperatures over which thermoregulation is effective is limited [5]. For example, at postnatal day 2 (P2), pups will initiate heat production at an air temperature of approximately 34 °C and heat production is maximal at approximately 31 °C. At this age, then, room temperature (i.e., 20 °C) represents an extreme thermal challenge that very quickly leads to significant hypothermia. Similarly, by P8, heat production is initiated at an air temperature of approximately 34 °C but at this age the pup can regulate effectively at air temperatures as low as 25 °C. In other words, the effective range of regulation expands as pups grow and as their thermal inertia increases. Still, note that room temperature (the temperature typically used to test geotaxis and other behavioral reflexes) represents an extreme challenge even to P8 rats, resulting in hypothermia and its attendant physiological consequences [7]. The continued increases in body size and growth of fur over the next week must occur before pups are able to combat effectively the challenge of exposure to room temperature.

Thus, testing developing animals of different ages at the same ambient temperature confounds age with body temperature. Interestingly, it has been noted that investigators seem to match the infant behavior of interest to particular testing temperatures [6]. For example, in addition to the examination of motor behaviors at room temperature, tests of learning and memory are typically administered at moderate air temperatures, the emission of ultrasonic vocalizations is best elicited at extreme air temperatures, and sleep is maximized at thermoneutrality [27]. In other words, investigators asking domain-specific questions of infant rats seem to have gravitated toward the use of particular air temperatures without explicitly acknowledging this fact. But this is an issue that demands our attention; indeed, even in adult mice tested in a Morris water maze, thermal factors have a significant impact on performance [18].

Of course, those interested in motor behavior in developing animals must avoid those air temperatures that stimulate sleep. But this does not mean that room temperature is a sound alternative for tests of motor behavior. Instead, investigators should begin to calibrate their testing conditions to the thermal inertia and thermoregulatory capabilities of their infant subjects. The result, we believe, will be increased sensitivity to developmental differences and increased ability to detect effects of teratogens on early behavior. Indeed, the demonstration [1] that rat pups exhibit positive geotaxis on a shallow incline may have been aided by testing 10-day-old pups at a moderate air temperature (i.e., 27 °C).

The elegant work of Alberts et al. [1] closes the book on negative geotaxis as it pertains to infant rats while it opens new avenues for research into the more complicated sensorimotor processes that govern infant behavior on more gentle slopes. Such complexity may not be welcomed by those seeking simple tests that can be quickly and easily administered to infants. Similarly, considerations of the thermal needs of infants may be viewed by some as a nuance that can be safely ignored. We believe, however, that more rapid and sure-footed progress in our understanding of normal and disrupted development will come when these complexities are appreciated and these nuances are embraced. In addition, we note that the demise of negative geotaxis stands as a reminder that behavioral metrics that stand on shaky conceptual ground need to be constantly reassessed, regardless of their popularity.

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