Environmental Effects on the Ontogeny of Exploratory and Escape Behaviors of Mongolian Gerbils

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Mongolian gerbils reared in standard laboratory cages and gerbils reared in cages containing a burrowlike shelter did not differ in their rate of development of escape responses to sudden visual stimulation. The presence of shelter in the rearing environment did, however, markedly slow the development of adult-like patterns of exploration. Reduced exposure to illumination, experienced by shelter-reared subjects, proved responsible for this retardation of development. The effect of shelter-rearing on the development of exploratory behavior is interpreted as demonstrating an environmentally induced maintenance of an adaptive juvenile pattern of behavior.

Gottlieb has proposed that experience can play any of 3 major roles in the development of behavior: (1) it can induce (channel, determine) development; (2) it can maintain (sustain, preserve) ongoing developmental states; and (3) it can facilitate development (Gottlieb, 1976; p.28). Recently, we employed Gottlieb's analysis of developmental processes to investigate the role that the physical rearing environment plays in the development of escape behaviors of Mongolian gerbils (Clark & Galef, 1979).

Mongolian gerbils maintained in cages that contain a tunnellike shelter, designed to simulate the species' typical rearing environment, respond throughout life to sudden visual stimulation by fleeing, hiding, and foot-thumping. In contrast, gerbils reared and housed in cages not providing access to shelter (open-reared subjects) exhibit this pattern of response to visual stimulation when young, but show considerable reduction in response to stimulation by the time they are 2 months old. Thus, access to shelter appears essential for the maintenance of a heightened reactivity, typical of gerbils observed in nature (Fetisov & Moskovskiy, 1948; Tanimoto, 1943; Thomas, 1908), that develops in all gerbils independently of whether shelter is available in their rearing environment (Clark & Galef, 1979).

The fact that both those gerbils exposed to an environment providing shelter during ontogeny and those lacking such exposure are highly reactive early in life indicates that experience with shelter is not a necessary condition for the induction of escape behaviors.

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However, such data provide no indication of whether shelter-rearing facilitates the achievement of adultlike levels of response. The present experiments were undertaken to determine whether shelter experience facilitates the ontogeny of escape and exploratory behaviors in gerbils.

In Experiment I we examined the effects of experience with shelter on the rate of development both of adultlike patterns of exploration and of adultlike responses to sudden stimulation. In Experiment II we determined those aspects of the shelter-rearing experience responsible for the effects of shelter-rearing on behavioral ontogeny discovered in Experiment I.

Experiment I

There is a psychologically trivial sense in which shelter-rearing affects the ontogeny of both exploratory and escape behaviors that influenced the design of the experiments described below. In comparison with open-reared gerbils, shelter-reared gerbils exhibit a significant retardation in the age at which their eyes open (Clark & Galef, 1980, 1981). Blind gerbils do not exhibit either patterns of exploratory behavior or patterns of response to sudden stimulation similar to those of their sighted fellows. Therefore, comparison of the behavior of shelter- and open-reared gerbils of the same chronological age would reveal a retardation in the development of shelter-reared subjects which would be an artifact of differences in the rate of sensory development resulting from open- and shelter-rearing. To control for these differences in sensory development, we examined the behavior of groups of open- and shelter-reared subjects, matched in the distribution of their ages at eye-opening, at various times after eye-opening had occurred. While such a procedure reduces the observed impact of shelter-rearing on rates of behavioral development, it does allow examination of the effects of shelter-rearing on rates of behavioral ontogeny independent of the effects of shelter-rearing on sensory development.

Method

Subjects

Subjects were 384 Mongolian gerbils (*Meriones unguiculatus*) selected from 240 litters born in the McMaster colony to multiparous breeding pairs acquired from Tumblebrook Farm (Brookfield, Mass.).

Subject assignment. Each of 192 shelter-reared and 192 open-reared subjects was assigned to testing at 1 of 6 ages. Thus, independent groups of 32 shelter-reared and 32 open-reared subjects were tested either on the day of eye-opening, or 24, 48, 72, 96, or 120 hr thereafter. Half of the subjects in each of these 12 groups (2 rearing conditions X 6 test ages) served as Experimental subjects and half as Control subjects in the test described below. To control for sex effects each of these 24 groups (2 rearing conditions X 6 test ages X 2 test conditions) was composed of 8 male and 8 female subjects. To control for litter effects only 1 or 2 subjects from any 1 litter were assigned to any 1 of the 24 groups; no group contained subjects from fewer than 12 litters. The distribution of ages at eye-opening of subjects was equated so that each group contained equal numbers of subjects whose eyes opened at 17, 18, 19, and 20 days postpartum.

Procedure

Rearing conditions. Breeding pairs were housed in polypropylene cages (35 X 30 X 15 cm) covered with .5-in. (1.27-cm) hardware cloth and carpeted with a thin layer of bedding material. The colony was maintained on ad lib food and water in a temperature-controlled colony room illuminated on a 12-hr light-dark cycle.

On the day of birth, a litter was moved with its parents to a new cage either providing or lacking shelter. Each litter to be reared in the absence of shelter was placed in a cage identical to the one in which it was born; a litter to be reared in a cage providing shelter was placed in an identical cage containing a plywood shelter (a 28 X 15 X 9-cm box) with a single entrance (5 X 5 cm).

Litters remained undisturbed in their respective rearing environments until testing except for examination thrice daily (at 0900, 1200, and 1700 hours) from Day 15 onward to determine each subject's age at eye-opening (defined as that day on which both eyes were first fully open) and for marking of pups by shaving on the day of eye-opening.

Testing. The apparatus and procedures used in testing subjects are described in detail in Clark and Galef (1979). In brief, individual subjects were placed in a 1.2-m^2 enclosure, containing a place of refuge, and their response to the sudden presentation of a novel visual stimulus was observed on closed-circuit television. (See Fig. 1.)

To familiarize subjects with the enclosure and the location of the refuge, and to provide a measure of exploration, each subject was allowed to explore the test apparatus until it had exited from the shelter 5 times. The experimenter recorded the latency of each subject to first enter the refuge and each subject's total latency to make 5 refuge exits. Subjects failing to enter the shelter within 45 min were discarded.

Immediately following a subject's 5th refuge exit, a moving visual stimulus (a lifelike Latex mask of a human face) was presented to each Experimental subject for 15 sec. During the 2 min following initiation of stimulus presentation, the experimenter recorded each subject's latency to reach the refuge, total amount of time spent in concealment, and any instances of foot thumping. Control subjects were treated identically to Experimental subjects except that no stimulus was presented to them after their 5th refuge exit and data were recorded during the 2-min period following the moment when the visual stimulus would have been presented to them if they had been Experimental subjects.

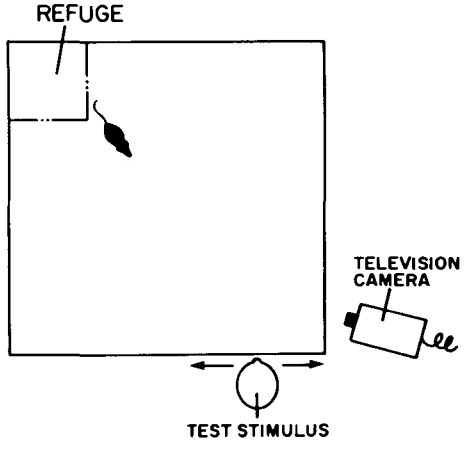

Fig. 1. Overhead schematic of the 1.2-m^2 test apparatus.

Results and Discussion

Effects of Rearing Environment on Ontogeny of Exploratory Behaviors

Data describing the behavior of open- and shelter-reared subjects in the test enclosure during the exploration period prior to stimulus presentation is presented in Figure 2, which shows the mean time required by subjects in the 2 groups to complete 5 refuge exits. As is clear from examination of the figure, and as statistical tests confirmed (t tests; see Figure 2 for results), there was a strong tendency, significant at 3 points in development, for shelter-reared subjects to be less willing than open-reared ones to move around the enclosure. This difference in exploration was the result both of a tendency on the part of shelter-reared subjects to spend longer periods of time in the refuge than open-reared subjects and of the former animals to remain immobile in the bare corners of the enclosure for many minutes on the first 3 days following eye-opening.

In the interest of brevity, we have not graphically presented data describing subjects' initial latencies to enter the refuge during the exploration period. These observiations also revealed a significantly greater latency in shelter- than open-reared subjects to first enter the refuge 24 and 48 hr after eye-opening (t-tests; both t's(62) > 2.47, both p's $< .02$).

The present data indicate that rearing in an environment which provides the relative sensory isolation of the natural gerbil burrow retards the development of young gerbils' tendency to explore in novel environments. This finding is consistent with a wealth of data on other rodent species suggesting that increased stimulation during infancy enhances the tendency of rodents to locomote in novel areas (see Daly, 1973 and Henderson, 1980 for reviews). While the present results show that shelter-rearing reduces the tendency of young gerbils to move about a novel arena, these data give no indication of the aspect or aspects of the shelter-rearing environment that produce this effect. Experiment II provides relevant data.

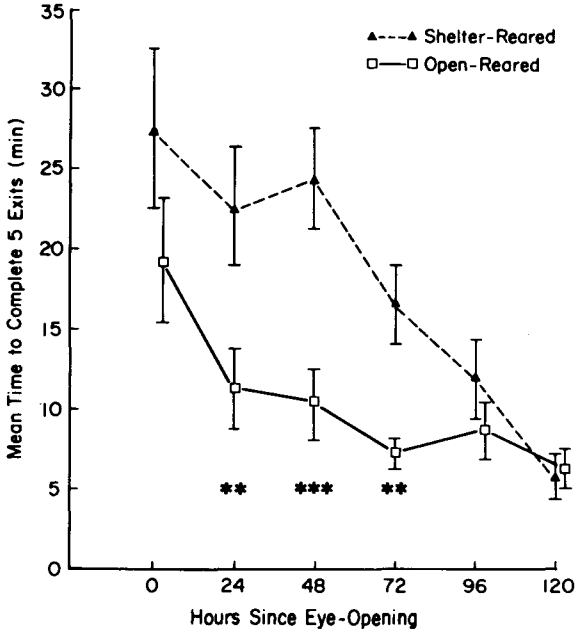

Fig. 2. Mean latency for open- and shelter-reared subjects to complete 5 refuge exists. Flags indicate ±1 SE. $^{**}p < .02$, $^{***}p < .001$; 2-tailed t-tests.

Development of Exploratory Behaviors

Adult gerbils examined in the test situation employed in the present experiment complete 5 refuge exists in an average of 4.25 min following placement in the arena (Clark, unpublished observations of sixty-five 61-day-old open-reared subjects). As can be seen in Figure 2, adultlike levels of performance were achieved more rapidly by open-reared than by shelter-reared subjects.

Effects of Rearing Environment on Ontogeny of Escape Behaviors

The behavior of subjects following stimulus presentation is described in Figure 3, which shows (A) the mean latency for subjects to reach the refuge following stimulus presentation, (B) the mean total time spent by subjects inside the refuge during the 2 min following stimulus presentation, and (C) the percentage of subjects foot-thumping during the 2 min following stimulus presentation. As is clear from inspection of the figure, and as statistical tests confirmed, shelter-rearing, which has been shown previously to be necessary for the maintenance of high levels of responsiveness to sudden visual stimulation (Clark & Galef, 1979), did not facilitate the development of such responsiveness. At no point in development did open- and shelter-reared subjects differ in their latencies to first reach the refuge (t tests; all t's $< .58$, all p's $> .20$), in the total amount of time they spent in concealment (t tests; all t's < 1.61, all p's $> .20$), or in the frequency with which they exhibited foot-thumping (Fisher's Exact Probability Tests; all p's $> .20$).

Development of Escape Behaviors

Adult shelter-reared gerbils examined in the test situation employed in the present experiment enter the refuge within 3 sec of stimulus presentation, spend approximately 80% of the test period in concealment, and foot-thump on approximately 75% of trials (Clark & Galef, 1979). As can be seen in Figure 3, such adultlike responses to stimulation were not reliably elicited on the day of eye-opening but emerged gradually with increas-

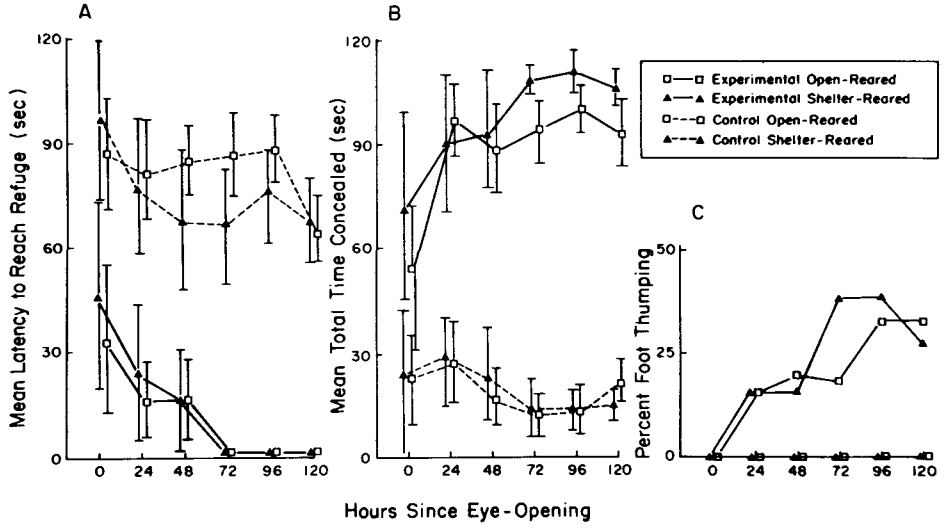

Fig. 3. Behavior of open- and shelter-reared subjects in the test apparatus at intervals between eye-opening and 120 hr thereafter. A: Mean latency to reach the refuge. B: Mean total time spent in the refuge during the 120-sec test period. C: Percentage of subjects foot-thumping. Flags indicate ±1 SE.

ing age and visual experience. Adultlike latencies to reach shelter were achieved within 72 hr of eye-opening and adultlike patterns of concealment 24 hr after eye-opening. Foot-thumping did not achieve adult levels even 120 hr after eye-opening, a findng consistent with our earlier data indicating that the likelihood of foot-thumping in response to sudden visual stimulation increases through 61 days of age (Clark & Galef, 1979).

Experiment II

The experiences of gerbils reared in environments containing shelter are different from those experienced by conspecifics reared in standard laboratory cages (Clark & Galef, 1977; Daly, 1973; Hutchings, 1968). In particular, the amount of exposure to light and the presence of opportunities to flee to a place of concealment differ significantly between animals reared in standard laboratory cages and those reared in environments providing shelter. The results of our previous studies indicate that the development, endocrine morphology, and behavior of gerbils are differentially affected by different aspects of the shelter-rearing experience. For example, the opportunity to move from an open area to an enclosed one maintains gerbils' response to sudden visual stimulation, increases relative adrenal gland size, and reduces body weight. The reduced exposure to illumination experienced by gerbils reared in cages providing access to shelter does not affect behavioral reactivity by profoundly affects rates of sexual development, reproductive organ and pituitary gland weights (Clark & Galef, 1981).

The present experiment was undertaken to determine those features of the shelter-rearing experience sufficient to produce the reduced levels of exploration found in shelter-reared subjects in Experiment I.

Method

Subjects

Sixty-four gerbils selected from 31 litters born and reared in the McMaster colony served as subjects. Housing and maintenance of mated pairs prior to the birth of their young were the same as those described in Method of Experiment I.

Procedure

Rearing conditions. Within 24 hr of birth, each litter and its parents were assigned to 1 of 2 rearing conditions. Litters to be reared in conditions of reduced illumination were placed in cages lacking shelter in a colony room maintained in constant darkness (*24-hr-Dark Open Group*).

A 2nd group of subjects (*Transparent-Shelter Group*) was housed in a colony room maintained on a 12-hr light-dark cycle and reared in cages containing transparent Plexiglas shelters. These subjects had the opportunity to flee to an enclosed space (which they invariably did in response to the approach of caretakers), but did not experience the reduced exposure to illumination that accompanies rearing in environments containing opaque shelters.

Testing. Forty-eight hours following eye-opening, subjects from each rearing environment were placed in the test enclosure described in Procedure of Experiment I and their latency to make 5 refuge exits was determined.

Results and Discussion

The main results of Experiment II are presented in Figure 4, which indicates the mean latency to complete 5 refuge exits by subjects in the 2 experimental groups. Data describing the behavior of open- and shelter-reared subjects in Experiment I tested 48 hr after eye-opening are presented for purposes of comparison. As is evident from inspection of the figure, and as statistical tests confirmed (t-test; $t = 3.95$, $p < .001$), subjects in the *24-hr-Dark Open Group* exhibited greatly reduced exploratory behavior in comparison with those in the *Transparent-Shelter Group.* Comparison of the behavior of subjects in the present experiment with that of the subjects of open- and shelter-reared groups of Experiment I reveals no effect of access to a transparent shelter on exploration and effects of dark-rearing on exploration that were as profound as those of shelter-rearing.

The data thus strongly suggest that the reduced exposure to illumination experienced by gerbils reared with access to an opaque shelter is responsible for their reduced tendency to explore in novel environments during the days immediately following eye-opening.

General Discussion

In their natural habitats, members of many rodent species spend all of the early part of their lives in an underground parental burrow (Daly, 1973). Maturation within a burrow both protects juvenile rodents from a spectrum of potentially noxious events (Schmidt-Nielsen, 1964) and exposes them to environmental conditions capable of influencing the course of development. In a series of studies, we have sought to discover the range of phenotypic characteristics development of which is affected by maturation in a burrowlike environment, the features of the sheltered environment responsible for observed phenotypic effects, and the ways in which these effects are achieved (Clark & Galef, 1977, 1979, 1980, 1981).

The results of the present experiments indicate that access to shelter, previously found necessary for the maintenance of escape behaviors (Clark & Galef, 1979), does not

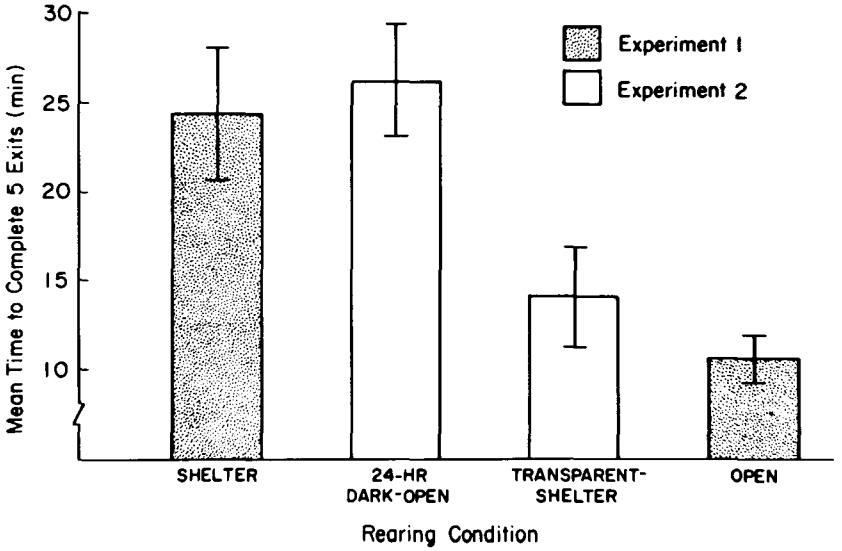

Fig. 4. Mean time for *48-hr-Dark Open*-reared subjects and *Transparent-Shelter*-reared subjects to complete 5 refuge exits. Data from Shelter- and Open-reared subjects presented for purposes of comparison. Flags indicate ±1 SE.

affect their rate of development except indirectly by delaying the onset of sensitivity to visual stimuli and consequent exhibition of organized flight. The present data further indicate that maturation in the relative darkness of a burrowlike shelter delays the expression of adultlike patterns of exploration.

It might be argued that in terms of Gottlieb's (1976) analysis of developmental processes it would be more appropriate to describe open-rearing as facilitating or accelerating development of exploratory behavior than to consider shelter-rearing as retarding such development. Although the former statement of the results is more easily incorporated into Gottlieb's framework than the latter, to us, emphasis of the facilitating effects of open-rearing rather than the retarding effects of shelter-rearing on development seems open to question.

Implicit in a focus of attention on environmental variables that accelerate the rate of acquisition of adultlike behavior is an assumption that the rate of acquisition of adult patterns of response provides an especially valid criterion for appraising the effects of environmental influences on development. Such an assumption is questionable on ecological grounds. If juvenile patterns of behavior are viewed as adaptations to the demands of the unique ecological niche occupied by young (Galef, 1980; Henderson, 1981; Oppenheim, 1980; Williams, 1966), then maintenance of juvenile behavior becomes a focus of interest in discussing the effects of species-typical experiences on developmental processes. Daly (1973) has argued that in natural conditions a readiness to explore novel environments is potentially harmful to young rodents. If so, it is more consistent with ecological realities to treat the neotonous behavior of Mongolian gerbils reared under conditions approximating those of natural burrows as demonstrating an environmentally induced maintenance of adaptive juvenile behaviors than to treat young gerbils reared in the open as exhibiting facilitated development of adultlike responses.

Notes

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