Visual cliff performance in 10 species of muroid rodents

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A total of 200 muroid rodents, 20 from each of 10 species from diverse ecological adaptations, were tested for depth perception near the age of weaning. Each animal was given 10 trials in a visual cliff. Seven of the 10 species, Israeli gerbils, California voles, house mice, meadow voles, cactus mice, cotton mice, and deer mice, showed some evidence of depth discrimination. By contrast, white-footed mice, prairie voles, and montane voles showed no evidence of such discriminative ability. Although there was no strong relationship apparent between the usual habitat of the species and their tendency to choose the shallow side in the visual cliff, a relationship was found among ecological factors, open-field behavior, and the latency to make a descent from the centerboard of the visual cliff.

In many habitats, the ability to perceive depth is of critical importance to young organisms when they first initiate independent locomotor activity. Only by attending to depth cues can the developing organism successfully negotiate its environment. The primary apparatus used in most recent studies of the development of depth perception in animals has been the visual cliff (Gibson & Walk, 1960; Shinkman, 1962; Walk & Gibson, 1961). Data on visual cliff performance have been collected using a wide variety of species (e.g., Routtenberg & Glickman, 1964; Walk & Gibson, 1961). Consistent with the demands of independent locomotion, it has generally been found that animals display effective visual cliff performance by the age of independent locomotion (Gibson, 1969). Thus, Walk and Gibson (1961) concluded that "all of the animals studied discriminated visual depth by the time locomotion was possible" (p. 42).

Despite the general finding of good depth perception in the visual cliff in most species, some exceptions have been found. For example, Mongolian gerbils appear deficient in depth perception as assessed using this method (Bradley & Shea, 1977; Thiessen, Lindzey, Blum, Tucker, & Friend, 1968). It has been proposed that variations in the development of depth perception may be correlated with the habitat of the species in question (Routtenberg & Glickman, 1964; Yerkes, 1904). For example, animals from a cliff environment might be expected to perceive depth more readily than those from a flat environment (e.g., Emlen, 1963). As elaborated by

Walk and Gibson (1961): "It is necessary, therefore, to take a lesson from the ethologists and consider how the kind of discrimination to be compared fits with the ecology and biological requirements of the species—its method of reproduction, defense, food-getting and territorial adjustment. A real comparative psychology will only be written in such a context" (p. 42).

Relationships between targeted behavioral variation and ecological factors are generally considered most easily demonstrated when groups of species of close taxonomic affinity, yet diverse ecological adaptation, are compared (King, 1963, 1970). The muroid rodents provide an ideal taxon for such comparisons (Dewsbury, 1974). In the present paper, we compare the visual cliff performance of 10 species of muroid rodents. These species are adapted for different life styles, ranging from semiarboreal patterns (e.g., cotton mice) to desert adaptation (e.g., cactus mice) and field dwelling (e.g., meadow voles). Animals were tested near the age of weaning—the time when substantial amounts of locomotor activity independent of the parents would be expected to begin.

METHOD

Subjects

The subjects were 20 animals of each of the following species of muroid rodents: montane voles (*Microtus montanus*), California voles (*Microtus californicus*), prairie voles (*Microtus ochrogaster*), meadow voles (*Microtus pennsylvanicus*), house mice (*Mus musculus*), Israeli gerbils (*Meriones tristrami*), deer mice (*Peromyscus maniculatus bairdi*), cotton mice (*Peromyscus gossypinus*), white-footed mice (*Peromyscus leucopus*), and cactus mice (*Peromyscus eremicus*). Animals were of both sexes, between the ages of 19 and 25 days; all were born and raised in the laboratory. For all species, the eyes of virtually all animals opened by Day 15 or earlier. In most cases, no more than three animals were selected from a single litter. Information regarding

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foundation and general characteristics of these animals has been summarized by Dewsbury (1974, 1975) and the references cited therein and for house mice of the wild genotype by Connor (1974), for Israeli gerbils by Thiessen, Wallace, and Yahr (1973), and for cotton mice by Lovecky (1976).

All animals were bred and maintained in clear plastic cages measuring 48 × 27 × 13 cm and fitted with metal tops of either mesh or parallel rods. Food and water were available ad lib. Voles were fed Purina Rabbit Chow (supplemented with lettuce for California voles and montane voles). All other animals were fed Purina Lab Chow. All animals were kept on 16:8 cycles of white light with lights going on between 1700 and 2000 h in different rooms. Dim red light shone at all times.

Apparatus

A Lafayette Instrument Company Model 86030 visual cliff was modified for use in this experiment. The apparatus was 76 cm square and 61 cm deep, with glass (0.39 cm thick) resting on both sides and 40 cm above the deep side pattern. The original red-and-white-check pattern with squares 5.14 cm square appeared on both the shallow and deep sides, but the side walls were lined with white poster board. A wood centerboard, 76 × 10 × 4 cm and painted white, was used. Illumination was provided by a floodlight that was equipped with a rheostat. The light was mounted on the ceiling 1.5 m above the centerboard of the visual cliff and was adjusted to minimize glare and shadow. Timing was done with a stopwatch.

Procedure

On the day before testing, all animals had their vibrissae clipped to the length of the surrounding muzzle hair. This was done to eliminate the use of tactual cues in the visual cliff (see Gibson & Walk, 1960).

Testing was done in the dark phase of the diurnal cycle, beginning at least 2 h after the white lights went out. Each animal received 10 massed trials in the visual cliff. Five releases were made from each end of the centerboard in a random progression. To minimize handling, the animals were placed in a small box, 10 × 15 × 10 cm, for release. The box was placed on the centerboard and the animal permitted to leave it. When all four feet left the box, the trial was begun and the box removed. A descent from the centerboard was defined as a trial in which the animal's front paws were placed on the glass over one side of the centerboard. Both the side chosen and the latency to descend were recorded. The animals were removed as soon as possible after they made a descent. If an animal did not descend from the centerboard within 1 min of the beginning of the test, a sheet of white poster board, 23 × 16.5 cm, was lowered at the end of the centerboard and moved toward the animal. If the animal did not descend within 1 min from the introduction of the poster board, the trial was recorded as a "nondescent" and the animal was removed from the apparatus.

RESULTS

The results are summarized in Figure 1 and Table 1. The primary dependent variable considered was the proportion of the total number of descents from the centerboard that were made to the shallow and to the deep side. Trials with no descent were excluded from such analyses. The proportion of trials with nondescent ranged from 0.0 in prairie voles to 0.14 in meadow voles and cactus mice. As there appeared to be no obvious relationship between the number of nondescents and other measures, they will not be considered further.

The mean proportion of shallow-side descents for each species is shown in Figure 1. These means were calculated by finding the proportion of descents that were to the shallow side for each animal and then taking the mean of these scores. Considerable variability is apparent, with Israeli gerbils having a mean proportion of 0.76 of their descents to the shallow side and white-footed mice just 0.48. A one-way analysis of variance revealed a significant difference as a function of species, $F(9,190) = 4.12$, $p < .01$. Tukey's honestly significant differences method of multiple comparisons was used to make pair comparisons. Both Israeli gerbils and California voles were found to have significantly greater shallow-side preferences than deer mice, montane voles, and white-footed mice. House mice, meadow voles, and cactus mice all differed significantly from white-footed mice.

Assessment of depth perception in each species can be made by determining whether each deviates significantly from chance performance levels (i.e., 0.50). Data from the 20 animals of each species were used to determine the 95% confidence limits about each mean proportion (Figure 1) (Hays, 1963). If the confidence limit for a species does not include the 0.50 level, then the species is regarded as performing at above chance levels. By this criterion, four species, white-footed mice, montane voles, deer mice, and prairie voles, failed to display nonrandom choice.

Figure 1. Mean proportion of shallow side descents to total descents for 10 species of muroid rodents. Ninety-five percent confidence intervals are shown for each species. Depth discrimination is regarded as present when confidence intervals do not include the chance (0.5) level.

Table 1
Choices on First Trials with Descent (Using Two Criteria), Mean Latencies to Descend, and Proportion Nondescents

Species	Percent of First Descent		Latency (seconds)		Proportion Nondescents (200 trials)
	to Shallow Side	with Stretch or Jump to Shallow Side	Mean	SE	
Israeli gerbils	85*	85*	33.0	8.0	.12
California voles	75*	75*	38.5	8.3	.02
House mice	75*	75*	15.4	4.6	.06
Meadow voles	75*	75*	49.1	9.6	.14
Cactus mice	65	75*	41.5	9.9	.14
Cotton mice	50	65	12.9	4.7	.05
Prairie voles	55	70	31.2	7.8	.00
Deer mice	80*	85*	30.3	6.8	.08
Montane voles	45	65	57.8	8.6	.06
White-footed mice	60	70	13.8	5.1	.02

* $p < .05$; binomial test (Siegel, 1956).

The remaining six species showed a significant preference for the shallow side. No species preferred the deep side. Species differences as assessed using these confidence limits are consistent with those assessed with the Tukey test.

Routtenberg and Glickman (1964) proposed that "site of first descent is likely to be the single best measure of depth discrimination per se" (p. 145). Therefore an additional data analysis was conducted, with the first descents analyzed separately. Percentages of first descents that were to the shallow side for each species are presented in Table 1. The statistical significance of the deviations of these values from chance was evaluated using binomial tests (Siegel, 1956). In general, the performance of different species on the first trial parallels their overall performance levels. Five of the 10 species displayed evidence of depth discrimination on the first trial. Deer mice, which showed no significant overall shallow-side preference, did show a significant first-trial preference. Cactus mice and cotton mice, which showed significant overall shallow-side preference, did not differ from chance when only first-trial performance was considered.

Animals sometimes appeared to either fall or dash from the centerboard. On such trials, it is not clear whether or not the animal has sufficient opportunity for true depth perception. Trials with stretching or true jumping motions clearly do permit an evaluation of depth by the animal (Collins, Lindzey, & Thiessen, 1969). A slight modification of the analysis of the first descent data can be made to consider choices on the first descent following stretching or jumping (see Table 1). Such an analysis revealed a pattern identical to that of the previous analysis, except that cactus mice now differed significantly from chance.

Data relating to the latencies to descend (excluding trials with nondescent) are presented in Table 1. The latencies to descend to the shallow vs. the deep side were tested for each species using Dunn's procedure

to control for error rate. No significant differences were found. Analysis of variance revealed a significant difference in the overall latency data as a function of species, $F(9,187) = 4.76$, $p < .01$. Individual comparisons using the Newman-Keuls method revealed that cotton mice, white-footed mice, and house mice displayed significantly shorter latencies to descend than montane voles, prairie voles, or meadow voles. A Spearman rank-order correlation coefficient revealed no significant correlation between the order of the species' proportions of descents and the order of the species' latencies to descend ($r_s = 0.18$) (see Table 1).

DISCUSSION

It is apparent from these data that the ability to perceive depth, at least as measured by performance in the visual cliff, is not a universal characteristic among rodents. Three of the species in this study, white-footed mice, prairie voles, and montane voles, showed no evidence of depth discrimination, either in the data from all tests or from the first descents following stretching or jumping. Although it is possible to conclude that the remaining seven species show evidence of at least some ability to perceive depth at around the time of weaning, it cannot be concluded that the remaining three species are unable to perceive depth. As with any test situation, many extraneous factors can affect performance and might interfere with efficient depth discrimination and choice. Unusual sensitivity to handling, the novel apparatus, confinement, or many other aspects of the test situation could impair performance.

There was no obvious relationship between taxonomic status and visual cliff performance. Species displaying both efficient and poor depth discrimination were found among both the *Microtus* and *Peromyscus* genera. Israeli gerbils, the species showing the highest mean proportion of choices to

the shallow side, are congeneric with Mongolian gerbils, a species that has been reported deficient in visual cliff performance (Bradley & Shea, 1977; Thiessen et al., 1968).

Ideally, there would be a correlation between visual cliff performance and the usual life-style of the species (Routtenberg & Glickman, 1964; Walk & Gibson, 1961; Yerkes, 1904). There appears to be none that is compelling. Among *Peromyscus*, both cotton mice and white-footed mice are semiarboreal species that are efficient at climbing (King, Price, & Weber, 1968; Layne, 1970). However, cotton mice displayed good depth discrimination; white-footed mice did not. The failure of white-footed mice is puzzling but somewhat consistent with their marginal performance in other test situations that require rapid habituation. Thus, they appear to be poor at digging when given 15-min tests, but can be seen to be efficient diggers in 24-h tests (King & Weisman, 1964). Similar behavior has been found in tests of visual discrimination and gnawing, where they are reported to display "marked inactivity in a strange, unpleasant situation changing to rapid, vigorous activity" (King et al., 1968, pp. 128-129).

As both prairie voles and montane voles are field dwellers, their failure to display efficient depth discrimination is less surprising. What is puzzling is the fact that while the latter species do not, California voles and meadow voles do display depth discrimination. There is no apparent ecological characteristic differentiating these species. Both prairie voles and montane voles tend to live in drier, more upland habitats than meadow voles (Getz, 1962; Murie, 1971). However, California voles are common in such habitats and montane voles can be found near water (Maser & Storm, 1970).

Data on latencies to descend appear more closely related to ecological factors than do the choice data. Three species formed a cluster as the fastest to descend, the semiarboreal cotton mice and white-footed mice, and the ubiquitous house mice. House mice live in diverse habitats, many of which require extensive climbing. As the remaining, slower species are generally found in fields or deserts, the latency data appear to show the clear correlation with ecological factors that was anticipated in the choice data (i.e., species likely to climb more in nature have shorter latencies than those that climb less).

Eight of the 10 species in this study, all except house mice and deer mice, were also studied in a comparative analysis of open-field behavior (Wilson, Vacek, Lanier, & Dewsbury, 1976). Those data were consistent with the latency data in the visual cliff and ecological factors. Cotton mice and white-footed mice entered the most squares of any species appearing in both studies, did the most jumping, and were the only species to climb. More recent observations

in the same apparatus indicate that house mice of the population studied herein also jump and climb. The consistency found among latency data, open-field behavior, and ecological factors, coupled with the discrepancy with discrimination data in the visual cliff, further suggests that the failure of white-footed mice, prairie voles, and montane voles to show evidence of depth perception may be more a function of the test situation than of deficient perceptual ability per se.

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