The effect of environment on visual cliff performance in the Mongolian gerbil

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Depth perception in the Mongolian gerbil was investigated as a function of age and environment. Thirty-two gerbils were raised in either a cliff or flat environment, and half the gerbils in each condition were tested on the visual cliff from 21 to 57 days of age. All gerbils were tested at 60-61 days on a standard visual cliff, a barrier cliff which prevented movement along the centerboard, and a jumping platform. While the gerbils did not display a preference for the shallow side when tested at 21 days, those living in a cliff environment showed rapid acquisition of such a preference, whereas those living in a flat environment did not. By 60-61 days, however, all gerbils demonstrated a strong preference for the shallow side on both versions of the visual cliff, regardless of environment or pretesting experience.

Following a now-classic study by Lashley and Russell (1934), many investigators have attempted to determine whether the perception of depth is innate or learned. The most popular apparatus for assessing the presence of depth perception has been the visual cliff (Gibson & Walk, 1960). When tested on this device, chicks, cats, dogs, mice, rats, goats, lions, tigers, rabbits, golden hamsters, Egyptian gerbils, sheep, pigs, jaguars, snow leopard cubs, monkeys, and human infants show a preference for the shallow side of the cliff (Gibson & Walk, 1960; Rosenblum & Cross, 1963; Routtenberg & Glickman, 1964; Thiessen, Lindzey, Blum, Tucker, & Friend, 1968; Walk, 1965; Walk & Gibson, 1961). In addition, many species have been tested shortly after birth, and the results indicate that the preference for the shallow side is present as soon as the infants are capable of independent locomotion (Gibson, 1969; Walk & Gibson, 1961). A conclusion frequently drawn from this research is that the perception of depth is innate in all species for which the avoidance of a sheer drop-off is a requirement for survival. Apparent exceptions to this generalization have been recorded; for example, both aquatic turtles and ducks perform poorly on the visual cliff (Gibson & Walk, 1960; Walk, 1965, Note 1). This is usually attributed to the lack of fear these animals would have for a cliff (presumably because of the nature of their aquatic environments), rather than to an absence of depth perception. Also, poor performance has been recorded in some experiments testing rats (Peretti, 1971; Schiffman, Lore, Passafiume, & Neeb, 1970), but this can be interpreted as indicating

a greater reliance on tactual as opposed to visual clues in governing the descent behavior of this animal. When the vibrissae are clipped so that the rats cannot rely on tactual cues, they show a preference for the shallow side, as do other species (Gibson & Walk, 1960; Schiffman et al., 1970; Walk & Gibson, 1961).

Recently, however, another species has shown inconsistent performance on the visual cliff. The Mongolian gerbil (*Meriones unguiculatus*) was first tested on the visual cliff because of the incidental observation that this animal often falls from high places. Initial tests indicated that the Mongolian gerbil displayed no systematic preference for the shallow side of the visual cliff (Thiessen et al., 1968). Subsequent research found that this species can discriminate depth, as measured by the increase in latency to descend from platforms of increasing heights (Cole & Topping, 1969; Collins, Lindzey, & Thiessen, 1969). However, since testing always occurred after 60 days of age, it is not clear whether this ability is innate, as it is presumed to be in most other species, or whether it is acquired during the pretest interval. In contradiction to Thiessen et al. (1968), Thiessen, Lindzey, and Collins (1969) reported that gerbils do display a preference for the shallow side of the cliff. Similarly, Peretti (1971) reported perfect performance for six Mongolian gerbils on the visual cliff, in contrast to inferior performance by albino rats. The age of testing in these two experiments was 52 and 30-51 days, respectively; hence, as in the platform tests above, these results do not prove that the gerbil is innately equipped to perceive depth.

Another question receiving attention concerns the effect of environmental factors on visual cliff performance. Although at least one class of depth information must be processed innately in order for a species to perform well on the visual cliff shortly after birth, experience might allow other classes of

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depth information to acquire cue value through contingent associations with that class detected by innate mechanisms (Walk & Gibson, 1961). For example, while young rats do not prefer descent to a textured pattern having physically larger and less densely packed texture elements of two patterns placed directly underneath the glass, older rats do show such a preference (Shinkman, 1962; Walk & Gibson, 1961). This suggests that texture size or density is acquired as a cue regulating descent behavior on the visual cliff.¹

Another effect of experience is to modify or disrupt the usual preference for the shallow side of the visual cliff. Tallarico and Farrell (1964) found that chicks raised on the deep side of the visual cliff showed a slight preference for the deep side when tested, whereas both shallow side and normally raised chicks showed the usual preference. Similar results have been obtained with rats (Carr & McGuigan, 1965; Kaess & Wilson, 1964; Rosen & Ison, 1964). Eichengreen, Coren, and Nachmias (1966) compared monocular and binocular visual cliff performance of infant rats having different early environmental histories. Half of the rats were raised in normal environments and half in a larger cage with climbing platforms which increased potential experience with depth cues and distance. The results showed that when tested monocularly "enriched" rats preferred the shallow side whereas normally reared rats did not. Both "enriched" and normal rats preferred the shallow side when tested binocularly.

Thiessen et al. (1969) investigated the effects of early experience on visual cliff performance in the Mongolian gerbil. They raised gerbils in one of three cage environments: (1) a patterned cliff environment, (2) an unpatterned cliff environment, and (3) an unpatterned flat environment. When tested at 52 days, all gerbils preferred the shallow side of the visual cliff, although this preference was slightly weaker in the unpatterned cliff environment than in either of the other two environments. Stronger effects of environment were observed in the latency data, with the patterned cliff environment producing the shortest, and the unpatterned flat environment the longest, latency to descend. Unfortunately, the preference data do not indicate whether the gerbils' ability to perceive depth at 52 days is dependent on, or simply incidental to, the environmental experience provided.

In order to assess whether or not the Mongolian gerbil can innately perceive depth, tests must be conducted as soon as possible after birth. Since gerbils do not open their eyes until about 20 days of age (Schwentker, 1963), testing cannot begin before this point. Furthermore, assuming that the Mongolian gerbil does not display an innate preference for the shallow side of the visual cliff when first tested, it

will be necessary to administer multiple tests over time to detect any developmental trends which may exist for the acquisition of a shallow side preference. Finally, the effects of early experience on the rate of acquisition can be evaluated by comparing the performance of gerbils raised in different cage environments. The following research was undertaken to investigate these questions.

METHOD

Subjects

The subjects were 32 Mongolian gerbils (*Meriones unguiculatus*) raised from mated pairs obtained from Tumblebrook Farms.

Design

The initial subject pool of 32 gerbils was randomly divided into two groups: a "pretested" group, which was tested on the visual cliff from 21 to 57 days of age and at 60-61 days, and a "naive" group, which was tested only at 60-61 days. One-half of the gerbils in each of these groups were randomly assigned to a cliff environment (CE) and the other half to a flat or noncliff environment (NCE). The design for the pretesting phase of the experiment was a 2 by 7 mixed factorial design, with two cage environments (CE vs. NCE) and seven testing ages (21, 23, 25, 27, 37, 47, and 57 days). The design for the posttesting phase (60-61 days) was a 2 by 2 factorial design, with two cage environments (CE vs. NCE) and two levels of previous experience with the visual cliff (pretested vs. naive). At 60-61 days, all four groups of gerbils were tested on two versions of the visual cliff (standard and barrier), and on a jumping platform placed at varying heights (7.6 to 38.1 cm). Finally, after 100 days of age, all four groups were tested on visual cliff having modified texture patterns on each side of the centerboard.

Apparatus and Materials

The cliff environment consisted of a large wire mesh cage (38.1 x 58.4 x 20.3 cm) with wood platforms stacked in staircase fashion to a height of 15.2 cm. Gerbils had to negotiate these obstacles to some degree in order to get to food and water. However, curiosity and the need to exercise motivated the gerbils to climb these artificially constructed cliffs in the absence of external incentives. The noncliff environment was an identically constructed cage, but without the wood platforms. The external visual environment was identical for both groups.

The visual cliff was 77.0 cm square and 61.0 cm deep. A piece of Plexiglas (.63 cm thick) was laid across the box at a height of 40.6 cm. A centerboard (77.0 x 10.2 cm) divided the Plexiglas into two rectangles of equal size. The shallow side of the cliff had a blue-and-white checkerboard pattern (3.8-cm squares) placed on the underside of the Plexiglas. On the deep side, an identical pattern was placed on the floor of the cliff 40.6 cm below the Plexiglas. The centerboard was covered with the same material. The entire box was lined with white posterboard, and a dome of Mylar drafting material was placed on top of the box to provide for even light dispersal and to minimize reflections. Illumination was provided by a desk lamp suspended 1 m above the box. The experimenter observed the subjects' performance from a peephole in a corner over the deep side. A modified version of the visual cliff utilized a barrier placed in the middle of the centerboard which served to constrict movement. The barrier consisted of two posterboard "walls" (23.0 x 16.5 cm) mounted vertically across the centerboard to form a 5.1-cm-wide alley in which the animal was placed.

The jumping platform consisted of a wooden platform (8.9 cm square) attached by an adjustable clamp to a 81.3-cm metal rod. The rod was mounted vertically on a 20.3-cm metal base, and

the platform could be raised and lowered to various heights. The Plexiglas on the visual cliff was removed and the jumping platform placed in the middle of the "shallow" side of the visual cliff. Wood shavings formed a 2.5-5.1-cm layer on the floor of the open field. Heights of 7.6, 15.2, 22.9, 30.5, and 38.1 cm were measured from the edge of the jumping platform to the wood shavings.

The modified pattern tests were all conducted using the barrier on the centerboard of the cliff. In the unpatterned test (U), the checkerboard pattern was removed and replaced with white posterboard which matched the lining of the rest of the cliff. For the random pattern test (P), 10 pennies were distributed (heads up) in nonsystematic fashion on each side of the centerboard with the white posterboard as background. The packed random pattern test (PP) consisted of 49 pennies nonsystematically arranged (heads up) on each side of the centerboard, again with the white posterboard as background. In the equated visual angle test (VA) black-and-white checkerboard patterns were placed on the shallow and deep sides of the visual cliff. Although the checks on each side of the cliff differed in physical size (1.27 vs. 11.43 cm), they subtended the same visual angle (14.25 deg) when viewed from 1.27 cm below the top of the centerboard. This assumes that the gerbil inspects the textured patterns from a partially stretched position, with head extended downward toward the textured surface.²

Procedure

The gerbils' vibrissae were clipped on the day their eyes opened, usually at 17-18 days of age, and trimmed every few days thereafter. The first visual cliff test was conducted at 21 days of age when the litters were weaned. Half of each litter was tested and half of both the tested and untested groups were placed in the cliff and noncliff environments. Litters and tested members within a litter were clipped for identification. Testing at ages 21, 23, 25, 27, 37, 47, and 57 days consisted of 10 trials per day on the visual cliff with a centerboard 3.81 cm high. All members of a litter were transported to the testing room each test day to equalize for handling effects. The gerbils were released at either end of the centerboard in a randomly determined order, with five releases at each end. The gerbils were released from a box to minimize handling bias, and the box was removed as soon as the gerbils emerged. The gerbils were picked up from the cliff in the same box as soon as possible after making a decision. If a gerbil had not made a decision after 2 min, a nondecision was recorded and the gerbil was removed until the next trial. All decisions, times, and miscellaneous behavior such as stretching, grooming, and chewing on the centerboard were recorded.

Testing at 60 and 61 days of age consisted of 10 trials each on the jumping platform, standard cliff, and barrier cliff. All gerbils were tested on the jumping platform on both days, and on one or the other of the visual cliff tests on each day. One half of the gerbils were tested on the standard cliff at 60 days and the barrier cliff at 61 days, while the other half received the reverse order. On a given day, the order of testing on the jumping platform and the visual cliff was also counterbalanced across gerbils, with one test occurring in the morning and one in the afternoon. Standard cliff tests were structured as before except that the centerboard was raised to 5.7 cm so that the larger gerbils could not make tactual contact on stretching. For the barrier cliff tests, the subjects were released from the box in the alleyway facing either the shallow or the deep side of the cliff and the box was removed. The order of release was determined randomly, with the restriction that there be five releases in each direction. The gerbils were picked up in the box as soon as possible after making a decision. If the gerbil had not made a decision after 2 min, a nondecision was recorded and the gerbil was removed until the next trial. In all visual cliff tests, the centerboard was turned over at varying points during each set of trials to control for olfactory cues. In addition, both sides of the centerboard and the cliff were washed

clean between subjects. Visible excretions were removed between trials.

The jumping platform trials were arranged in blocks of two, each of the five heights being tested twice before changing to a different height. The order of the heights was determined randomly. The gerbils were placed on the platform from the box and given 2 min to descend. If descent did not occur in that time, the gerbil was removed and placed in the wood shavings until the next trial as a control procedure. Gerbils making decisions were left to explore the shavings until the next trial. The wood platform was cleaned between subjects, and visible excretions were removed between trials. Orientation behavior on the platform, as well as whether the descent was a jump, slide, or fall, was recorded. A jump was a descent which left the gerbil well away from the base of the platform. A slide was a descent which left the gerbil under or quite near the platform, usually consisting of a descent from a deep stretch when the gerbil reached the point where it could not regain the platform. A fall was an obvious mistake, such as going off the board backwards, sideways, or walking forward into the air.

Testing after 100 days of age on the four modified pattern tests followed the same general procedure as described above for the visual cliff. However, because the modifications required were substantial and could not be easily alternated between the four conditions (U, P, PP, VA), it was not possible to counterbalance the order of testing for these conditions. Consequently, all gerbils were tested on the modified pattern tests in the same order: equated visual angle (VA), unpatterned (U), random pattern (P), and packed random pattern (PP). By this stage of the experiment, 31 of the original 32 gerbils were still available for testing.

RESULTS

The results are organized into three major sections: (1) visual cliff data for the pretested CE and NCE groups from 21 to 57 days; (2) visual cliff and jumping platform data for the pretested (CE and NCE) and naive (CE and NCE) groups at 60-61 days of age; and (3) modified visual cliff data for all groups collected after 100 days of age. Unless otherwise indicated, all significance tests are evaluated at the .05 level and all tests are two-tailed.

Pretest Data

The basic unit of analysis was the proportion of trials (out of 10) that the gerbil descended to the shallow side.³ Figure 1 presents the mean proportion of shallow-side descents for the CE and NCE groups as a function of testing age. Above-chance performance on the visual cliff may be determined for any condition by observing whether or not the 95% confidence limits about the mean include the dashed horizontal line.⁴ The CE group shows a significant shallow-side preference by age 23 days and continuing thereafter. In contrast, the NCE group shows no evidence of a significant preference for the shallow side except at 47 days, although the mild upward trend of this group continues through age 57 days.

The trends in Figure 1 were evaluated by a 2 by 7 mixed model analysis of variance. The main effects of Environment and Age and the Environment by Age interaction, were all significant: $F(1,14) = 67.26$,

Figure 1. Mean proportion shallow-side preference on the visual cliff as a function of environment (CE vs. NCE) and age (21-57 days).

$p < .0001$; $F(6,84) = 5.12$, $p < .0002$; $F(6,84) = 3.53$, $p < .0038$. The environmental factor accounted for 43.5% of the variation in the data. The Subjects by Age interaction accounted for 32.4% of the variation in the data, indicating some degree of subject-to-subject variation in the trends plotted in Figure 1. This may be seen in the large confidence intervals for the CE group at 23 and 25 days (Figure 1), which resulted from some gerbils' acquiring a strong shallow-side preference at an earlier age than others. Likewise, the large confidence interval at 57 days for the NCE group resulted from two gerbils' decreasing in preference for the shallow side, while the others maintained or increased their preference.⁵

An analysis of the simple effects of age for each environmental group was conducted. Age had a significant effect on shallow-side preference only for the CE group [$F(6,84) = 6.66$, $p < .0001$], although the mild upward trend of the NCE group does approach significance [$F(6,84) = 2.00$, $p < .075$]. As is evident from Figure 1, the Environment by Age interaction results from the markedly different trends in the acquisition of shallow-side preference for the CE and NCE groups.

Observational data collected during the pretesting phase indicated a high incidence of falls from the centerboard on the first test, in which 69% (CE) and

63% (NCE) of the total number of descents were falls. Performance on the visual cliff was quite erratic on this test, probably because the gerbils were tested shortly after being weaned and separated from their parents, and because this was their first introduction to the novel environment of the testing apparatus. By the second test (23 days), only 10% (CE) and 36% (NCE) of the total number of descents were falls, and thereafter almost all descents represented "voluntary" decisions by the animals to descend from the centerboard.

Figure 2 presents the mean latency of descents as a function of trial block (1-5) and environment (CE vs. NCE) for each test period (23-57 days). The data for the first test (21 days) are not plotted because of the high incidence of falls occurring on this test. In general, latencies decrease from 23 to 37 days, and then increase slightly for the tests at 47 and 57 days. A 2 by 5 by 7 mixed model analysis of variance was performed on the latency data. The main effect of trial block was significant and that of age nearly so: $F(4,56) = 3.88$, $p < .0076$; $F(6,84) = 2.08$, $p < .0631$. Of the two-way interactions, only the Trial Block by Age interaction was significant, $F(24,336) = 2.72$, $p < .0001$. Finally, the Environment by Trial Block by Age triple interaction achieved borderline significance, $F(24,336) = 1.54$, $p < .0525$. We can inter-

Figure 2. Mean latency to descend on the visual cliff as a function of within-day trial block (1-5), environment (CE vs. NCE), and age (23-57 days).

pret the triple interaction by noting the changes in the simple Environment by Trial Block interactions at each age of testing, as plotted in Figure 2. Whereas the within-test latency trends are similar for the CE and NCE groups at 27 and 37 days, they are quite dissimilar at 23 and 47 days (other ages represent cases in between these extremes). During the early stages of the acquisition of significant shallow-side preferences in the CE group (23 and 25 days), the within-test trends show decreasing latencies from the first to the fifth trial blocks. Later on, this trend disappears (37 days) and is eventually replaced by a trend showing increasing latencies from the first to the fifth trial block (47 and 57 days). The within-test latencies of the NCE group, on the other hand, show no systematic trends.

Tests at 60-61 Days

Table 1 presents an overall summary of the preference data on the visual cliff. The mean propor-

tion of shallow-side descents is indicated for all groups, test periods, and varieties of visual cliff. In this section, we consider the visual cliff and jumping platform data collected at 60-61 days. The shallow-side preference data for the CE pretested, CE naive, NCE pretested, and NCE naive groups are listed in the column beneath the 60-61-day heading of the table. Proportions in parentheses indicate shallow-side descents on the barrier cliff. Performance on the standard version of visual cliff ranged from .84 to .97, indicating significant preferences for the shallow side in each of the groups (none of the 95% confidence limits included $p = .50$). The large differences in proportion of shallow-side descents between the CE and NCE groups evident throughout the pre-testing period have greatly diminished by this point. Furthermore, performance on the visual cliff by naive animals not exposed to the extensive pretesting regime is equally good, regardless of whether these animals were raised in a cliff environment (CE) or a flat environment (NCE). A one-way analysis of variance indicated that the mean proportion of shallow-side descents did not differ significantly across the four groups, $F(3,28) = 1.64$. Performance on the barrier cliff was even more uniform, ranging from .93 to 1.0. Consequently, there is no evidence for differential performance on the visual cliff among the four groups when measured at 60-61 days of age.

Analysis of the latency data revealed no significant differences among the four groups on either version of the visual cliff. However, the mean latency to descend on the barrier cliff was significantly less than that of the standard cliff for the NCE pretested, CE naive, and NCE naive groups; $t(7) = 3.39$, $p < .05$; $t(7) = 4.14$, $p < .05$; $t(7) = 3.23$, $p < .05$, respectively. Overall, the mean latency on the barrier cliff was 10.5 sec as opposed to 25.5 sec on the standard cliff. This difference is understandable insofar as the barrier cliff prevents the animal from exploring the full length of the centerboard before descending.

The other test used to evaluate depth discrimination

Table 1
Mean Proportion of Shallow-Side Preferences on Visual Cliff*

Environment	Age in Days									100-215**			
	21	23	25	27	37	47	57	60-61		U†	P	PP	VA
Cliff										(.49)	(.72)	(.76)	(.93)
Pretested	.63	.75	.86	.91	.97	.95	.96	.97	(.93)				
Naive								.96	(.97)				
Noncliff										(.58)	(.78)	(.84)	(.93)
Pretested	.55	.56	.45	.49	.55	.61	.66	.84	(1.0)				
Naive								.93	(1.0)				

*Numbers in parentheses indicate barrier cliff tests.

†U indicates unpatterned test, P indicates random pattern test, PP indicates packed random pattern test, and VA indicates equated visual angle test.

**Data collapsed across pretested and naive groups.

Table 2
Descent Behavior from Platform at 60 and 61 Days

Descent Behavior	Platform Height (cm)				
	7.6	15.2	22.9	30.5	38.1
Observational					
Jump	114	65	22	16	7
Slide	13	57	92	92	101
Fall	0	4	12	11	15
Nondescent	1	2	2	9	5
Latency (sec)					
Mean	6.4	15.8	20.5	32.6	30.9
SD	13.5	19.3	20.2	32.4	27.9

at 60-61 days was the jumping platform. Table 2 presents the frequency of jumps, slides, falls, and nondescents from the platform as a function of height, as well as the overall mean latencies to descend. The data are pooled across all groups. The increases in slides, falls, nondescents, and latencies which occur with increasing platform height provide additional evidence that the gerbils are capable of discriminating depth at this age.

Modified Pattern Tests

Table 1 presents the mean proportion of shallow-side descents for the CE and NCE groups (collapsed across pretested and naive animals) as a function of the pattern used on modified versions of the visual cliff. Performance on the unpatterned test (U), which had a white field on each side of the cliff, was not significantly above chance for either group (confidence limits included $p = .50$). This confirms the fact that the previously demonstrated preferences for the shallow side were controlled by the textured pattern, rather than by "irrelevant" features of the apparatus, such as visual or olfactory cues, which may have become inadvertently associated with the shallow side. When tested using the black and white checked pattern equated for visual angle (VA), both groups showed strong and significant preferences for the shallow side. On tests conducted with pennies (P, PP) randomly distributed over a white field on each side of the visual cliff (and serving as the only source of texture information), above-chance preferences for the shallow side were obtained for both groups. This preference is somewhat stronger for the condition having a higher density of texture elements (PP vs. P), and in both cases falls in between that observed for the U and VA conditions.

There were no significant differences in mean proportion of shallow-side preference between the CE and NCE groups on any of the modified pattern tests. Consequently, the data were pooled across environments and a one-way analysis of variance for repeated measures was conducted. The results indicated that the mean proportion of shallow-side descents differed significantly across the four pattern

tests, $F(3,90) = 32.7$, $p < .0001$. Multiple pairwise comparisons were conducted on the pooled means using the Subject by Treatment error term from the analysis of variance and Dunn's procedure to control for error rate (Kirk, 1968, p. 79). All pairwise comparisons among the U, P, PP, and VA conditions were significant (t values ranging from 3.16 to 9.17, 90 df, $p < .008$) except for the P vs. PP comparison, $t(90) = 1.26$.

Significant between-groups differences (CE vs. NCE) in mean latency to descend were not obtained on any of the four tests. However, a repeated measures analysis of variance conducted on the pooled CE and NCE data indicated a significant difference in the mean latencies to descend across the four tests, $F(3,90) = 5.17$, $p < .0026$. This resulted from a mean latency in the U condition of 15.9 sec as compared to mean latencies ranging from 7.9 to 9.6 sec in the P, PP, and VA conditions. Multiple pairwise comparisons confirmed that the U condition differed significantly from each of the remaining conditions (t values ranging from 2.85 to 3.60, 90 df, $p < .008$), although none of the latter conditions differed significantly from one another (all t values < 1.0).

DISCUSSION

Considering the preference data first, the results indicate that environmental factors can have a powerful influence on the rate of acquisition of significant shallow-side preferences in the Mongolian gerbil. Gerbils raised in a cage having artificially constructed cliffs to negotiate demonstrate extremely rapid acquisition of a preference for the shallow side of the visual cliff, whereas those raised in a cage lacking this environmental feature do not (Figure 1). However, the impact of this environmental factor is confined to rate of acquisition, and does not appear to affect asymptotic performance. By 60-61 days, all gerbils display strong preferences for the shallow side regardless of cage environment or pre-testing experience (Table 1). This lack of differentiation in performance for the two environmental groups is maintained throughout the modified pattern tests administered after 100 days.

Several interpretations may be applied to the preference data. It might be argued that the ability to discriminate depth on the visual cliff is acquired in the Mongolian gerbil. Task-specific visual experience, such as encounters with real cliffs, increases the rate of acquisition of this discrimination. Animals not exposed to such task-specific environmental features would still acquire the discrimination eventually, through nonspecific visual experiences resulting from climbing the sides of the cage, jumping, and other activities requiring visuomotor coordination. This

view would account for the differences in the CE and NCE trends of Figure 1, as well as for the convergence of performance observed at 60-61 days and thereafter. However, it directly opposes the conclusion reached for most other species tested on the visual cliff; i.e., that the ability to discriminate depth on the visual cliff is present shortly after independent locomotion is achieved, and is therefore probably innate (Gibson & Walk, 1960). Furthermore, the rate of acquisition in the environmentally favored group (CE) is almost too rapid to be plausible under an "empiricist" hypothesis.

Another interpretation might argue that the ability to discriminate depth is innately present in the Mongolian gerbil, but that performance on the visual cliff is also contingent on the development of an appropriate fear response motivating avoidance of the deep side, as suggested by primate research (Walk & Gibson, 1961; Wilson & Riesen, 1966). The presence of real cliffs in the home environment of the CE group might facilitate the rapid acquisition of this fear response as a result of actual experience in negotiating cliffs, thereby causing avoidance of the deep side on the visual cliff. The slowly increasing trend of the NCE group would be accounted for by the retarded development of the fear response resulting from the lack of relevant environmental features appropriate for generating it. However, a problem with this view is that the frequent deep-side descents made by the NCE group during the pretesting phase are never negatively reinforced by the consequences of an actual fall. Hence, it is hard to understand why a fear response would ever develop in this group. Nevertheless, the NCE group does eventually show a strong preference for the shallow side (60-61 days).

A third interpretation represents a form of compromise between the nativist-empiricist positions. The visual system of the Mongolian gerbil is assumed to be innately organized to extract certain kinds of depth information, but the manifestation of this ability in performance is strongly affected by environmental factors. From this view, the cliffs in the home cage of the CE group provide an environmental pressure sufficient to "trigger" an innately organized system into becoming functional in controlling behavior on the visual cliff. The extremely rapid acquisition of a strong shallow-side preference in this group supports this view. The lack of such pressures in the NCE group would account for the retarded development of shallow-side preferences in this group. Although it might seem a contradiction to suggest that an innately organized system requires certain kinds of experience in an environment to become functional in controlling behavior, there is now considerable evidence to suggest that this is true with regard to various properties of the visual system (see Barlow, 1975, and Tees, in press, for reviews).

Considering the latency data, the following generalization may be tentatively offered. The more "difficult" the discrimination of depth in any given instance, the longer the latency to descend. The discrimination of depth on the visual cliff will be more difficult during the initial period of acquisition, and, within a given test day during this period, on the initial trials of the tests. As performance on the visual cliff stabilizes (either across or within tests), latencies should decrease. These trends are observed in Figure 2 for the group demonstrating acquisition of a shallow-side preference during the pretesting period (CE). From 23 to 37 days, the overall latencies for the CE group decrease as discriminative ability improves across tests. Similarly, within-test latencies tend to decrease for all test days during acquisition except those at 37 days, by which time asymptotic performance on the cliff has been achieved. The within- and across-test increases in latencies observed after this point (47 and 57 days) are probably due to a "boredom" or habituation effect. Observational data indicated that the gerbils in the CE group had become thoroughly acclimatized to the apparatus by this point. Consequently, they often remained on the centerboard engaged in grooming and other extraneous behavior before descending. This tendency became more pronounced with repeated tests on the same day, which would account for the increasing latencies. The NCE group shows no consistent evidence of a strong preference for the shallow side during the pretesting period. Consequently, the behavior of this group on the visual cliff is not under the control of a developing discriminative capacity, and the within- and across-test latencies should not reflect this factor. Indeed, this group displays no systematic within-test trends (Figure 2).

The latency data collected on tests conducted after the pretesting period also support the generalization that the more difficult the discrimination, the longer the latency to descend. When tested on the unpatterned version of the visual cliff (U), in which texture information is not present to assist the discrimination, long latencies were obtained in comparison to any of the tests having a textured pattern (P, PP, VA). Also, latency to descend from the jumping platform was an increasing function of platform height, which replicates previous research (Cole & Topping, 1969). In this and the previous cases discussed, the relevant factor causing increased latencies may not be the difficulty of discrimination per se, but rather the increase in fear which would be correlated with situations generating a difficult discrimination. In any event, the generalization offered above seems to provide a reasonable characterization of the latency data.

Whenever a species displays a preference for the shallow side of the visual cliff, the question arises as to the stimulus information controlling this

behavior. In the standard visual cliff, most of the cues to depth are potentially available: relative texture size and density, texture gradient, motion parallax, flow pattern, etc. The potential value of accommodation, convergence, and binocular disparity depends, of course, on the structure of the visual system of the particular species. In any event, the usual strategy is to selectively eliminate these potential sources of depth information and note when discriminative capacity breaks down (Walk, 1965). While the present experiment was not designed to determine the source of depth information controlling the shallow-side preferences of the Mongolian gerbil, the modified pattern tests conducted after 100 days do provide preliminary evidence on this issue. The fact that performance on the visual cliff was not affected by equating the visual size of the texture elements on the deep and shallow sides of the cliff (VA) indicates that relative texture size and density are not the controlling factors. This result is in accord with other evidence (Walk, 1965; Walk & Gibson, 1961). Further, since all modified pattern tests were conducted with a barrier to eliminate movement along the centerboard, the availability of motion parallax information is greatly reduced. Yet, on the VA pattern test and on all barrier tests conducted at 60-61 days, exceptionally strong preferences for the shallow side are in evidence (Table 1). In fact, these preferences are as strong as those observed at 60-61 days on the standard (unrestricted) cliff. Consequently, motion parallax information resulting from movement *along* the centerboard is not required in order for the Mongolian gerbil to successfully discriminate depth on the visual cliff.

A possible hint as to the factor controlling the gerbils' performance on the barrier version of the visual cliff comes from observational data. When these animals were tested with a barrier restricting their movement along the centerboard, a marked increase in the amount of head bobbing was noted. Typically, the animal would peer over one side of the centerboard, bob two or three times, turn around in the narrow alley created by the barrier, and peer over the opposite side again bobbing as it did so. This entire process was usually repeated before the animal descended to the shallow side. Since the expansion rate of a textured surface is in part a function of distance, the head-bobbing activity could provide information as to which of the textured surfaces is more distant (Walk, 1965). Further, this source of information is available even when the texture elements are equated for visual size (VA). Consequently, the flow pattern of the texture elements resulting from head bobbing might be the controlling factor on tests conducted with the barrier.⁶

In conclusion, the present research demonstrates that the Mongolian gerbil does not display a prefer-

ence for the shallow side of the visual cliff when first tested at 21 days. However, a group given the opportunity to negotiate cliffs in the cage environment shows an above-chance preference for the shallow side after only 48 h of exposure, whereas a group lacking this experience does not show a consistent preference for the shallow side until 60-61 days. These data suggest that, although the visual system of the Mongolian gerbil is innately organized to extract information about depth, the manifestation of this capacity in performance on the visual cliff requires some minimal contact with environmental features demanding its utilization.

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NOTES

1. However, the view that the cue "large is close" is acquired and therefore secondary to motion parallax has recently come into question (Davidson & Whitson, 1973; DeHardt, 1969; Schiffman & Walk, 1963; Walk & Walters, 1973).

2. If the checked patterns are inspected from a higher position, then the optical size of a deep-side check is somewhat larger than that of a shallow-side check; e.g., 13.87 vs. 11.43 deg when measured from the top of the centerboard. Hence, insofar as texture size controls behavior on the visual cliff, this would result in the gerbils' selecting the deep side of the cliff for descent. Since this experimental condition is intended to evaluate the adequacy of depth cues other than relative size in determining selection of the shallow side, it provides a conservative test because of the opposing texture size difference.

3. Note that this specification of the dependent variable pools both deep-side descents and nondescents in the same category: i.e., failure to select the shallow side within the 2-min period allotted per trial. An animal that does not descend in the 2-min period may, of course, be capable of discriminating depth (competence) but for some reason does not channel this ability into behavior (performance). Equally likely, however, is the

possibility that the animal does not descend precisely because it cannot discriminate depth. In any event, pooling nondescents with deep-side descents provides a conservative, if stringent, evaluation of the gerbils' ability to discriminate depth. Since nondescents were infrequent (occurring in only 3 out of 100 trials on the average), this procedure does not have any significant impact on the pattern of results. This is demonstrated by reanalyzing the data, using as the basic unit of analysis the proportion of shallow-side descents relative to the total number of "decision" trials, i.e., trials in which the gerbil descended to one side or the other (10 or less). When nondescents are excluded from the analysis in this way, the same overall results are obtained as that reported in the text (Figure 1). This alternative analysis of the preference data is available upon request from the senior author.

4. The use of confidence limits for purposes of statistical inference is discussed by Hays (1963, p. 312). In the present case, the 95% confidence limits about the mean proportion were computed using the following formula: $\bar{X} \pm S_{\bar{X}} t_{os} (7 \text{ df})$. If this interval does not include the population mean stipulated under the null hypothesis (.50 in the present instance), then the sample result may be considered significant at the .05 level. In this application, the confidence interval provides the equivalent of a one-sample *t* test of the null hypothesis.

5. Because of these differences in variability of performance across conditions, and because the basic data were proportions (thus introducing potential "ceiling" effects), the assumptions of homogeneity of variance and normality of distribution of within-group errors may have been violated. Consequently, an arcsin transformation ($X' = 2 \arcsin \sqrt{X}$; Kirk, 1968, p. 66) was performed on the preference data in an attempt to eliminate or reduce the effects of these violations. This transform reduced the maximum ratio between sample variances from 36.0 to 12.3, and distributed the individual proportions within groups in a far less skewed fashion. An analysis of variance performed on this transformed data produced the same results as the original analysis (see text): $F(1,14) = 68.61, p < .0001$; $F(6,84) = 6.33, p < .0001$; $F(6,84) = 4.18, p < .0011$. However, the Subject by Treatment interaction still accounted for a substantial proportion of the variation in the transformed data (29.4%). This state of affairs implies some degree of heterogeneity of covariance (Keppel, 1973, p. 463) which was not removed by the transform. Monte Carlo investigations on the effects of violating the homogeneity of covariance assumption (Collier, Baker, Mandeville, & Hayes, 1967) indicate that relatively extreme departures from this assumption do result in a positive bias in the tests on the repeated-measure factor and the interaction. However, since the actual alpha level rarely exceeds .08 when using a nominal alpha level of .05, this bias can be ignored for most practical purposes, especially when the obtained significance levels provide an adequate margin (e.g., $p < .01$).

6. Walk (1965) considers expansion rate to be a form of motion parallax information. The term "motion parallax" is most frequently used to refer to that information deriving from the different rates of "sheer" of the texture elements across the visual field resulting from lateral movement along the centerboard. Expansion rate or flow pattern information results from an approach to or recession from the textured surface, as would occur with head bobbing. While also a movement-related cue to depth, it is not obvious that an innately organized system designed to extract motion parallax information (in the sense noted above) would necessarily be equipped to extract flow pattern information as well. Hence, it would seem desirable to keep these two forms of movement-related depth cues conceptually distinct.

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