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STATEMENT OF SIGNIFICANCE OF THESIS RESEARCH

THESIS TITLE: THE EFFECTS OF THE PHYSICAL ENVIRONMENT DURING MATURATION ON SUBSEQUENT REACTIVITY TO VISUAL STIMULATION IN MONGOLIAN GERBILS (*Meriones unguiculatus*)

AUTHOR: MERTICE CLARK

Historically, three mechanisms have been proposed to account for the observation that individual members of a species exhibit behaviour patterns which are characteristic of that species and different from those of other species. First, possession of similar behavioural repetoires among species members could result from similarities in the geneotype of species members. Second, behavioural similarity could arise from the cultural transmission of behaviour patterns from adults to juveniles. And, third, the relative constancy of the physical environment in which members of a species are reared could lead to the acquisition of similar patterns of behaviour among species members. Previous research concerned with the factors responsible for the homogeneity of behaviour of members of a species has attempted to assess the contribution either of genetic factors or the cultural transmission of behavioural patterns to behavioural homogeneity and has, in general, ignored the possible contribution of the constancy of the physical rearing environment to the development of species typical behaviours.

The present series of investigations were undertaken to examine the role of the physical environment experienced during ontogeny in the development of behaviour. Animals were reared in an array of different environments and their response to the presentation of a sudden visual stimulus assessed at maturity. It was found that rearing in enclosures providing shelter markedly increased the responsiveness of subjects to sudden visual stimulation.

The finding described above is particularly relevant to the issue of the causes of differences in the behaviour of wild and domesticated strains of animal species. Comparison of the behaviour of wild and domesticated strains of a number of mammalian species reveals consistent differences in their behaviour. In particular, descendants of domesticated strains appear far less responsive to a variety of types of stimulation than do descendants of wild strains. Perhaps in consequence, members of domesticated populations have often been characterized by observers as less emotional, timid, or savage than their wild progenitors.

The vast majority of accounts of the underlying cause of these differences in the behaviour of wild and domesticated animals have assumed that they are the direct results of differences in the genetic constitution of compared populations. In terms of the most frequently employed of the genetic hypotheses of the nature of domestication, behaviours such as intraspecific aggression and flight from or attack of man, which are adaptive in the wild, are maladaptive in captivity and are therefore consistently selected against. The hypothesized result of this artifical selection is the evolution of a new strain which resembles its wild progenitor, both behaviourally and morphologically, less and less with the passage of time, until the domesticated strain becomes unsuited to life in its original habitat. Thus, domestication is, at least potentially, an irreversible event in the history of a species.

Other investigators, however, have proposed that the relative tractability and docility of domestic individuals is the result of different individual experiences in captivity rather than differences in the genetic constitution of domesticated and wild populations. If individual experience in captivity is responsible, at least in part, for observed differences in the behaviour of wild and domesticated strains, than one would expect a rapid reversion to behaviour typical of wild populations in domesticated animals reared in environments similar to their natural habitats. The data presented in the present thesis suggest that in the case of the Mongolian gerbil, at least, much of the disparity in the behaviour of wild and domesticated strains of the species is the result of differences in the early rearing environment of the relevant strains and not in their genetic substrate.

EFFECTS OF THE PHYSICAL ENVIRONMENT ON REACTIVITY IN GERBILS

EFFECTS OF THE PHYSICAL ENVIRONMENT DURING MATURATION ON SUBSEQUENT REACTIVITY TO VISUAL STIMULATION IN MONGOLIAN GERBILS (*Meriones unguiculatus*)

By

MERTICE MADORA CLARK, B.A.

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ABSTRACT

Mongolian gerbils (Meriones unguiculatus) living in their natural habitat flee to their burrows and footthump in response to the appearance of humans, while conspecific individuals reared in open-laboratory cages approach and investigate humans attempting to handle them. The present series of investigations was undertaken to determine the role of the differences in the physical rearing environment of laboratory- and wild-born gerbils in the development of their response to the visual stimuli provided by humans.

A testing procedure was developed to quantify the response of gerbils to the sudden presentation of a human-like visual stimulus and the behaviour of gerbils reared under a variety of conditions assessed in this test situation. It was found that gerbils reared in the laboratory, in gerbil-constructed tunnel systems, responded to the sudden presentation of a human-like visual stimulus by fleeing to shelter, footthumping and remaining concealed for long periods, while many gerbils reared in open-cages responded to presentation of the stimulus by approaching and visually fixating it.

Analysis of the features of the tunnel environment responsible for the potentiation of the flight and concealment response in tunnel-reared animals revealed that the critical factor in tunnel-rearing was the provision of shelter during maturation. Neither the isolation from illumination nor the isolation from stimuli associated with human handlers, resulting from rearing in a tunnel, was responsible for the observed effects of tunnel-rearing. The experience of moving in and out of cover, provided by rearing in environments having shelter available, appeared to potentiate the flight and concealment response.

Observation of behaviour in a second situation measuring reactivity, that is willingness to descend from the centerboard of a visual-cliff, revealed that the effects of rearing with shelter available were not restricted to situations involving flight to shelter in response to sudden visual stimulation. Willingness to descend from the centerboard was markedly increased by rearing in environments providing shelter.

It was further found that even a relatively brief exposure to an environment providing opportunity for flight and concealment was sufficient to potentiate the entire behavioural syndrome in open-reared gerbils. Gerbils reared in normal laboratory cages would exhibit the pattern of flight and concealment in response to sudden stimulation, normally observed in tunnel-reared gerbils, if they were placed in a tunnel system for 24 hours. However, behaviour of tunnel-reared gerbils was not affected by 24-hour exposure in an open-cage.

Taken together, the results of the present experiments suggest that the syndrome of reactive behaviour exhibited by wild, as compared with laboratory-reared, gerbils is the result of differences in the physical environment in which they are reared. Experience of a sheltered area early in life, for either brief or extended periods, is sufficient to potentiate reactive behaviour in gerbils at maturity.

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CHAPTER I

Historical Background and Introduction

Historical Background

Although it is generally accepted that individual members of a species exhibit elements of behaviour that are species characteristic (Mayr, 1970), the factors responsible for this observed homogeneity of patterns of movement among species members have been a source of contention between psychologists and ethologists for several decades (Lorenz, 1956, 1965, 1970; Eibl-Eibesfeldt & Kramer, 1958; Hebb, 1953; Lehrman, 1953, 1956, 1962, 1970; Schneirla, 1956, 1966). European ethologists, in particular Lorenz and his associates, have consistently maintained that species-typical behaviours are transmitted from parent to offspring via the mechanisms of Mendelian genetics in much the same fashion as morphological or anatomical features and that experiences occurring during the life of the organism are of minimal importance in affecting their ontogeny (Lorenz, 1956, 1970; Eibl-Eibesfeldt & Kramer, 1958). Lorenz (1970), for example, has argued that as long as the environment in which an organism is reared is sufficiently supportive to permit the development of the behaviour pattern of interest, its topography is not modifiable by experience. Consequently, while environmental factors might affect the intensity or frequency of occurrence of species-typical behaviours, such factors could not modify their form.

Understandably, North American psychologists, whose predominant research interests have centered on the role of experience in the ontogeny of behaviour, accused ethologists of underestimating the contribution of the social and physical environment in which members of a species are reared to the development of what psychologists conceived of as species-typical behaviours. Unfortunately, psychologists and ethologists were, for many years, arguing at cross-purposes in that the particular behaviours that ethologists were describing as genetically determined were of a different type than those that psychologists were referring to as modifiable by experience (Moltz, 1965).

This failure of communication concerning the appropriate unit of analysis of behaviour patterns is made clear in the following exchange:.

Lehrman (1953), the leading proponent of the psychological position in the nature-nuture controversy, argued that,

> "(An. . .) example of behavior appearing to fulfil the criterion of "innateness" may be found in the maternal behavior of the rat (p. 342)."

To which Lorenz (1956) responded,

> "in the paper mentioned, Dr. Lehrman extensively describes the maternal behaviour of the Rat, showing in what way learning enters into it. No ethologist ever doubted that it did and none ever believed, as the author evidently implies that we do, that this extremely complicated set of widely differing behaviour elements was wholly innate, but we do contend that the motor patterns which we call instinctive movements are. And to disprove this our critics must take one typical example of such a motor pattern which possesses the typical wide distribution characteristic of a taxonomic unit and typically high species predictability already mentioned. Then they must proceed to show that, as Prof. Hebb asserts "an environment equally invariable in most or all important matters" is necessary to produce species predictability. Let me propose, for a suitable object, the movement with which Oscines (Song Birds) and Anatidae distribute oil from the oil gland over their plumage.....Now let our critics do their utmost, changing whatever they can change in environment, or even excising the gland altogether and see whether they succeed in making a song-bird do the Anatidae's movement and vice versa. I give them a free hand to use all the methods of animal training known hitherto, starting with the moment the bird hatches, or even before that (p. 53)."

While Lehrman (1956), at the same conference, presented a paper stating,

> "that my problem here has not been the coordination of the fixed movement patterns, but their organization into a pattern such that the animal's motivational states, and the relationships between motivation and movements, are appropriate to the inter-individual relationships in the species (p. 519)."

As the above dialogue illustrates, ethologically oriented behaviourists were concerned with the ontogeny of the microelements of behaviour (the fixed or modal action pattern) while their psychologically trained colleagues were concerned with the development of more global or integrated patterns of behaviour.

The failure of the participants in the nature-nurture controversy of the 1950-1960's to recognize this dichotomy in the behaviours to which they were referring as "instinctive" was, in large part, due to the ethologists failure to clearly define the behavioural elements that they wished to describe as independent of experiential input in their development. Tinbergen (1951), for example, commented:

> "What is to be called an instinctive act? Is it the pattern as a whole or ~~is it~~ one of the partial patterns or even as Lorenz has proposed, the consummatory act? I would prefer to apply the name to all levels. For instance, reproduction in the male stickleback is, as a whole, an instinctive activity. But its component parts, nest building and fighting may also be called instinctive activities (p. 110)."

Additional confusion resulted from the fact that the criteria used by ethologists for distinguishing innate from acquired behaviours, i.e. species-specificity and stereotypy (Lorenz, 1956, 1970), could be applied to many global patterns of behaviour (Lehrman, 1953) which most ethologists would not consider to be innate in the sense of genetically determined.

The nature-nurture controversy, although doing little to resolve the dispute between the parties involved, did, however, raise an important and legitimate issue. Even granting that the fixed action patterns in which ethologists were interested were genetically determined, a question still remains as to the factors responsible for the similarity observed in the topography of more global patterns of behaviour.

Psychologists pointed to two alternative mechanisms by means of which the early experience of organisms could lead to the development of similar global patterns of behaviour in all members of a given species. First, it is possible that acquired patterns of behaviour could be socially transmitted from adult species members to their offspring (see Davis, 1973, and Galef, in press, for recent reviews of this literature). It is, for example, believed that the habit of washing sweet potatoes in salt water is learned by juvenile Japanese Macaques as a result of observing their parents engage in this behaviour (Kawai, 1965).

Second, behavioural homogeneity could be achieved as a result of the relative constancy of the the physical environment in which the members of any species develop. In addition to sharing common genetic material, the young of any species may be reared in an environment which is as characteristic of that species as its genotype (King, 1968). Thus, the constancy of species-typical behaviours may result from a constancy in genotype-environment interaction rather than a constancy in genotype alone (Smith & Guthrie, 1921; Hebb, 1953). In other words, the structure of the environment may channel the development of behavioural patterns in one of the many directions available in the genotype

(Lehrman, 1953, 1962, 1970; Moltz, 1965).

Historically, it is the second of these mechanisms which has received the greatest attention in the theoretical statements of psychologists attempting to explain the development of species-typical global patterns of behaviour. Psychological theory has emphasized the importance of the relative constancy of the physical environment in which the members of any species are raised in the production of species-typical behavioural homogeneity.

Introduction

Given the major role attributed by psychologists to the physical environment in the ontogeny of global species-typical patterns of behaviour, it is surprising that relatively few studies have directly investigated the effects of the physical rearing environment on them. The design of such investigations is relatively straightforward. One need only rear animals of constant genotype in environments differing from one another in carefully specified ways (Stone, 1947) and, at maturity, compare subjects' patterns of motor activity in some standard situation. Unfortunately, most of the studies purporting to investigate the role of the rearing environment in the ontogeny of species-typical patterns of behaviour have failed to satisfy these criteria. The numerous investigations in the literature on the effects of poorly defined "enriched", "deprived", "restricted", or "isolated" rearing environments on learning ability (see Meyers, 1971, for a recent review of this voluminous literature) are not really to the point, in that learning ability is not a species-typical pattern of behaviour in any of the usual senses of that term. Studies of the influence of early experience on species-typical preferences (for food, Kuo, 1967; habitat, Welker, 1963; sexual partner, Lorenz, 1970; and oviposition site, Thorpe & Jones, 1937) are, similarly, not directly relevant to the question of the effects of the physical environment on the development of species-typical patterns of behaviour. Such studies do not attempt to modify patterns of behaviour, but rather to influence the stimuli eliciting them.

The major problem in initiating studies dealing directly with the influence of the physical environment on the development of species-typical behaviours lies in the identification of promising areas for investigation. In general, the relative invariance of the behaviour patterns of members of a species have made it difficult to locate situations in which differences in rearing environment are correlated with differences in behaviour.

Examples of variability in species behaviour correlated with diversity in rearing environment are, however, to be found in the comparison of the behaviour of wild and domesticated strains of many species. Usually, wild-reared individuals are timid, savage, and emotional (Richter, 1954; Stone, 1932) while those maintained in the laboratory are curious, docile, and placid (Boice, 1966).

It is, of course, possible that the differences in the observed behaviours of wild and domesticated strains are due to changes in the gene pool of the domesticated strain as a result of intensive inbreeding (Spurway, 1955) or artificial selection for docility (Castle, 1947; Richter, 1954). However, a number of investigators have suggested that differences in behaviour between wild and laboratory strains of the same species may, in fact, develop as a consequence of differences in the environment in which they are reared (Donaldson, 1932; Friedman, 1964; Kavanau, 1964).

For example, as a result of consideration of his studies of the experiences sufficient to tame the Virginia opposum, Friedman (1964) suggested that it is possible that members of domesticated species have to be tamed anew in each generation. In support of this hypothesis, a variety of naturalistic observations suggest that domesticated strains can rapidly revert to the patterns of behaviour of wild strains as a result of escape or release from laboratory settings. Rasmussen (1938) has reported that domesticated rats allowed to run free for several days, became shy and wild and severely bit the experimenter when he attempted to handle them. Similarly, Minckler and Pease (1938) have described a colony of albino rats, which managed to survive two winters living in a Montana garbage dump and had proliferated to such an extent that they were considered to be a health hazard. It is unfortunate that these authors did not report observations on the effects of life in the wild on behaviour or temperament, but their report of survival and reproduction in the wild is sufficient to establish that changes produced by domestication are not sufficient to render domesticated animals incapable of adapting their behaviour to the demands of more severe environments.

One difference in the physical environment inhabited by wild and domesticated strains is that many of the species commonly studied in behavioural laboratories (gerbil, hamster, mouse, and rat) live in burrows in their natural habitat (Bannikov, 1954; Calhoun, 1962; Tanimoto, 1943; Telle, 1966; Won, 1961), while in the laboratory they are most commonly maintained in cages devoid of shelter. It is possible that rearing in an open environment is a critical factor in producing, in each generation, the tameness and docility characteristic of these domesticated strains.

Daly (unpublished, 1971) investigated the effects of burrow- and laboratory cage-rearing on the behaviour of Golden Hamsters (Mesocricetus auratus, Nehring, 1898). He concluded that the main effect of rearing environment was to render burrow-reared animals more timid (timidity being defined as "cautious approach to unfamiliar environments") than cage-reared ones. Unfortunately, the data obtained in Daly's experiment are difficult to interpret because the burrow manipulation was only partially successful. Of the five litters reared in enclosures permitting burrowing, only one litter was actually reared below the surface. The burrow systems of the other four litters collapsed. Data from the one successful litter were not presented separately and, as a result, it is not possible to determine whether or not the rearing manipulation had any effect on behaviour.

In the present thesis the effects of rearing in burrow systems on the behaviour of a small desert rodent, the Mongolian gerbil (Meriones unguiculatus, Milne-Edwards, 1867), are investigated. Like most domesticated strains, the laboratory-reared gerbil is extremely docile, shows no fear of human handlers and rarely flees from or bites them (Schwentker, 1961). The behaviour of laboratory-reared gerbils is, however, very different from that of gerbils observed in their natural habitat. Anderson (in Allen, 1940) reports that he could approach within 8 ft. of wild gerbils but that they would then flee into their burrows and foot-thump (see also Daly & Daly, 1973; Won, 1961).

Gerbils have been maintained in captivity for some 20 years, a period sufficient for genetically induced changes in behaviour to occur which could result in relative tameness (King & Donaldson, 1929; Robinson, 1965). However, the results of an experiment by Thiessen (1973) suggest that differences in the physical environment inhabited by wild and laboratory strains may be responsible for the observed differences in their behaviour.

Thiessen (1973) released a number of Mongolian gerbils into a large outdoor enclosure and, although a high rate of predation and heavy rains considerably reduced their numbers, he observed three or four surviving pairs for several months. These gerbils dug complex burrow systems and, once established in them, became wary and could only be seen by an observer if he waited patiently for considerable periods of time. It is possible that the subjects managing to survive the initial high rates of predation were initially more wary than their deceased fellows; however, the observation that living in a burrow system was associated with an increase in wariness is suggestive. The present thesis extends, under controlled conditions, the observation by Thiessen of the effects of burrow maintenance on the behaviour of the Mongolian gerbil in response to the presence of human observers.

CHAPTER II

The Effects of Laboratory- and Tunnel-Rearing on Reactivity to Sudden Stimulation

If the difference in the response of laboratory- and wild-reared gerbils to the presence of humans reflects the effects of being reared in diverse physical environments, then gerbils reared in a laboratory environment which simulates that of their natural habitat might be expected to exhibit the flight, concealment and footthumping response to the presence of humans which is seen in wild gerbils. In the first experiment, gerbils of a common genetic background were reared either in standard laboratory cages or in tunnel systems constructed by their parents, and their responsiveness to a novel, moving, visual stimulus (a mask of a human head) was assessed at maturity. In order to determine whether any observed behavioural differences were due to differences in visual capacity, all subjects were first tested on the visual-cliff (Walk & Gibson, 1961), an apparatus commonly used to detect visual deficits.

Method

Subjects

Subjects were 64 Mongolian gerbil pups (Meriones unguiculatus, Milne-Edwards, 1867), the direct descendents of 16 breeding pairs acquired from Tumblebrook Farm, Brant Lake, New York. Each of the 16 breeding pairs reared one litter in each of the two rearing conditions (LDO and LDT) described below. To control for possible litter effects (Henderson, 1963, 1967; King, 1969), only two pups (when possible one male and one female) were used from each of the litters reared in each condition. Twenty-six of the subjects in each rearing-condition were assigned to the experimental group and the remaining six subjects to the control group.

General Maintenance

Upon arrival in the laboratory, multiparous female gerbils and their mates were established in a temperature-controlled colony room (72°F), illuminated by overhead fluorescent lights from 9 am to 9 pm, with total darkness prevailing for the remainder of the day. Food and water were available continuously.

Experimental Rearing Conditions

Group LDO

Subjects were reared on a 12-hourlight-dark cycle (LD) in an open (O) laboratory cage, devoid of shelter. The cages used were formed of translucent plastic (14 in. long x 12 in. wide x 6 in. high) and contained wood shavings to a depth of 1/2 in. The cover of each cage was constructed of 1/2 in. hardware cloth. Cages were inspected each morning for the birth of litters and to determine the date of eye-opening of young. A litter was weaned and its members individually marked for identification by shaving portions of their bodies 27 days after the median day of eye-opening of that litter. The median day of eye-opening of a litter was defined as the first day on which half of the pups in that litter had both eyes fully open (mean = 18.5 days post partum, S.E. = 1.7). Litters were handled only when wood shavings were changed, once on the day of median eye-opening and once again 27 days later.

Group LDT

Subjects were reared on a 12-hour light-dark cycle (LD) in a tunnel (T) system. Cages for tunneling were constructed by filling a sheet metal enclosure (3 ft. long x 3 ft. wide x 4 ft. high) to a depth of 18 in. with wetted packed earth. Breeding pairs constructed complex tunnel systems within these cages 3 to 4 days following introduction into them. All litters were born and reared inside the burrow and were rarely seen on the surface, making direct determination of the date of birth and of eye-opening impossible. However, preliminary observation had revealed that shortly after giving birth to a litter, a female gerbil would exclude her mate from the burrow system and block all entrance holes with earth. Consequently, whenever an adult male was seen on the surface and the entrances to the tunnel were blocked, it was assumed that a litter had been born. Confirmation of the birth of a litter was accomplished by placing "Have-A-Hart" mouse traps inside the tunnel cage on days 16 through 19 following the presumed birth of a litter and trapping all enclosure inhabitants. In every instance in which a litter was thought to be inhabiting the tunnel, young pups were trapped. Immediately after the eyes of the trapped young had been checked for opening, the pups were released back into the tunnel system. Twenty-seven days after median eye-opening had occurred, each litter was permanently removed from its tunnel system, marked for identification purposes, and housed in a translucent plastic cage (14 in. long x 12 in.

wide x 6 in. high) containing a wooden box (7 in. long x 11 in. wide x 6 in. high) with one (2 x 2 in.) entrance hole.

General Procedure

Thirty days after median eye-opening had occurred in a litter, subjects in that litter were tested on the visual-cliff, receiving one test trial a day for five consecutive days (method of testing on the visual-cliff and the data collected in this apparatus will be discussed in detail in Chapter IX). At the conclusion of visual-cliff testing, subjects were left undisturbed for one week and were then tested in the shelter-field enclosure described below. Subjects were 58-64 days *post partum* at the time of shelter-field testing. Immediately prior to testing in the shelter-field enclosure, the wooden shelter in the cages of LDT litters was removed and subjects permitted 20 minutes to light adapt.

Shelter-Field Apparatus

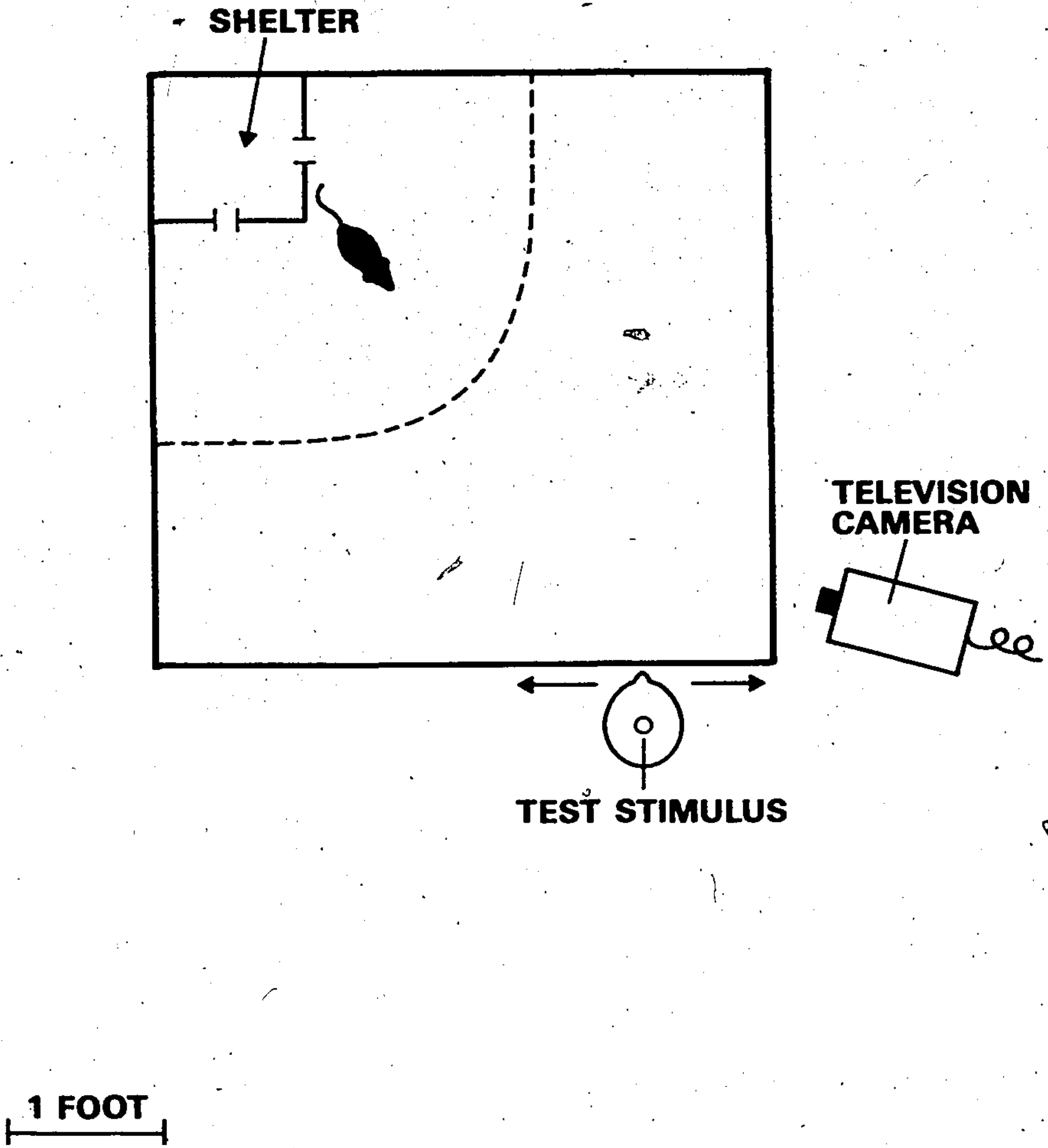
Testing was conducted in a 4 x 4 ft. enclosure with walls 3 ft. high. A wooden shelter (12 in. long x 12 in. wide x 6 in. high) with two 2 x 2 in. entrance holes was located in the upper left hand corner of the enclosure (see Figure 1). Behaviour occurring in the shelter-field enclosure was monitored via closed-circuit television.

Insert Figure 1 about here

The visual stimulus presented to subjects while in the enclosure is illustrated in Figure 2. It consisted of a rubber mask of a male

FIGURE 1

Overhead Schematic View of the Shelter-Field Enclosure


SHELTER
TELEVISION CAMERA
TEST STIMULUS
1 FOOT

human face placed on a styrofoam wig-stand which was mounted on a pole.

Insert Figure 2 about here

Shelter-Field Test Procedure

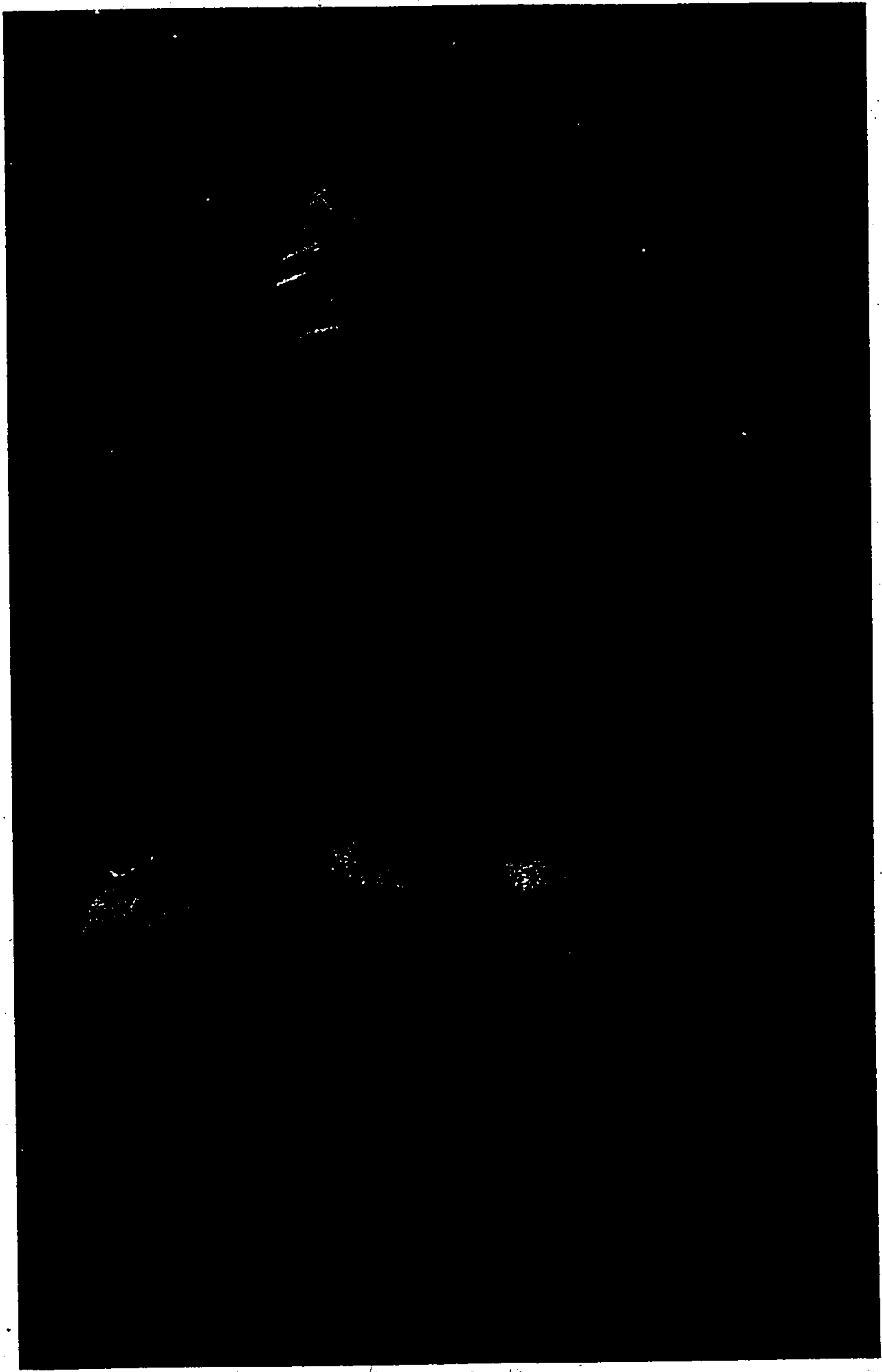
A major difference in behaviour between gerbils reared in the wild and those reared in the laboratory is in their response to the sudden appearance of humans. The shelter-field test described below was designed to study this response to the sudden introduction of a novel, human-like stimulus in a quantifiable fashion. Although the shelter-field situation is, in many respects, a novel test situation for assessing reactivity, it does incorporate features of more traditional methods for measuring emotionality. The relationship of the shelter-field test to these measures is discussed in detail in Chapter VIII.

Basically, the shelter-field test consists of two subtests, referred to below as the pretest and posttest. During the pretest, subjects (experimental and control) were permitted to explore the open and sheltered portions of the enclosure. In the posttest, experimental subjects were exposed to the test stimulus while control subjects were permitted to move in the enclosure undisturbed.

Pretest (experimental and control groups). Individual subjects were placed in the lower right-hand corner of the shelter-field enclosure and the time required by each subject to enter the shelter recorded. During the 3-minute period immediately following initial shelter exit (the pretest period), the observer recorded the amount of time the subject spent within the shelter. Movement into or from the shelter

FIGURE 2

The Test Stimulus Presented to Experimental Groups
at the Commencement of the Posttest Period
in the Shelter-Field Enclosure



was defined as occurring when the subject had all four feet inside or outside of its entrance. Subjects failing to enter the shelter within 10 minutes of placement in the enclosure were removed from it and retested on the following day.

If a subject exhibited freezing behaviour during the 3-minute pretest period, recording was stopped and resumed when the subject resumed locomotion. Freezing was defined as the assumption of a crouched posture accompanied by complete immobility (Brady & Hunt, 1951; Doyle & Yule, 1959; Levine, 1956; Miller, 1951).

Posttest (experimental group). Following the 3-minute pretest period, the visual stimulus (illustrated in Figure 2) was presented to each subject when (1) that subject was within 18 in. of the wooden shelter and oriented towards the lower right corner of the enclosure and (2) it had been moving in the preceding 5-second period.

The test stimulus was introduced over the lower right corner of the enclosure, moved horizontially from left to right three times and then held in an upright position. The total period of exposure of the test stimulus lasted 30 seconds. During the 2-minute period subsequent to the introduction of the test stimulus, the experimenter recorded the time required for the subject to reach shelter, the time to first emerge from shelter, the total time spent in concealment, and instances of footthumping.

Posttest (control group). Subjects in control groups were treated identically to those in experimental groups except that no test stimulus was presented at the beginning of the posttest period. The presence of the control groups thus provides an indication of how animals behave during the posttest period when allowed to explore the enclosure undisturbed.

Data Analysis

Pretest data were analyzed by Kruskal-Wallis One Way Analysis of Variance and posttest data by Mann-Whitney U test for N's < 8, Mann-Whitney U test for N's > 20, and Chi Square (Siegel, 1956; Bradley, 1968). All tests were two-tailed with the rejection level at 0.05.

Results and Discussion

Pretest

Six subjects in the LDT Experimental Group behaved so as to make both their pre- and posttesting impossible and they were excluded from the experiment. On five consecutive days, two of these subjects remained immobile in the open portion of the enclosure and four subjects entered the shelter and did not emerge.

The data in Table 1, which presents the pretest behaviour of LDO and LDT experimental and control subjects, reveal that subjects in all groups spent approximately 25% of the pretest period inside the shelter. A Kruskal-Wallis One Way Analysis of Variance of these pretest data revealed no significant differences in the amount of time spent in shelter by the four groups ($H = 5.5$, $df = 3$, $p > 0.05$). This finding indicates that subsequent differences in concealment behaviour during the posttest period cannot be attributed to differences in the tendency of tunnel- and open-reared subjects to seek shelter in the absence of stimulation.

Insert Table 1 about here

Posttest

There are several comparisons of posttest performance that are of interest and to facilitate presentation of the results each comparison will be discussed separately.

LDO control vs LDT control. Inspection of the data describing posttest behaviour of LDO and LDT control groups, presented in Table 2, reveals that during the posttest period the behaviour of the two control groups was remarkedly similar. No significant differences were found either in the latency to first reach shelter ($\underline{U} = 9$, $\underline{p} > 0.05$), in latency to first emerge from shelter ($\underline{U} = 17$, $\underline{p} > 0.05$), or in total time spent in shelter ($\underline{U} = 9$, $\underline{p} > 0.05$).

Insert Table 2 about here

These findings indicate that any observed differences in posttest behaviour of experimental groups must result from responses to stimulus presentation rather than baseline differences in activity during the posttest period.

Experimental vs control. As is also seen in Table 2, posttest behaviour of experimental and control groups differed markedly. Both LDO and LDT experimental groups reached the shelter sooner, spent more time under shelter before emerging, spent more total time in shelter, and had a higher frequency of footthumping than did their respective controls. These differences in posttest performance of experimental and control groups were most noticeable in the case of subjects reared in a tunnel-

TABLE 1

MEDIAN AMOUNT OF TIME SPENT IN SHELTER DURING THE PRETEST PERIOD BY EXPERIMENTAL AND CONTROL GROUPS IN LDO AND LDT

Rearing condition	Group			
	Experimental		Control	
	n	Median	n	Median
LDO	26	45.0	6	48.5
LDT	26	47.0	6	54.0

TABLE 2

POSTTEST PERFORMANCE OF EXPERIMENTAL AND CONTROL GROUPS

Group	Rearing condition	Median latency to reach shelter	Median latency to first emerge from shelter	Median total time spent in shelter	Entry <3 seconds (flight)		Footthumping	
					n	%	n	%
Experimental	LDO (n = 26)	2.0	11.0	60.5	15	57.6	4	15.4
	LDT (n = 20)	1.0	119.0	119.0	20	100.0	8	40.0
Control	LDO (n = 6)	13.0	6.5	29.5	0	00.0	0	00.0
	LDT (n = 6)	12.5	6.0	40.5	0	00.0	0	00.0

cages although the same trend was apparent in open-reared subjects.

LDO experimental vs LDT experimental. The main effects of tunnel-rearing, as compared with open-rearing, are to be found in the posttest behaviour of LDT and LDO experimental groups. As can be seen in Table 2, all 20 of the LDT experimental subjects fled to shelter within 3 seconds of presentation of the test stimulus while only 15 of the 26 LDO subjects did so. Analysis of the number of fleeing and nonfleeing subjects revealed that this difference between LDO and LDT experimental groups was highly significant ($\chi^2 = 8.91$, Yates correction, $df = 1$, $p < 0.005$). Comparison of the latency to first emerge from shelter and total time spent concealed by LDT and LDO experimental subjects revealed that the LDT group exhibited longer latencies before first emerging (Mann-Whitney U test, transformed z score = 2.84, $p < 0.001$) and spent significantly more total time concealed during the posttest period than did the LDO group (Mann-Whitney U test, transformed z score = 3.75, $p < 0.001$). However, no significant differences were found in the number of LDO and LDT subjects footthumping ($\chi^2 = 2.93$, Yates correction, $df = 1$, $p > 0.05$).

Fleeing vs nonfleeing subjects. Experimental subjects who took shelter in the first 3 seconds of the posttest period were considered to have "fled" in response to the presentation of the test stimulus, while those who required more than 3 seconds to reach shelter were considered not to have fled. A criterion of 3 seconds to reach cover following stimulus presentation was selected to differentiate fleeing from nonfleeing subjects because, as examination of the fourth column of data in Table 2 reveals, none of the control subjects reached shelter during the initial 3 seconds of the posttest period. Thus, a 3 second criterion is a useful discriminator of flight in response to stimulus presentation from random shelter entry.

To some extent, differences in posttest performance of the LDO and LDT experimental groups reflected the fact that the LDO group consisted of two subgroups of subjects, those which fled immediately following stimulus presentation and those which did not. The LDT group, on the other hand, consisted only of subjects which fled immediately following presentation of the test stimulus. Differences in posttest performance of the LDO and LDT experimental groups were somewhat attenuated if analysis of posttest performance was based only on the data obtained from those subjects which fled in response to the test stimulus. Latency scores for the LDT experimental group during the posttest period remained unaffected, as all LDT subjects fled on presentation of the test stimulus. However, as can be seen in Table 3, which presents separately the posttest data of fleeing and nonfleeing subgroups of the LDO experimental group, median scores for time to first emerge and total time spent in shelter for the fleeing LDO subgroup became 51.0 and 90.0 seconds respectively. Significant differences, however, still remained between LDT and LDO fleeing subjects in time to first emerge from shelter (Mann-Whitney U test, transformed z score = 1.98, $p < 0.05$) and total time spent in concealment (Mann-Whitney U test, transformed z score = 2.79, $p < 0.01$).

Insert Table 3 about here

As can also be seen in Table 3, the behaviour of the fleeing subgroup of LDO differed dramatically from that of the nonfleeing subgroup. Nonfleeing individuals showed longer latencies to reach shelter, shorter

TABLE 3

POSTTEST PERFORMANCE OF FLEEING AND NONFLEEING SUBGROUPS OF THE LDO EXPERIMENTAL GROUP

Subgroup	Median latency to reach shelter	Median latency to first emerge from shelter	Median total time spent in shelter
Fleeing (n = 15)	1.0	51.0	90.0
Nonfleeing (n = 11)	26.0	7.0	32.0

latencies to emerge from shelter and spent less total time in concealment during the posttest period than did the subgroup which fled in response to the test stimulus.

A further difference between fleeing and nonfleeing subjects, to be discussed in greater detail in Chapter VIII, was in the presence and absence of footthumping. Footthumping was exhibited only during the posttest period and only by experimental subjects reaching shelter during the initial 3-seconds of the posttest period. Footthumping subjects engaged in the activity immediately after reaching shelter.

Summary

The results of the present experiment indicate that the behaviour of gerbils in response to the abrupt presentation of a visual stimulus varies, in several important respects, as a function of the conditions under which they are reared. First, gerbils reared in tunnel systems were more likely to respond to stimulus presentation by fleeing to shelter then were gerbils reared in standard laboratory cages. Second, following stimulus presentation, tunnel-reared gerbils showed increased latencies to leave shelter and spent a greater amount of time in concealment than did gerbils reared in open cages. Third, behaviour of tunnel-reared and open-reared gerbils which fled in response to stimulus presentation differed in that the former animals showed longer latencies to first leave cover and spent more total time concealed than did the latter.

The fact that concealment behaviour in the absence of stimulus presentation did not differ between tunnel- and open-reared subjects indicates that differences between them in response to stimulus presentation cannot be attributed to differences in baseline exploratory behavior.

It seems reasonable to conclude, on the basis of the data in the present chapter, that the physical environment in which gerbils are reared can influence the nature of their response to the sudden presentation of a human-like visual stimulus. In general, the effects of rearing gerbils in a tunnel environment would apparently be to establish the syndrome of response to the appearance of humans normally seen in wild-reared gerbils.

In the following chapters we will be concerned with the determination of those features of the tunnel environment responsible for the increased responsiveness of individuals reared in this environment.

CHAPTER III

Analysis of the Tunnel Environment

The physical environments in which tunnel- and laboratory-reared gerbils matured differed along at least three major dimensions. The tunnel system provided (1) a hole through which gerbils could flee, (2) an enclosed hiding place, and (3) a three-dimensional substrate. In contrast, the laboratory cage provided opportunity for neither flight nor concealment and gerbils reared in laboratory cages were restricted in activity to a two-dimensional surface. In the present experiment each of these features, differentiating tunnel from cage environments, were added singly to the basic open-cage design to allow assessment of their individual contribution to the differences in behaviour observed in open- and tunnel-reared animals.

Method

Subjects

Subjects were 128 gerbil pups selected from 64 litters born and reared in the laboratory.

Experimental Rearing Conditions

Each breeding pair was established in a translucent plastic cage and maintained in a temperature controlled colony room, illuminated on a 12-hour light-dark cycle (LD). Marking, handling and cage-cleaning procedures were these described in Chapter II. Nine days after the birth of a litter, 16 mothers and their young were randomly assigned to each of the four housing conditions described below.

As can be seen in Figure 3, which illustrates the four housing conditions used, house-open cages (LDHO) provided a hole to run through, cliff-open cages (LDCO) a three-dimensional substrate, house cages (LDH) a hole and an enclosed hiding place, and cliff-house cages (LDCH) a hole, enclosed hiding place, and experience with a three-dimensional substrate. By rearing pups in this array of environments and then testing them in the shelter-field enclosure, it should be possible to determine the contribution of each environmental feature to the difference in response of open- and tunnel-reared subjects to the novel, moving stimulus discussed in Chapter II.

Insert Figure 3 about here

General Procedure

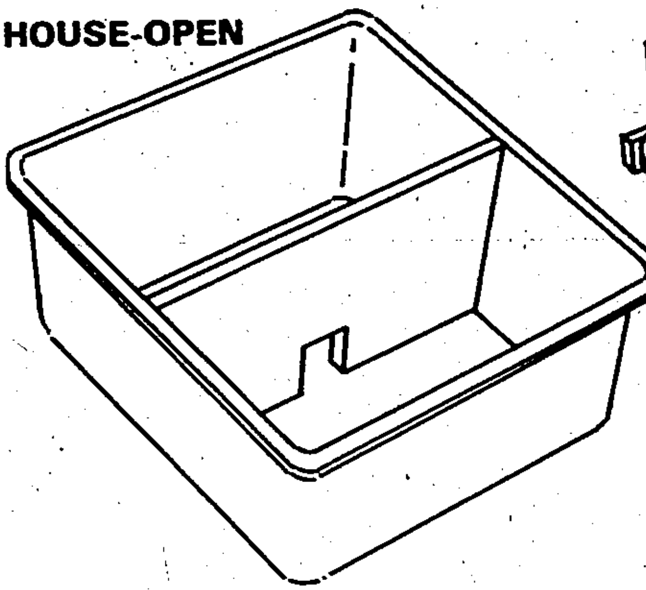
Procedures for visual-cliff and shelter-field testing were identical to those described in Chapter II. For the shelter-field test, two subjects were selected from each of the 16 litters in each housing condition. Twenty-six of each group of 32 subjects were assigned to the experimental group and six to the control group.

Results

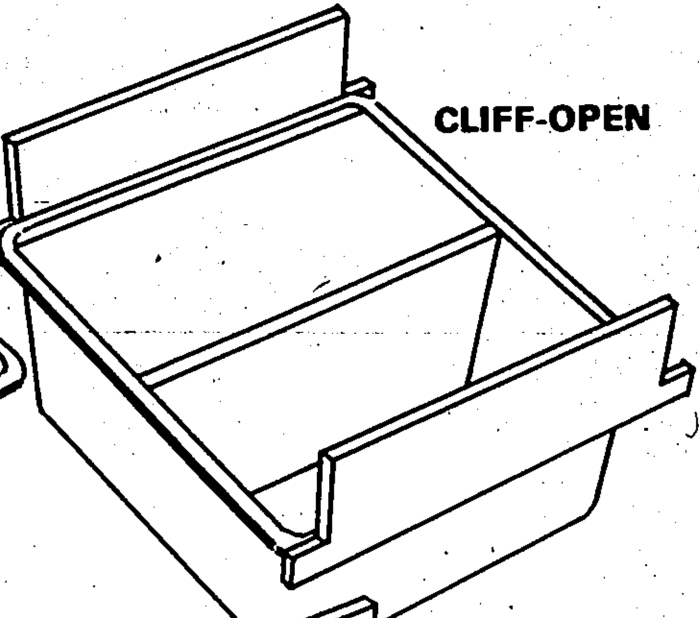
The main results of the present experiment are presented in Table 4. Data obtained from the LDO and LDT groups of Chapter II are included for purposes of comparison. Examination of Table 4 reveals that

FIGURE 3

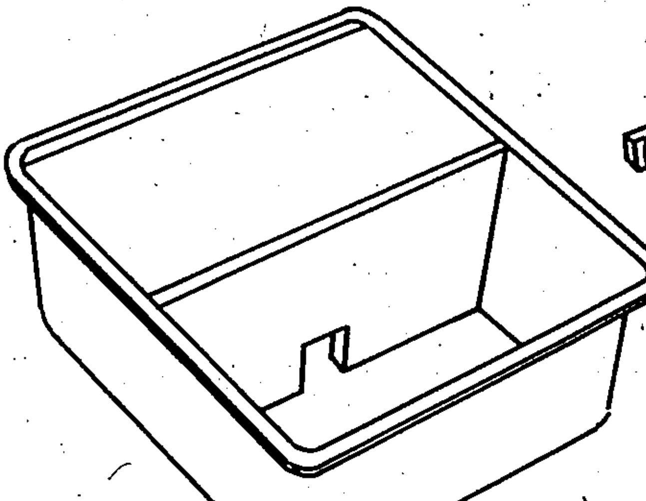
Schematic diagrams of the house-open (HO), cliff-open (CO), house (H), and cliff-house (CH) cages used for rearing. The hardware cloth used to cover the tops of the cages is not shown. In H and HO cages, the hardware cloth was flush with the top edge of the plastic cages and in CO and CH cages, it was raised 5 in. above the plastic cage edge.



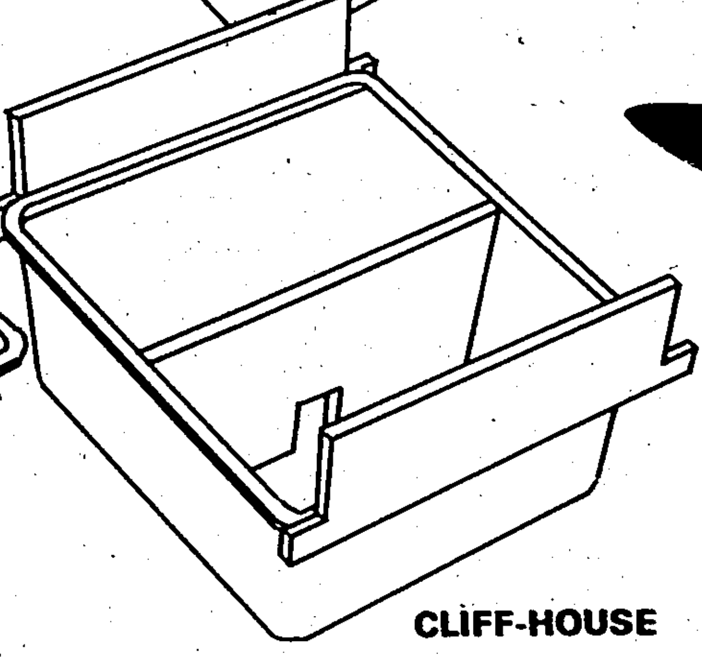
HOUSE-OPEN



CLIFF-OPEN



HOUSE



CLIFF-HOUSE

during the posttest period control subjects did not differ, as a function of rearing condition, in latency to reach shelter (Kruskal-Wallis, $\underline{H} = 4.9$, $\underline{df} = 5$, $\underline{p} > 0.05$), in time to first emerge from shelter (Kruskal-Wallis, $\underline{H} = 4.5$, $\underline{df} = 5$, $\underline{p} > 0.05$), or in total time spent in concealment (Kruskal-Wallis, $\underline{H} = 3.0$, $\underline{df} = 5$, $\underline{p} > 0.05$).

Insert Table 4 about here

Rearing condition, however, did significantly affect the responsiveness of experimental groups to stimulus presentation. In particular, for those groups which had a hiding place available during ontogeny (LDH, LDCH, LDT), median latency to reach shelter was reduced (Extension of the Median test, $\underline{X}^2 = 16.3$, $\underline{df} = 5$, $\underline{p} < 0.025$), median latency to emerge from shelter increased (Extension of the Median test, $\underline{X}^2 = 33.7$, $\underline{df} = 5$, $\underline{p} < 0.005$), and total time spent in shelter increased (Extension of the Median test, $\underline{X}^2 = 36.7$, $\underline{df} = 5$, $\underline{p} < 0.005$).

As was the case in Chapter II, experimental subjects in each housing condition could be subdivided into fleeing and nonfleeing subjects using a criterion of 3 seconds to reach shelter following presentation of the test stimulus during the posttest period. Tables 5 and 6 present the data describing the behaviour of each of these subgroups independently. As can be seen in Table 5, the percentage of experimental subjects categorized as fleeing in response to presentation of the test stimulus increased regularly as a function of increasing similarity of housing conditions during maturation to the tunnel-rearing environment ($\underline{X}^2 = 25.8$, $\underline{df} = 5$, $\underline{p} < 0.01$). Also, there was a significant tendency for fleeing subjects reared in environments providing the opportunity for concealment

TABLE 4

POSTTEST PERFORMANCE OF EXPERIMENTAL AND CONTROL GROUPS

Group	Rearing condition	Median latency to reach shelter	Median latency to first emerge from shelter	Median total time spent in shelter
Experimental	LDO (n = 26)	2.0	11.0	60.5
	LDCO (n = 26)	6.0	11.0	40.5
	LDHO (n = 26)	1.0	12.5	49.0
	LDH (n = 26)	1.0	85.0	109.5
	LDCH (n = 26)	1.0	85.0	111.0
	LDT (n = 20)	1.0	119.0	119.0
Control	LDO (n = 6)	13.0	6.5	29.5
	LDCO (n = 6)	7.5	3.5	30.5
	LDHO (n = 6)	22.0	7.0	31.0
	LDH (n = 6)	14.0	7.0	33.0
	LDCH (n = 6)	19.0	2.0	19.5
	LDT (n = 6)	12.5	6.0	40.5

(LDH, LDCH, LDT) to spend more time in the shelter before emerging (Extension of the Median test, $X^2 = 14.5$, $df = 5$, $p < 0.025$), and to spend a greater proportion of the posttest period under shelter (Extension of the Median test, $X^2 = 13.5$, $df = 5$, $p < 0.025$) than subjects reared in environments lacking cover (LDO, LDCO, LDHO).

Insert Table 5 about here

Extension of the Median tests revealed no differences on any measure of posttest behaviour either among fleeing subgroups having cover available during rearing (LDH, LDCH, LDT) or among fleeing subgroups having no cover available during rearing (LDO, LDCO, LDHO) (all p's > 0.05).

Nonfleeing experimental subjects did not show significant differences among groups, as a function of rearing environment, in latency to first reach shelter (Kruskal-Wallis, $H = 2.9$, $df = 4$, $p > 0.05$), in latency to first emerge from shelter (Kruskal-Wallis, $H = 6.6$, $df = 4$, $p > 0.05$), or in total time spent in concealment (Kruskal-Wallis, $H = 3.8$, $df = 4$, $p > 0.05$).

Insert Table 6 about here

Comparisons of the behaviour of nonfleeing experimental subjects with that of controls (Table 4) revealed a significant increase in latency to reach shelter on the part of nonfleeing experimental subjects (Mann-Whitney U test, transformed z score = 2.18, $p < 0.05$), but no differences between nonfleeing experimental subjects and control subjects in latencies to first emerge from shelter (Mann-Whitney U test, transformed z score = 0.09, $p > 0.05$) or in total time spent in concealment (Mann-Whitney U

TABLE 5

POSTTEST PERFORMANCE OF EXPERIMENTAL SUBJECTS WHICH FLED TO PRESENTATION OF THE TEST STIMULUS

Rearing condition	Flight			Concealment		Footthumping	
	Entry < 3 seconds		Median latency to reach shelter	Median latency to first emerge from shelter	Median total time spent in shelter		
	n	%				n	%
LDO (n = 26)	15	57.6	1.00	51.0	90.0	4	26.6
LDCO (n = 26)	13	50.0	1.00	45.0	80.0	5	39.2
LDHO (n = 26)	20	76.9	1.00	31.0	68.0	4	20.0
LDH (n = 26)	22	84.6	1.00	96.0	114.0	5	22.7
LDCH (n = 26)	24	92.3	1.00	98.5	112.5	8	33.3
LDT (n = 20)	20	100.0	1.00	119.0	119.0	8	40.0

TABLE 6

POSTTEST PERFORMANCE OF NONFLEEING EXPERIMENTAL SUBJECTS

Rearing condition	n	Median latency to reach shelter	Median latency to first emerge from shelter	Median total time spent in shelter
LDO	11	26.0	7.0	32.0
LDCO	13	18.0	2.0	25.0
LDHO	6	20.5	5.5	21.5
LDH	4	29.0	2.0	21.0
LDCH	2	72.5	1.0	12.0

test, transformed _z_ score = 0.55, $p > 0.05$).

Insepection of the pretest data, presented in Table 7, reveals that the amount of time spent in the shelter by all groups was essentially constant. A Kruskal-Wallis One Way Analysis of Variance of the pretest data, presented in Table 7, revealed no significant differences in the median amount of time spent in the shelter during the pretest period among the 12 groups ($H = 14.3$, $df = 11$, $p > 0.05$).

Insert Table 7 about here

Discussion

The results of the present experiment indicate that the increased responsiveness to the presentation of the visual stimulus to be seen in tunnel-reared, as compared with open-reared, subjects resulted from the shelter which the tunnel system provides for gerbils reared in it. Neither provision of a cliff, nor of a hole through which to run, significantly increased responsiveness in the shelter-field enclosure, while provision of shelter produced the entire behavioural syndrome of flight and concealment normally seen in tunnel-reared subjects.

An additional finding of the present study was that, in comparison with control subjects, nonfleeing subjects showed a significant increase in latency to reach shelter. Observation of the behaviour of nonfleeing subjects revealed that this longer latency to enter shelter following stimulus presentation resulted from a marked tendency of these subjects to approach and fixate the stimulus. The nonfleeing subjects

TABLE 7

MEDIAN AMOUNT OF TIME SPENT IN SHELTER DURING THE PRETEST PERIOD BY EXPERIMENTAL AND CONTROL GROUPS

Rearing condition	Group			
	Experimental		Control	
	n	Median	n	Median
LDO	26	45.0	6	48.5
LDCO	26	42.0	6	43.0
LDHO	26	38.0	6	41.5
LDH	26	43.0	6	50.0
LDCH	26	44.0	6	40.0
LDT	20	47.0	6	54.0

were not simply indifferent to stimulus presentation but rather might be described as curious or inquisitive in a situation in which fleeing subjects were timid or fearful.

The dichotomy in response of nonfleeing and fleeing subjects in the present experiment to presentation of the visual stimulus could be attributed to differences in the intensity of fear elicited by stimulus presentation. A number of investigators have suggested that the response of animals to mildly fear-inducing stimuli is to approach and explore them, while their response to intensely fear-inducing stimuli is to flee and escape (Halliday, 1967; Montgomery & Monkman, 1955). In this view the effects of rearing in environments providing shelter would be to increase the probability of gerbils responding to a sudden visual stimulus with high levels of fear.

An organism maturing within an environment providing shelter may, if it makes use of that shelter, have a different range of experiences than one maturing in an open environment. The presence of a physical shelter enables an organism to modulate the amount of light to which it is exposed, to reduce its exposure to visual and auditory stimuli arising in the outside world, and to experience flight from an exposed area to one offering concealment. In the following three chapters an assessment will be made of the contribution to reactivity in the shelter-field test of each of these three types of experience which are available only to shelter-reared subjects.

CHAPTER IV

The Effects of Dark Rearing

Litters reared in cage conditions lacking shelter (LDO, LDCO, LDHO) were continuously exposed to the 12-hour light-dark cycle prevailing in the colony room and had no way to modulate the amount of light to which they were exposed. Animals reared in cages containing enclosed shelters (LDH, LDCH, LDT), on the other hand, could reduce the amount of light to which they were exposed by spending time inside the available shelter. In fact, immature animals living in environments providing shelter spent most of their time under it and, hence, in the dark.

Many experimenters have reported that rearing in the dark can have an effect on subsequent emotionality (Tees, 1969; Walk, 1960). For example, Gantz and Fitch (1968) noted that dark-reared cats appeared frightened (moved little, shivered, and vocalized) and Gibson, Walk, and Tighe (1959) observed that rats reared in the dark were more hesitant to eat food in a novel environment and exhibited more freezing and hesitation behaviour than their cyclic-reared counterparts.

Because dark-rearing has been demonstrated to be a factor in potentiating fear responses, it is possible that the observed differences in behaviour between shelter- and open-reared subjects resulted from differences in the amount of illumination to which they were exposed during rearing. In the present experiment, groups of subjects were reared in darkness in open-cages (referred to below as group DDO) to assess the effects of low illumination levels during infancy onlater behaviour.

Method

Subjects

Subjects were 32 gerbil pups randomly selected from 16 litters born and reared in the laboratory.

Procedure

Nine days following the birth of a litter, mother and young were removed from the breeding colony and transferred to a darkened room in open-cages. No attempt was made to completely eliminate exposure of the pups to light, as rigorous light deprivation in infancy is known to produce severe visual deficits in a number of species (Dews & Wiesel, 1970; Glees & Clarke, 1941; Hein & Held, 1967; Hubel & Wiesel, 1970; Riessen, 1950, 1960). Instead, the dark colony room was kept in darkness but illumination was provided occasionally when animals were fed, watered, cleaned, marked and observed for eye-opening.

All other maintenance and testing procedures were identical to those described in Chapter II.

Results

The main results of the present experiment are presented in Tables 8 and 9. Data from the LDO group of Chapter II are included for purposes of comparison. As is evident from examination of the data, both from all subjects (Table 8) and from fleeing subjects alone (Table 9), the effects of dark-rearing were generally to reduce responsiveness to stimulus presentation. In fact, subjects reared on a 12-hour light-dark cycle (Group LDO) fled significantly more frequently, showed longer latencies to first emerge from shelter, and spent more total time in the shelter than did the dark-reared subjects (Mann-Whitney U tests for N's >20, all p's < 0.05).

Insert Tables 8 and 9 about here

That these differences in the behaviour of dark- and cyclic-reared experimental subjects in response to stimulus presentation were not the result of changes in baseline levels of activity is indicated by the fact that corresponding effects were not to be found in the comparison of the behaviour of LDO and DDO control groups (Mann-Whitney U tests N's < 20, all p's > 0.05).

Discussion

As was shown in Chapter III, the main effects of rearing in environments containing shelter were (1) to increase the precentage of subjects exhibiting flight behaviour, (2) to increase the latency to first emerge from shelter, and (3) to increase total time spent in shelter in response to stimulus presentation.

Animals reared with cover available spent more time in the dark during ontogeny than those reared in open environments and, therefore,

TABLE 8

POSTTEST PERFORMANCE OF EXPERIMENTAL AND CONTROL GROUPS

Group	Rearing condition	Median latency to reach shelter	Median latency to first emerge from shelter	Median total time spent in shelter
Experimental	LDO (n = 26)	2.0	11.0	60.5
	DDO (n = 26)	19.5	4.5	28.0
Control	LDO (n = 6)	13.0	6.5	29.5
	DDO (n = 6)	20.0	9.5	31.5

TABLE 9

POSTTEST PERFORMANCE OF FLEEING SUBJECTS

Rearing condition	Flight			Concealment		Footthumping	
	Entry < 3 seconds		Median latency to reach shelter	Median latency to first emerge from shelter	Median total time spent in shelter		
	n	%				n	%
LDO (n = 26)	15	57.6	1.0	51.0	90.0	4	26.6
DDO (n = 26)	7	26.9	1.5	7.0	75.0	1	14.3

it seemed possible that differences in exposure to light during development might be responsible for the increased responsiveness to stimulus presentation to be observed in gerbils reared with cover available to them. The results of the present experiment, however, indicate that such an interpretation of the observed effects of rearing with cover available is an invalid one. Rearing in the dark served to reduce rather than augment responsiveness to stimulus presentation; i.e., it reduced the percentage of animals fleeing, decreased latency to first emerge from shelter, and decreased total time spent in shelter in response to stimulus presentation.

CHAPTER V

The Effects of Isolation Rearing

A second plausible explanation of the observed differences in behaviour between animals reared in cages providing cover and those reared in open-cages is in terms of differences in their relative exposure to moving visual stimuli during development. Animals reared in tunnel, house, and cliff-house environments spent much of their time within an enclosed space and thus were seldom exposed to the visual stimuli provided by activity in their immediate vicinity. If in the open portions of their cages when a human approached, their response was to immediately flee to shelter. Animals reared in open-cages were frequently exposed to visual stimuli resulting from activity in their colony room and had an opportunity to become habituated to the stimuli emitted by caretakers. It is thus possible that the differences in response to stimulus presentation in the test situation described in Chapter III resulted from differences in habituation to visual stimulation during rearing. There is considerable support for such an interpretation in the literature.

Fentress (1968a) housed groups of captured adult voles for 2-3 months in environments differing in the amount of cover that they provided before observing the voles' response to an object moving overhead. A greater percentage of animals which had been housed in pens with some form of cover available, than of those housed in pens lacking shelter, responded to the test stimulus by fleeing. Fentress suggested that these data could be interpreted as indicating that animals reared in pens lacking shelter were habituated to stimuli passing overhead and had therefore become unresponsive to such stimuli.

The literature is, in fact, rich in reports indicating that animals reared in isolation, either from conspecifics or other sources of stimulation, show exaggerated responses to normally neutral stimuli following their removal from isolation conditions (Fuller, 1967; Konrad & Bagshaw, 1970). For example, several investigators have reported that isolation-reared Scottish terriers exhibit a number of patterns of behaviour not exhibited by normally reared individuals, including bizarre postures (Clarke, Heron, Featherstonhaugh, Forgays, & Hebb, 1951), whirling fits (Thompson & Heron, 1954a; Thompson, Melzack & Scott, 1956), disruption of exploratory activity (Thompson & Heron, 1954b; Thompson & Melzack, 1956) and deficits in response to pain (Melzack & Scott, 1957). Fuller (1967) has suggested that these behavioural abnormalities may result from habituation in isolation to low levels of stimulation and that isolated animals respond to moderate levels of stimulation with behaviour seen in normally reared animals only to intense stimuli.

In order to assess the effects of isolation from exposure to visual stimulation during maturation on performance in the shelter-field test, the behaviour of gerbils reared in visual isolation was compared to that of individuals reared in a normal colony room.

It was decided to rear animals in isolation under conditions of constant illumination, as pilot experiments had shown that animals reared in constantly illuminated open-cages were least likely to flee in response to presentation of a moving stimulus. Therefore, any effects of isolation on subsequent performance in the shelter-field test should be most evident in animals reared in constantly illuminated open-cages.

Method

Subjects

Subjects were 58 gerbils selected from 29 litters. Twenty-four animals, randomly selected from 12 litters, were reared in open-cages in a constantly illuminated colony room and 34 animals, from 17 litters, were reared in open-cages in the constantly illuminated isolation enclosure described below.

Apparatus

The isolation enclosure, illustrated in Figure 4, was constructed of wood, with fluorescent lighting fixtures mounted on its cover, and was subdivided internally by wooden partitions so as to contain four individual cages.

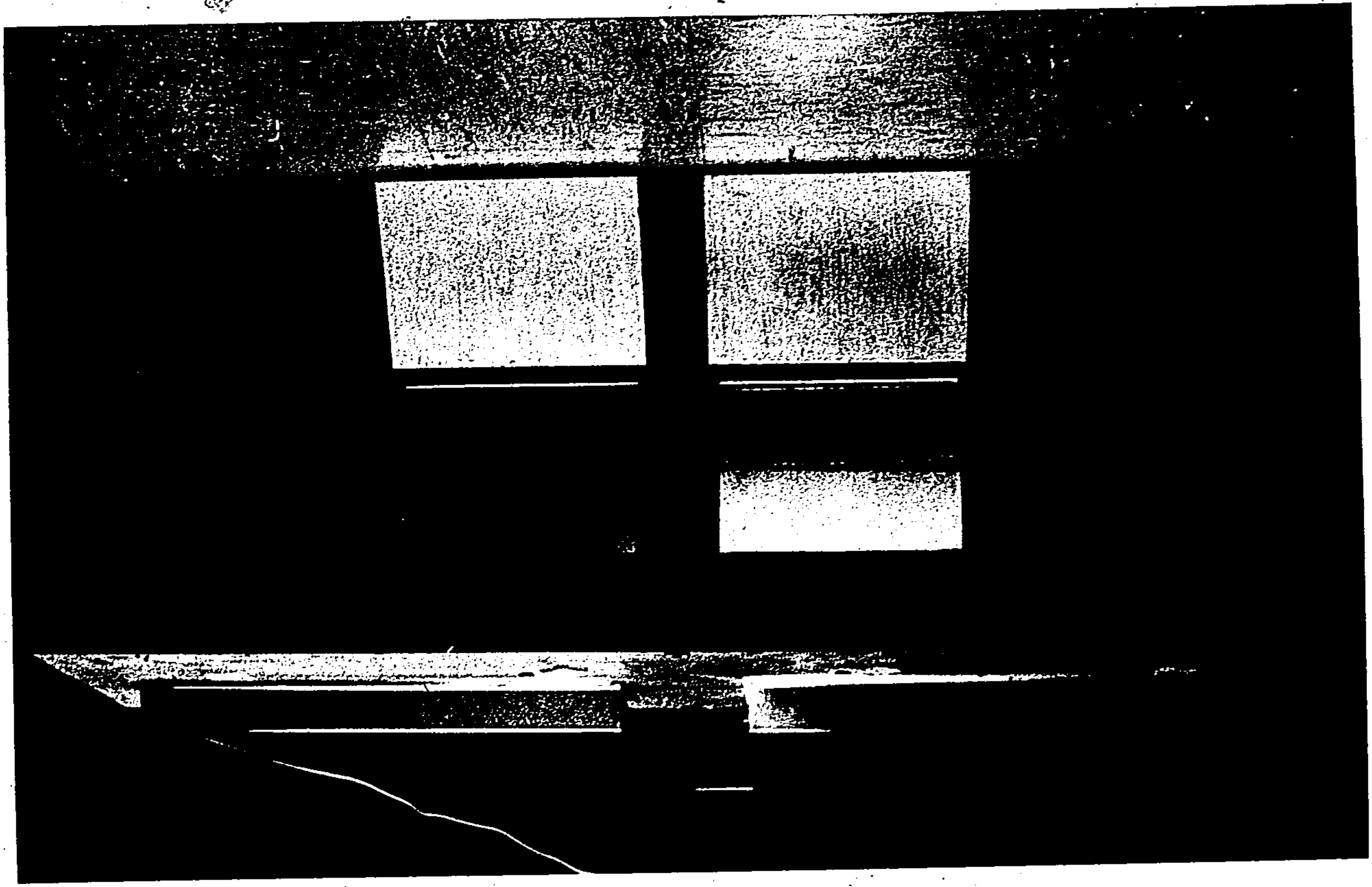
Insert Figure 4 about here

Procedure

General maintenance, rearing, and testing procedures were identical to those described in Chapter II except that isolation-reared subjects were left totally undisturbed until they were marked for identification 27 days after median eye-opening (eye-opening was observed through peepholes in the top of the isolation enclosure) and when they

FIGURE 4

Apparatus Used for the Rearing of Litters in Isolation



were removed for testing on the visual-cliff and in the shelter-field enclosure.

Shelter-Field Test Procedure

Twelve animals in each group (isolation- and nonisolation-reared) were used as control subjects in the shelter-field test and the remainder as experimental subjects.

Testing in the shelter-field enclosure was conducted as in previous experiments except that the visual stimulus was presented for 15 seconds rather than 30 seconds.

Results and Discussion

As was mentioned in the introduction to the present chapter, subjects reared in constant-light in open-cages were selected for isolation-rearing because pilot observations had indicated that subjects reared in constant-light tended to show little response to stimulus presentation during the shelter-field posttest. Comparison of the posttest performance of nonisolation-reared experimental subjects with that of nonisolation-reared control subjects, presented in Table 10, revealed, as expected, that stimulus presentation did not significantly affect the behaviour of experimental subjects during the posttest period on any measure (Mann-Whitney *U* tests, all *p*'s > 0.05). Similarly, data comparing isolation-reared experimental and control subjects' posttest behaviour, which are also presented in Table 10, revealed only small modifications in behaviour as a result of stimulus presentation. There was a significant increase in the experimental group's latency to first emerge from shelter (Mann-Whitney U test, transformed z score = 1.96, $p = 0.05$), but no significant effects of stimulus presentation on latency to reach shelter, or on total time spent in shelter (Mann-Whitney U test, both p's > 0.05).

Comparison of the posttest behaviour of isolation and nonisolation reared experimental subjects also revealed little effect of isolation-rearing on posttest behaviour. Isolation-rearing produced a significant effect on median latency to first emerge from shelter (Mann-Whitney U test, transformed z score = 2.12, $p < 0.05$), but no significant effects on latency to first reach shelter or total time spent in concealment (Mann-Whitney U test, both p's > 0.05).

Insert Table 10 about here

Analysis of the data obtained from fleeing subjects, presented in Table 11, revealed similarly that rearing in isolation had no significant effect on the percentage of experimental animals fleeing to shelter (Fisher's Exact Probability test, $p = 0.52$), or on total time spent in concealment (Mann-Whitney U test, $U = 5$, $p > 0.05$), but did significantly increase latency to first emerge from shelter (Mann-Whitney U test, $U = 0$, $p < 0.05$).

Insert Table 11 about here

In general, the data reviewed thus far would seem to indicate that isolation-rearing acted to increase responsiveness to stimulus presentation, but not sufficiently to account for differences in behaviour observed in previous experiments between subjects reared in environments

TABLE 10

POSTTEST PERFORMANCE OF EXPERIMENTAL AND CONTROL GROUPS

Group	Rearing condition	Median latency to reach shelter	Median latency to first emerge from shelter	Median total time spent in shelter
Experimental	Isolation (n = 22)	5.5	38.5	58.5
	Nonisolation (n = 12)	11.0	7.5	35.0
Control	Isolation (n = 12)	11.0	9.0	42.0
	Nonisolation (n = 12)	7.5	4.5	27.5

TABLE 11

POSTTEST PERFORMANCE OF ISOLATED AND NONISOLATED SUBJECTS

FLEEING TO PRESENTATION OF THE TEST STIMULUS

Rearing condition	Flight			Concealment		Footthumping	
	Entry <3 seconds		Median latency to reach shelter	Median latency to first emerge from shelter	Median total time spent in shelter		
	n	%				n	%
Isolation (n = 22)	9	40.9	1.0	66.0	81.0	0	00.0
Nonisolation (n = 12)	4	33.3	2.0	24.5	62.0	0	00.0

that either did or did not provide shelter. There were, in addition, two anomalous findings in the data from the present experiment which further reduce the likelihood that the relative isolation of subjects reared with shelter available was responsible for their increased responsiveness to stimulus presentation.

First, analysis of the pretest behaviour of isolated as compared with nonisolated subjects, presented in Table 12, revealed that isolation-reared subjects spent significantly more of the pretest period in concealment than did nonisolation-reared subjects ($F = 8.15$, $df = 2/57$, $p < 0.01$; Walker & Lev, 1953; see Appendix A for the Analysis of Variance summary table). Second, comparison of the posttest behaviour of isolation- and nonisolation-reared control groups, presented in Table 10, revealed a significant increase in total time spent in concealment (Mann-Whitney U test, $U = 35$, $p < 0.02$) on the part of the isolation reared control group. Thus, isolation-rearing produced changes in behaviour in the absence of stimulus presentation, while rearing in environments providing shelter did not do so.

Insert Table 12 about here

These findings suggest that the mechanism underlying differences in the responsiveness of isolated and nonisolated experimental subjects in the posttest period may be different from that responsible for differences in the responsiveness of open-reared and shelter-reared experimental animals discussed in Chapter III. In particular, the increases in concealment behaviour exhibited by isolation-reared subjects

TABLE 12

MEAN AMOUNT OF TIME SPENT IN THE SHELTER DURING THE PRETEST PERIOD BY EXPERIMENTAL AND CONTROL GROUPS

Rearing condition	Group					
	Experimental			Control		
	n	$\overline{X}$	S.E.	n	$\overline{X}$	S.E.
Isolation	22	64.6	4.8	12	67.0	12.0
Nonisolation	12	43.2	7.4	12	38.7	4.5

in response to stimulus presentation appear to be mediated by changes in exploratory behaviour in the shelter-field enclosure while the increased concealment behaviour of tunnel-reared subjects do not. It would thus seem reasonable to conclude that, although isolation-rearing can change responsiveness in the shelter-field test, rearing in relative isolation is not, in fact, responsible for the differences in the behaviour observed in the tunnel- and open-reared subjects of Chapter II.

CHAPTER VI

The Effect of a Brief Exposure to a Tunnel Environment on the Behaviour of Open-Reared Gerbils

In previous chapters, data have been presented indicating that differences in the posttest performance of tunnel- and open-reared subjects are not the result of rearing in darkness or rearing in isolation from large, moving objects. It remains possible, however, that the experience of moving into an enclosed area from an exposed one is sufficient in itself to potentiate response to stimulus presentation in the shelter-field test. If such experience is sufficient for the development of flight and concealment behaviour, then one might expect that even a brief exposure to an environment providing the opportunity for flight to shelter would be adequate to potentiate flight and concealment during the posttest period. In the present experiment, open-reared subjects were placed in a gerbil-constructed tunnel system for 24 hours prior to testing in the shelter-field enclosure in order to examine the effects of a brief experience with an area providing an opportunity for concealment on posttest performance.

Method

Subjects

Subjects were 72 gerbil pups, 18 of which were randomly selected from 6 litters reared in tunnel-systems, and 54 of which were randomly selected from 18 litters reared in open-cages.

Procedure

Rearing, handling and testing procedures for open- and tunnel-reared gerbils were identical to those described in Chapter II until visual-cliff testing had been completed. One week following visual-cliff testing, appropriately reared subjects were assigned to one of the four experimental or two control groups described below.

Experimental open-undisturbed (n = 18) and *experimental tunnel-undisturbed* (n = 6) subjects were left in the environment in which they had been reared (open-cage or tunnel) for an additional 24 hours before being tested in the shelter-field enclosure. *Experimental open-tunnel* (n = 18) subjects were reared in open-cages and placed in an enclosure containing an uninhabited, gerbil-constructed tunnel system for 24 hours before being tested in the shelter-field enclosure, while *experimental tunnel-open* (n = 6) subjects were reared in tunnel systems and placed in an open-cage for 24 hours before shelter-field testing.

All experimental groups received a 15-second presentation of the visual stimulus at the end of the pretest period in the shelter-field enclosure.

Control open-tunnel (n = 18) and *control tunnel-open* (n = 6) subjects were treated identically to their respective experimental groups (i.e., subjects reared in open-cages were given 24-hours experience in a tunnel system and subjects reared in tunnel-systems were given 24-hours experience in open-cages) except that they were not presented with the visual stimulus in the shelter-field enclosure at the beginning of the posttest period.

Results

Experimental open-undisturbed vs experimental open-tunnel

As is clear from examination of Table 13, which presents the data describing the posttest behaviour of open-reared groups, placing open-reared subjects in a tunnel system for 24 hours prior to shelter-field testing markedly decreased the latency of experimental open-tunnel subjects to reach shelter (Mann-Whitney U test, $U = 37$, $p < 0.002$), and significantly increased both their latency to first emerge from shelter (Mann-Whitney U test, $U = 48$, $p < 0.002$) and the total time spent in concealment (Mann-Whitney U test, $U = 51$, $p < 0.002$) in comparison with experimental open-undisturbed subjects.

Insert Table 13 about here

Table 14, which presents data obtained from fleeing subjects only, reveals that placing open-reared subjects in a tunnel environment for 24 hours increased the percentage of open-reared subjects fleeing in response to stimulus presentation ($X^2 = 15.1$, $df = 1$, Yates correction, $p < 0.05$) had a marked effect on their latency to first emerge from shelter (Mann-Whitney U test, $U = 24$, $p < 0.05$) and on the total time which they spent in shelter (Mann-Whitney U test, $U = 21$, $p < 0.05$).

Insert Table 14 about here

A One Way Analysis of Variance (Mendenhall & Ott, 1972) of the pretest data, shown in Table 15, revealed no significant differences in the mean amount of time spent in shelter by the three open-reared groups

TABLE 13

POSTTEST PERFORMANCE OF THE OPEN-REARED GROUPS

Group	Manipulation	Median latency to reach shelter	Median latency to first emerge from shelter	Median total time spent in shelter
Experimental open (n = 18)	Placed in tunnel	1.0	72.0	110.5
Experimental open (n = 18)	Undisturbed	19.0	11.5	45.0
Control open (n = 18)	Placed in tunnel	30.5	7.0	22.0

TABLE 14

POSTTEST PERFORMANCE OF FLEEING SUBJECTS IN OPEN-REARED GROUPS

Group	Manipulation	Flight			Concealment		Footthumping	
		Entry <3 seconds		Median latency to reach shelter	Median latency to first emerge from shelter	Median total time spent in shelter		
		n	%				n	%
Experimental open (n = 18)	Placed in tunnel	18	100.0	1.0	72.0	110.5	9	50.0
Experimental open (n = 18)	Undisturbed	6	33.3	2.0	42.0	75.0	2	33.3

(F = 2.89, df = 2/53, $p > 0.05$; the Analysis of Variance summary table is to be found in Appendix B).

Insert Table 15 about here

Experimental tunnel-undisturbed vs experimental tunnel-open

Table 16 presents data from animals left undisturbed in the tunnel and those placed in an open-cage for 24 hours prior to shelter-field testing. As is evident from examination of the table, placing tunnel-reared animals in an open-cage for 24 hours had no effect on shelter-field behaviour. No significant differences were found in the number of experimental subjects fleeing from the test stimulus, in latency to first emerge from shelter in the posttest period (Mann-Whitney U test, $U = 14$, $p > 0.05$), in total time spent in the shelter (Mann-Whitney U test, $U = 6$, $p > 0.05$) or in the number of subjects footthumping (Fisher's Exact Probability test, $p > 0.05$), as a result of the experimental manipulation.

Insert Table 16 about here

There were also no significant differences between pretest concealment behaviour of the three tunnel-reared groups ($F = 2.41$, df = 2/17, $p > 0.05$; see Appendix C for the relevant Analysis of Variance summary table), as inspection of the data in Table 17 reveals.

Insert Table 17 about here

TABLE 15

MEAN AMOUNT OF TIME SPENT IN THE SHELTER DURING THE PRETEST PERIOD BY OPEN-REARED GROUPS

Group	Manipulation	$\overline{X}$	S.E.
Experimental open (n = 18)	Placed in tunnel	40.1	4.7
Experimental open (n = 18)	Undisturbed	49.8	4.3
Control open (n = 18)	Placed in tunnel	41.6	4.2

TABLE 16

POSTTEST PERFORMANCE OF TUNNEL-REARED GROUPS

Group	Manipulation	Flight			Concealment		Footthumping	
		Entry <3 seconds		Median latency to reach shelter	Median latency to first emerge from shelter	Median total time spent in shelter		
		n	%				n	%
Experimental tunnel (n = 6)	Placed in open cages	6	100.0	1.0	118.0	118.0	4	66.7
Experimental tunnel (n = 6)	Undisturbed	6	100.0	1.0	105.0	116.0	3	50.0
Control tunnel (n = 6)	Placed in open cages	0	00.0	10.5	5.0	35.5	0	00.0

TABLE 17

MEAN AMOUNT OF TIME SPENT IN THE SHELTER DURING THE PRETEST PERIOD BY TUNNEL-REARED GROUPS

Group	Manipulation	$\bar{X}$	S.E.
Experimental tunnel (n = 6)	Placed in open cages	57.9	6.1
Experimental tunnel (n = 6)	Undisturbed	59.2	6.1
Control tunnel (n = 6)	Placed in open cages	55.2	8.8

Discussion

The results of the present experiment indicate that the differences in behaviour between animals reared in open laboratory cages and those reared in tunnel systems could be produced by simply exposing open-reared subjects to a tunnel environment for 24 hours. The 24-hour experience of a tunnel system was sufficient to potentiate the entire behavioural syndrome differentiating open-reared from tunnel-reared subjects. This finding has three implications: (1) it strengthens our earlier conclusions (Chapters IV and V) that neither rearing in relative darkness nor rearing in isolation from exposure to humans were necessary conditions for potentiating flight and concealment responses in tunnel-reared subjects, (2) the data indicate that rearing in open-cages did not produce visual deficits resulting in lack of responsiveness to the visual stimulus presented in the shelter-field test, and (3) it offers support for the hypothesis, developed in Chapter III, that the experience of running into concealment was the critical factor in the ontogeny of the behavioural syndrome shown by tunnel-reared gerbils in response to visual stimulation. It is, of course, possible that 24 hours spent in the dark or in isolation from visual stimulation were responsible for the observed effects of spending 24 hours in an environment providing cover but, in view of the fact that dark-rearing and isolation-rearing did not produce them, this seems unlikely.

The finding that the effects of tunnel-rearing were not reversed by 24 hours spent in open-cages suggests that once the flight and concealment responses were established, as the result of experience in the appropriate environment, they were relatively resistent to reversal by experience in a more open environment.

CHAPTER VII

Correlates of Within-Group Variability

Previous chapters have emphasized the importance of the physical environment in which gerbils are reared as a factor influencing the type of response which these animals exhibit when exposed to sudden visual stimulation. The majority of animals reared in the LDH, LDCH and LDT conditions responded to stimulus presentation by fleeing to shelter, while many of the animals in LDO, LDCO, and LDHO conditions responded to stimulus presentation by approaching the stimulus. However, as has been noted, there were subjects reared in environments providing shelter (LDH, LDCH, LDT) which approached the stimulus and animals reared in open environments which fled in response to its presentation. Several factors which might be responsible for this within-group dichotomy in response are examined in this chapter.

Each group in the preceding experiments was comprised of both male and female subjects and it is conceivable that sex of a subject was, in some measure, responsible for determining its behaviour in response to stimulus presentation. Examination of the data in Table 18, which presents an analysis of the behaviour of male and female subjects in experiments described in detail in Chapters III and IV, revealed that there were no significant differences either in the percentage of male and female subjects fleeing in response to stimulus presentation or in the median amount of time spent in concealment during the posttest period by male and female subjects. There is thus no support in the data for the hypothesis that differences in within-group response to stimulus presentation were the result of sex differences.

Insert Table 18 about here

It is possible that differences in behaviour among animals within any group which fled and did not flee in response to stimulus presentation during the posttest period reflected differences in their pretest behaviour. Table 19 examines the pretest behaviour of animals in experiments in Chapters III and IV in terms of their later response to stimulus presentation. As is evident from examination of the table, there was a difference in the pretest behaviour of potential fleeing and nonfleeing subjects. Within each housing condition, potential fleeing subjects spent a greater amount of the pretest period concealed than did potential nonfleeing subjects.

Insert Table 19 about here

Pearson product moment correlations between the time spent in shelter by individual subjects during the pretest and posttest periods, presented in Table 20, similarily reveals a relationship between the behaviour of individual subjects before and after stimulus presentation. In general, experimental animals which spent a large proportion of the pretest period concealed responded to stimulus presentation by spending a large proportion of the posttest period concealed.

Insert Table 20 about here

TABLE 18

POSTTEST PERFORMANCE OF MALE AND FEMALE EXPERIMENTAL SUBJECTS

Rearing condition	Males		Females			Median total time spent in shelter (posttest)		
	n	% fleeing	n	% fleeing	p[a]	Males	Females	U[b]
LDO (n = 26)	18	61.0	8	50.0	0.29	60.0	61.0	60 *
LDCO (n = 26)	10	40.0	16	56.2	0.16	25.5	49.0	46 *
LDHO (n = 26)	15	67.0	11	91.0	0.25	40.0	49.0	80 *
LDH (n = 26)	14	79.0	12	92.0	0.20	107.6	119.0	60 *
LDCH (n = 26)	12	100.0	14	86.0	0.28	112.5	107.5	50 *
LDT (n = 20)	11	100.0	9	100.0	[c]	118.0	119.0	39 *
DDO (n = 26)	10	30.0	16	25.0	0.33	35.0	18.0	63 *

[a] Fisher's exact probability, two-tailed.

[b] Mann-Whitney U value.

[c] Analysis not appropriate.

* *Not significant.*

TABLE 19

MEDIAN AMOUNT OF TIME SPENT IN THE SHELTER DURING THE PRETEST PERIOD BY POTENTIAL FLEEING AND NONFLEEING SUBJECTS

Rearing condition	Fleeing		Nonfleeing		U [a]
	n	Median	n	Media	
LDO (n = 26)	15	59.0	11	35.0	32 **
LDCO (n = 26)	13	48.0	13	35.0	42 *
LDHO (n = 26)	20	40.0	6	18.0	2.62 b *
LDH (n = 26)	22	46.0	4	17.0	2.08 b *
LDCH (n = 26)	24	44.0	2	32.0	1.18 b ns
LDT (n = 20)	20	47.0	--	----	
DDO (n = 26)	7	48.0	19	19.0	30 *

a U value, Mann-Whitney U test for N's <20.

b Transformed z score, Mann-Whitney U test for N's >20.

* $p < 0.05$, two-tailed test.

** $p < 0.02$, two-tailed test.

ns Not significant.

TABLE 20

PEARSON PRODUCT MOMENT CORRELATIONS BETWEEN TIME SPENT IN SHELTER DURING THE PRETEST AND TIME SPENT IN SHELTER DURING THE POSTTEST

Rearing condition	r
LDO (n = 26)	0.44 *
LDCO (n = 26)	0.39 *
LDHO (n = 26)	0.48 *
LDH (n = 26)	0.46 *
LDCH (n = 26)	0.49 **
LDT (n = 20)	0.24
DDO (n = 26)	0.57 **

* $p < 0.05$, two-tailed test.

** $p < 0.01$, two-tailed test.

The data discussed thus far indicate that differences in both flight and concealment behaviour in response to stimulus presentation reflect within-group differences in pretest concealment behaviour. It should be kept in mind, however, that between-group differences in pretest behaviour cannot explain between-group differences in posttest behaviour. As was shown in Tables 1 and 7, there were no differences among groups in pretest behaviour as a function of rearing condition. Still the finding that pretest behaviour is a good predictor of posttest behaviour within a given group raises an interesting question. Does pretest behaviour affect posttest behaviour or do both pretest and posttest measures reflect some underlying differences in arousal between animals responding to stimulus presentation and those failing to do so? The experiment described below was undertaken to determine whether or not the relationship between pretest and posttest behaviour was causal as well as correlational.

It was demonstrated in Tables 19 and 20 that experimental subjects fleeing in response to stimulus presentation during the posttest period spent a greater amount of time during the pretest period under shelter than did nonfleeing individuals and that experimental subjects spending a greater amount of time during the pretest period under shelter spent a greater proportion of the posttest period concealed. If the differences in pretest behaviour caused these differences in posttest behaviour, then forcing animals to spend additional time under shelter during the pretest period should both increase the proportion of subjects fleeing in response to stimulus presentation and increase the amount of time they spend in concealment during the posttest period. In the present experiment, groups of subjects were left in in the pretest condition until they had spent 90 seconds in the shelter and the effects of this treatment on posttest flight and concealment behaviour assessed.

Method

Subjects

Subjects were 75 Mongolian gerbils, randomly selected from 38 litters reared on a 12-hour light-dark cycle in open laboratory cages.

Procedure

Rearing, marking and handling procedures were identical to those described in Chapter II.

Shelter-Field Test Procedure

Fifty-seven of the 75 subjects were left undisturbed in the shelter-field enclosure until they had spent a total of 90 seconds in the shelter (Constant-time group) at which time 39 subjects were exposed to the visual stimulus for 15 seconds. Eighteen Constant-time control animals were left undisturbed after spending 90 seconds under shelter. Eighteen additional subjects (Self-timed group) were left in the shelter-field enclosure for 180 seconds before receiving 15 seconds of visual stimulation.

Results

Constant-time experimental subjects required a mean of 316.2 seconds (S.E. = 27.2) to accumulate 90 seconds under shelter during the pretest period, while Self-timed experimental subjects spent a mean of 51.4 seconds (S.E. = 13.3) of their 180-second pretest period under shelter.

The main results of the present experiment, data describing the posttest behaviour of Constant-time and Self-timed experimental groups, are presented in Table 21. It is clear from examination of the table that forcing subjects to spend 90 seconds in the shelter during the pretest period had profound effects on posttest behaviour. The Constant-time experimental group showed significant decreases in latency to reach shelter (Mann-Whitney *U* test, transformed *z* score = 2.48, $p < 0.01$) and significant increases both in latency to first emerge from shelter (Mann-Whitney *U* test, transformed *z* score = 3.06, $p < 0.01$) and in total time spent in concealment (Mann-Whitney *U* test, transformed *z* score = 3.12, $p < 0.01$) in comparison with the Self-timed experimental group.

Insert Table 21 about here

Table 22 presents the data obtained from fleeing subjects in the Constant-time and Self-timed experimental groups. As a result of the pretest manipulation, there was an increment in the percentage of animals fleeing ($X^2 = 4.3$, Yates correction, *df* = 1, $p < 0.05$) and fleeing animals during the posttest period in the Constant-time group showed significant increases in latency to first emerge from shelter (Mann-Whitney *U* test, transformed *z* score = 2.00, $p < 0.05$) and in total time spent in shelter (Mann-Whitney *U* test, transformed *z* score = 2.45, $p < 0.01$).

Insert Table 22 about here

TABLE 21

POSTTEST PERFORMANCE OF EXPERIMENTAL AND CONTROL GROUPS

Group	Median latency to reach shelter	Median latency to first emerge from shelter	Median total time spent in shelter
Constant-time (experimental, n = 39)	1.0	80.0	110.0
Self-timed (experimental, n = 18)	7.5	9.5	54.0
Constant-time (control, n = 18)	19.5	6.5	24.5

TABLE 22

POSTTEST PERFORMANCE OF CONSTANT-TIME AND SELF-TIMED FLEEING SUBJECTS

Group	Flight			Concealment		Footthumping	
	Entry <3 seconds		Median latency to reach shelter	Median latency to first emerge from shelter	Median total time spent in shelter		
	n	%				n	%
Constant-time (n = 39)	28	72.0	1.0	99.0	117.0	16	57.0
Self-timed (n = 18)	7	39.0	1.0	85.0	102.0	2	29.0

Discussion

The results of the experiment described above indicate that increasing the time spent in concealment during the pretest period can significantly increase responsiveness during the posttest period. However, the manipulation employed, that of forcing subjects to accumulate 90 seconds in the shelter, is confounded because Constant-time animals not only spent more time in concealment during the pretest period than Self-timed subjects, but also spent more time in the test enclosure and engaged in a greater number of entrances to and exits from the shelter in the pretest period than did the members of the Self-timed group. It has not been possible to experimentally disassociate these three variables in order to determine which aspect of the pretest experience of Constant-time subjects was responsible for their increased responsiveness during the posttest period.

One interpretation of this finding is that the extended pretest period experienced by the Constant-time subjects acted, as did the 24-hour exposure to a tunnel environment, to provide Constant-time open-reared subjects with experience of an environment providing the opportunity for concealment. This experience during the pretest might then have potentiated flight and concealment behaviour during the posttest. We have not yet directly investigated the possibility that very brief exposure to an environment providing shelter outside the shelter-field situation itself, is sufficient to increase flight and concealment behaviour in response to sudden stimulation.

The results of the analysis in the present chapter indicates that the differences between fleeing and nonfleeing subjects within groups were (1) not a function of sex and (2) that, within a group, fleeing and nonfleeing subjects could be differentiated on the basis of their pretest concealment behaviour. The implications of the second of these findings is not clear in that a factor correlated highly with within-group differences in posttest behaviour failed to correlate with between-group differences in posttest behaviour. It is possible that animals with no experience of concealment during infancy were able to take advantage of the very brief opportunity provided by the pretest period to potentiate, at least to a limited extent, the flight and concealment which, as was demonstrated in Chapter VI, could be potentiated by a 24-hour experience of opportunity for concealment.

CHAPTER VIII

The Relationship of the Shelter-Field Test to Measures of Animal Emotionality

The measurement of animal emotionality is a problem of long-standing within psychology and a variety of procedures have been developed for assessing the effects of genotype and early experience on the emotional behaviour of nonhuman subjects (Archer, 1973; Candland, 1971; Hall, 1941). Among the many measures employed, those of freezing, latency to enter a novel enclosure, time spent concealed in a covered area, response to sudden stimulation and behaviour in the open field have historically been of greatest importance. The shelter-field test used in experiments described here for quantifying responsiveness to sudden visual stimulation incorporates several of these more traditional measures of emotionality. In the present section, the relationship between behaviour observed in the shelter-field test and the measures of emotionality referred to above will be discussed.

Freezing

Freezing, which has been defined as crouching and remaining immobile, is one of the more commonly employed measures of emotionality in small rodents, the assumption being that emotional subjects will freeze more frequently than nonemotional ones (Doyle & Yule, 1959; Hall, 1936; Higginson, 1930; Levine, 1956; Schaefer, 1963; Yoshioka, 1943). In the shelter-field test, many subjects were observed to freeze in the enclosure during the pretest period and it might be expected that subjects which exhibited this behaviour in the pretest would be more likely to flee at the presentation of the test stimulus in the posttest than subjects which did not freeze. As is apparent from Table 23, which presents an analysis of the relationship between freezing during the pretest period and flight during the posttest period, there was a marked tendency for rearing conditions which increased fleeing (LDH, LDCH, LDT) to increase freezing ($\underline{X}^2 = 19.2$, $\underline{df} = 5$, $\underline{p} < 0.01$). However, subjects in each rearing condition which exhibited freezing behaviour during the pretest period were no more likely to flee during the posttest period than those which did not freeze during the pretest.

Insert Table 23 about here

Latency to enter shelter

It has been argued that emotional animals should be more hesitant to approach and enter a novel area than nonemotional ones. The "hole in the wall" test (McClearn, 1959), in which subjects are placed in a compartment providing escape through a small opening, measures latency to escape as an index of emotionality. In the shelter-field test, the equivalent of the "hole in the wall" measure is to be found in the determination of subjects' latency to first enter shelter prior to the commencement of the pretest period. Pearson product moment correlations of this measure with posttest measurements of concealment were either nonsignificant or significantly negative (see Table 24).

Insert Table 24 about here

TABLE 23

ANALYSIS OF THE RELATIONSHIP BETWEEN FREEZING AND FLEEING BEHAVIOUR IN THE SHELTER-FIELD TEST FOR SUBJECTS IN CHAPTERS III AND IV

Rearing condition	Freezing	Fleeing	Fleeing		Not fleeing		p[a]
			Freezing	Not freezing	Freezing	Not freezing	
LDO (n = 26)	6	15	3	12	3	8	0.32
LDCO (n = 26)	8	13	4	9	4	9	0.33
LDHO (n = 26)	8	20	5	15	3	3	0.20
LDH (n = 26)	13	22	10	12	3	1	0.25
LDCH (n = 26)	13	24	11	13	2	0	0.24
LDT (n = 20)	15	20	15	5	0	0	b
DDO (n = 26)	7	7	0	7	7	12	0.08

[a] Fisher's exact probability.

[b] Analysis not appropriate.

TABLE 24

PEARSON PRODUCT MOMENT CORRELATIONS BETWEEN LATENCY TO FIRST ENTER SHELTER PRIOR TO COMMENCEMENT OF THE PRETEST PERIOD AND TOTAL TIME SPENT IN THE SHELTER DURING THE POSTTEST PERIOD BY SUBJECTS IN CHAPTERS III AND IV

Rearing condition	r
LDO (n = 26)	0.02
LDCO (n = 26)	-0.12
LDHO (n = 26)	0.30
LDH (n = 26)	-0.47 *
LDCH (n = 26)	0.20
LDT (n = 20)	0.02
DDO (n = 26)	-0.06

* $p < 0.05$, two-tailed test.

Time spent in concealment

A number of investigators have proposed that emotional animals will spend a greater percentage of time under shelter than unemotional ones (Billingslea, 1941; Stone, 1932). As discussed in Chapter VII, data from the shelter-field test revealed a significant correlation between the pretest concealment and posttest concealment behaviour within each rearing condition. Animals which fled to the presentation of the test stimulus spent more time under shelter in both pre- and posttest periods than did nonfleeing subjects.

Presentation of sudden stimulation

The response of animal subjects to the presentation of a sudden stimulus, either auditory or visual, has often been used as a measure of reactivity (Archer, 1974; Dykman, Murphree & Peters, 1969; Fentress, 1968 a , 1968 b ; Moyer, 1963; Patrick, 1931) and forms the basis of the shelter-field test. In many earlier studies, stimulation was presented to subjects in a barren environment and freezing in response to presentation of the stimulus was the measure employed. In the shelter-field enclosure, freezing was never observed in response to stimulus presentation and, as discussed in Chapter III, subjects either fled from or actively investigated the stimulus.

In the shelter-field test there are available three measures of response to stimulus presentation: time to first enter shelter, time to first emerge from shelter, and the proportion of the posttest period spent in shelter. Each has some validity as a measure of responsiveness. The most reactive subjects should be those fleeing most rapidly, those most hesitant to emerge from under shelter and those spending the greatest proportion of time under shelter during the posttest period. If, in fact, these three aspects of behaviour represent a single arousal syndrome, one would expect latency to reach shelter to be inversely correlated with both latency to emerge from shelter and proportion of time spent in concealment during the posttest. As can be seen in Table 25, which presents Pearson product moment correlations between both latency to reach shelter and time to first emerge and latency to reach shelter and proportion of time spent in shelter; time to enter shelter was, in fact, highly negatively correlated with both latency to emerge from shelter and proportion of time spent in shelter for all experimental groups. Examination of the same correlations in control groups, however, revealed an irregular pattern of mainly nonsignificant correlations.

Insert Table 25 about here

Footthumping and the shelter-field test

As was indicated in Chapter II, only subjects exhibiting the flight response to presentation of the visual stimulus engaged in footthumping behaviour. That footthumping is an index of high arousal states is indicated by consideration of the circumstances in which footthumping is known to occur in gerbils. In the wild, it has been observed to occur when gerbils have fled from an observer into their burrow, while they were being handled in traps, and during both sexual and agonistic intraspecific encounters (Daly & Daly, 1973). In the laboratory, footthumping has been observed following electrical brain stimulation (Kramis & Routtenberg, 1969), following electric shock delivered to the foot (Routtenberg & Kramis, 1967), following intromission (Kuehn & Zucker,

TABLE 25

PEARSON PRODUCT MOMENT CORRELATIONS BETWEEN (a) TIME TO ENTER SHELTER AND TIME TO FIRST EMERGE FROM SHELTER AND (b) TIME TO ENTER SHELTER AND PROPORTION OF TIME SPENT IN SHELTER BY EXPERIMENTAL AND CONTROL SUBJECTS IN CHAPTERS III AND IV

Group	Rearing condition	(a)	(b)
		r	*r*
Experimental	LDO (n = 26)	-0.45 *	-0.38 *
	LDCO (n = 26)	-0.41 *	-0.50 **
	LDHO (n = 26)	-0.46 *	-0.69 **
	LDH (n = 26)	-0.53 **	-0.75 **
	LDCH (n = 26)	-0.40 *	-0.76 **
	LDT (n = 20)	[a]	[a]
	DDO (n = 26)	-0.39 *	-0.63 **
Control	LDO (n = 6)	0.73	0.94 **
	LDCO (n = 6)	0.88 *	0.09
	LDHO (n = 6)	-0.28	-0.29
	LDH (n = 6)	0.47	0.24
	LDCH (n = 6)	-0.50	-0.48
	LDT (n = 6)	-0.01	-0.04
	DDO (n = 6)	-0.07	0.32

[a] Correlation not applicable.

* $p < 0.05$, two-tailed test.

** $p < 0.01$, two-tailed test.

1968), during aggressive encounters (Gallup & Waite, 1970), following handling and following introduction of a novel stimulus into a gerbil's home environment (Spatz & Granger, 1970). As both Spatz and Granger (1970) and Routtenberg and Kramis (1967) have indicated, footthumping in gerbils appears to be correlated with high levels of arousal. The fact that subjects which fled in the shelter-field test in response to stimulus presentation were the only subjects to footthump suggests that they were the more highly aroused or reactive individuals.

<u>Open field performance</u>

The advantages of both reasonable validity and consistency of correlations among emotionality measures will become apparent in consideration of the most commonly employed measure of animal emotionality, the open field.

High levels of emotionality in the open field are assumed to be associated with excessive elimination (Broadhurst, 1957, 1958 a; Hall, 1934) and low rates of ambulation (Dennenberg, 1967; Hall, 1936). Unfortunately, highly emotional strains, such as the wild rat (Galef, 1970; King & Donaldson, 1929; Richter, 1954; Stone, 1932) do not differ from less emotional domesticated strains in either of these two measures of emotionality (Boice, 1966; Broadhurst, 1958 b; Farris & Yeakel, 1945). Thus, the validity of attempts to measure emotionality in terms of defecation, urination, and locomotion in the open field is dubious. Further, as Archer (1974) has demonstrated, there is often no consistent correlation between locomotion and elimination in the open field enclosure. For example, increasing the size of the test enclosure alters locomotory patterns, but leaves defecation and urination unaffected, while increasing light intensity alters patterns of defecation without affecting locomotion (Broadhurst, 1957). In other experiments, elimination and locomotion have been reported to be negatively correlated (Dennenberg & Morton, 1962), positively correlated (Brain & Nowell, 1969), and uncorrelated (Anderson, 1938).

Discussion

In general, the quantification of animal emotionality has proved to be a difficult problem in that animals described as emotional in one test situation are not necessarily the ones appearing emotional in a second situation (Anderson, 1938; Bindra & Thompson, 1954; Billingslea, 1940, 1941, 1942; Willingham, 1956; O'Kelly, 1940). As Yoshioka (1932) has stated, it is difficult to predict the excitability of an animal in a new situation on the basis of its behaviour in a previous one. Each situation may arouse the same individual differently. For example, Anderson (1938) found that correlations of exploration in the open-field with four other measures of emotionality were not significant, ranging from -0.02 to -0.17.

There is, of course, a similar problem with the shelter-field test. It is possible that animals appearing to be reactive in the shelter-field enclosure would not appear so in other testing situations. The problem in the present series of experiments is, perhaps, particularly pressing in that there is a confounding between the independent and dependent variables, i.e., rearing in conditions providing shelter provided experience with an environment very similar to that in which shelter-field testing was conducted. It would be particularly helpful, therefore, to have available a second measure of reactivity as disparate as possible from the shelter-field situation in order to determine that the effects of rearing conditions seen in the shelter-field test are not unique to that testing situation.

As mentioned above, all subjects in the preceeding experiments were tested on the visual-cliff prior to testing in the shelter-field enclosure. Although the visual-cliff has been primarily used as a measure of visual acuity, several investigators have suggested that visual-cliff performance is influenced by the emotionality of subjects (Lore & Sawatski, 1969; Routtenberg & Glickman, 1964; Thiessen, Lindzey, Blum, Tucker & Friend, 1968). With particular reference to gerbils, Thiessen and his co-workers (1968) have suggested that random performance and short latencies of choice behaviour on the visual-cliff may be the result of an emotional factor rather than visual deficits. Other investigators have presented data describing behaviour on the visual-cliff which are most readily interpreted in terms of the reactivity of the subject, although those workers have not discussed the data in that framework (Nealey & Edwards, 1960; Rosenblum & Cross, 1963; Walk & Gibson, 1961).

In the following chapter, the behaviour of gerbils on the visual-cliff is described in terms of its relationship to their performance in the shelter-field enclosure in order to determine the reliability of the shelter-field test as a measure of the effects of the physical-rearing environment on behaviour.[1]

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[1] See Appendix D

CHAPTER IX

The Relationship of Behaviour on the Visual-Cliff to Behaviour in the Shelter-Field

Our initial intention was to use performance on the visual-cliff as an index both of visual deficits (Gibson, Walk & Tighe, 1959; Gantz & Fitch, 1969; Hein & Diamond, 1972) and of reactivity. However, as consideration of the data described in the present chapter will make clear, the behaviour of subjects was such as to preclude use of the visual-cliff as a procedure for assessing visual acuity. The chief weakness of the visual-cliff test is that, although consistent preferences by a subject or group of subjects for the shallow side of the apparatus is readily interpretable as demonstration of the ability to discriminate the deep from the shallow side, all other outcomes are resistent to interpretation. If subjects refuse to make a choice or descend randomly to deep and shallow sides, it is impossible to determine the causes of this failure to discriminate. Fortunately, the results of the experiment reported in Chapter VI indicate that differences in behaviour in the shelter-field test among subjects maturing in different rearing environments were not the result of differences in visual acuity. Therefore, it was not necessary to use visual-cliff performance to detect visual deficits in order to interpret the data reported in Chapters II through V. We will, instead, concentrate on the data obtained on the visual-cliff as an index of reactivity.

Method

Subjects

Subjects were 78 open-reared, 78 house-open reared, 78 house-reared, 78 cliff-house reared, and 20 tunnel-reared gerbils.

Procedure

General Maintenance

All tunnel-reared subjects were maintained on a 12-hour light-dark cycle, as were 26 of each of the groups of 78 subjects. A further 26 subjects from each rearing condition were maintained in constant light and the last 26 in constant dark. Methods of rearing, handling and marking were those described in Chapter II.

Visual-Cliff Apparatus

A modified Model II visual-cliff (Walk & Gibson, 1961) was constructed by suspending a plexiglass plate (24 x 24 x 1/4 in.) 12 inches above the floor of a plywood box (24 in. long x 24 in. wide x 36 in. high). Blue-and-white checkered (1 x 1 in.) material was inserted directly below one-half of the plexiglass plate (the shallow side) and 12 inches below the other half (the deep side). A wooden centerboard (24 in. long x 3-3/4 in. wide x 3 in. high) bisected the plexiglass surface, concealing the junction of the deep and shallow sides. Illumination of the deep and shallow sides was equated by adjusting fluorescent lamps located under the centerboard until they appeared equally bright in a Nikon photomic FT_N Finder. Behaviour in the visual-cliff apparatus was observed via closed-curcuit television.

Visual-Cliff Procedure

Prior to testing, all subjects reared in environments providing darkness were light-adapted for 20 minutes. Subjects were then tested individually on the visual-cliff in a quiet, well-illuminated room. Each subject was placed at one end of the centerboard, facing the opposite end, and left undisturbed until it either descended to the plexiglass surface or had remained on the centerboard for 5 minutes, at which time it was returned to its home cage. Each subject was tested once a day for five consecutive days with the experimenter recording the latency for the subject to leave the platform and the side to which it descended. The centerboard and plexiglass surface were cleaned with a moist cloth at the conclusion of each test trial.

Shelter-Field Test Procedure

One week following completion of visual-cliff testing, all subjects were tested in the shelter-field enclosure as described in Chapter II.

Results

The main results of the present experiment are presented in Table 26. As is apparent from inspection of the data, the number of subjects descending from the centerboard on one or more trials varied as a function of rearing condition, with subjects reared with shelter available showing a greater probability of descending than those reared without shelter available ($\underline{X}^2 = 25.5$, $\underline{df} = 4$, $\underline{p} < 0.01$). Furthermore, subjects which fled in response to presentation of the test stimulus in the shelter-field enclosure were far more likely to descend from the centerboard in the visual-cliff apparatus than those which did not flee.

Insert Table 26 about here

Table 27 presents data describing the latency to descend and initial choice (deep or shallow side) of subjects on the visual-cliff. As can be seen by examination of the table, subjects in all groups showed a slight and, in most cases, significant preference for the shallow side. There were, however, no significant differences among groups in initial choices to the shallow or deep side as a function of rearing condition ($\underline{X}^2 = 1.74$, $\underline{df} = 4$, $\underline{p} > 0.05$).

Insert Table 27 about here

Comparison of the latencies to descend and the percent of shallow-side choices of subjects fleeing and not fleeing during the shelter-field posttest are presented in Table 28. Analysis of the data revealed that the latency of nonfleeing subjects to descend from the centerboard on the visual cliff was significantly longer than that of fleeing subjects (all $\underline{p}$'s > 0.05) and that nonfleeing subjects were somewhat more likely to chose the shallow side than fleeing subjects.

Insert Table 28 about here

Discussion

The observations described above offer support for the suggestion that the effects of the physical rearing environment on reactivity were

TABLE 26

ANALYSIS OF THE RELATIONSHIP BETWEEN DESCENT ON THE VISUAL-CLIFF AND FLIGHT IN THE SHELTER-FIELD

Rearing condition	Subjects descending from visual-cliff platform		Subjects fleeing in the shelter-field enclosure		Fleeing		Not fleeing		Chi square
	n	%	n	%	Descend	Not descend	Descend	Not descent	
Open (n = 78)	45	57.7	32	41.0	29	3	16	30	21.9 *
House-open (n = 78)	53	67.9	51	65.4	45	6	8	19	39.9 *
House (n = 78)	66	84.6	72	92.3	63	9	3	3	a
Cliff-house (n = 78)	64	82.0	68	87.2	59	9	5	5	a
Tunnel (n = 20)	19	95.0	20	100.0	19	1	0	0	a

* $p < 0.001$, two-tailed test.

[a] Statistical analyis not appropriate.

TABLE 27

PERCENTAGE OF INITIAL DESCENTS TO THE SHALLOW SIDE AND LATENCY FOR SUBJECTS TO DESCEND FROM THE VISUAL-CLIFF PLATFORM

Rearing condition	Initial choices to the shallow side			Latency	
	n	%	z [a]	$\overline{X}$	S.E.
Open	45	66.7	2.39 *	71.3	12.5
House-open	53	71.2	2.75 **	78.2	11.6
House	66	60.6	1.85 ns	41.3	7.5
Cliff-house	64	65.1	2.62 **	72.0	10.2
Tunnel	19	62.7	0.36 [b] ns	19.6	3.7

a Transformed z score, binomial test.

b Binomial probability value.

* $p < 0.05$, two-tailed test.

** $p < 0.01$, two-tailed test.

ns Not significant.

TABLE 28

VISUAL-CLIFF PERFORMANCE OF DESCENDING SUBJECTS WHICH FLED AND DID NOT FLEE IN THE SHELTER-FIELD ENCLOSURE

Rearing condition	Descend from the visual-cliff platform									
	Fled in shelter-field test					Did not flee in shelter-field test				
	Shallow initial choices			Latency		Shallow initial choices			Latency	
	n	%	$\underline{z}$ [a]	$\overline{X}$	S.E.	n	%	$\underline{p}$ [b]	$\overline{X}$	S.E.
Open (n = 45)	29	55.2	0.56 ns	23.8	3.3	16	87.5	0.004 **	158.0	20.5
House-open (n =53)	45	71.1	2.98 **	43.4	6.3	8	75.0	0.290 ns	225.9	12.1
House (n = 66)	63	60.3	1.76 ns	31.4	6.2	3	66.7	0.410 ns	233.0	30.2
Cliff-house (n=64)	59	63.2	2.10 *	50.9	7.5	5	80.0	0.380 ns	256.3	12.2
Tunnel (n = 19)	19	62.7	0.36 [b]ns	19.6	3.7	0	----	-----	-----	----

[a] Transformed $\underline{z}$ score.

[b] Binomial probability value.

* $\underline{p} < 0.05$, two-tailed test.

** $\underline{p} < 0.01$, two-tailed test.

ns Not significant.

not specific to the shelter-field test. Subjects reared in conditions providing shelter had both a greater probability of descending from the centerboard on the visual-cliff and a higher probability of fleeing in the shelter-field enclosure.

The observation that flight in the shelter-field enclosure was correlated with short latencies to descend from the centerboard on the visual-cliff indicates that the shelter-field test has predictive validity in an alternative testing situation. The finding that rearing in enclosures providing shelter increases probability of descent on the visual-cliff, as well as increasing flight and concealment behaviour in the the shelter-field test, suggests that the increased responsiveness of subjects reared in environments providing shelter in the shelter-field enclosure was not due to similarities between shelter-rearing environments and the shelter-field testing situation. On the contrary, rearing in environments providing shelter seems to produce a general increment in reactivity in Mongolian gerbils.

The fact that subjects in every rearing condition showed a preference for the shallow side indicates that the choice of a side to which to descend on the visual-cliff was to some extent directed by visual cues. However, the observation that higher probabilities of shallow side choice were associated with long latencies of descent and an absence of flight in the shelter-field enclosure suggests that subject reactivity is a factor in determining visual-cliff performance. The data suggest that reactive animals were less visually directed than nonreactive ones and may have been to some extent simply seeking to escape from the exposed centerboard.

CHAPTER X

Conclusions

The results of the experiments reported above support the hypothesis that the physical environment in which animals are reared has an important influence on the ontogeny of behaviour (King, 1968; Lehrman, 1953, 1956, 1970). The dichotomy of response of wild- and laboratory-reared gerbils to sudden visual stimulation is seen to result from differences in the physical environment in which gerbils are reared by their parents in the laboratory and in their natural habitat. By implication, the stereotypy observed in the response of wild gerbils to the approach of humans could be interpreted as resulting from the constancy of the environment in which wild-reared gerbils mature. Thus, the constancy in the behaviour of each new generation of wild gerbils may result from the choices of members of the preceding generation of sites in which to rear their offspring. If this hypothesis is correct, then the response of gerbils in the wild to humans is an instance of the social transmission of an acquired characteristic, falling within the bounds of the definition proposed by Galef (in press). That is, long-term homogeneity of behaviour is, in this case, the result of a social interaction.

It is often assumed that the relative docility and tameness of domesticated strains results from changes in the gene pool caused by the workings of artificial selection on populations reproducing in captivity (Hale, 1962). Although artificial selection is certainly responsibile for differences in the behaviour of domestic and wild strains of many species (e.g., the rat and mouse), the results of the present investigation suggest that domestication may result from even short-term alterations in experience produced by rearing in captivity as well as by alterations in the genetic substrate caused by selective breeding. The rapidity with which many domesticated populations revert to feral behaviour upon release into natural environments (Minckler & Pease, 1938) supports this interpretation.

It is thus possible that the phenomenon of domestication is not, in fact, a unitary one but can result from either of two mechanisms or their interaction. Both changes in genetic material resulting from artificial selection and changes in responsiveness to stimulation resulting from early experiences in captivity are sufficient to produce tameness and docility in naturally wild populations.

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APPENDICES

APPENDIX A

ANALYSIS OF VARIANCE SUMMARY TABLE OF PRETEST DATA PRESENTED IN TABLE 12

Source	df	SS	MS	F
Factor A (isolation vs nonisolation)	1	5814.30	5814.30	8.15 *
Factor B (experimental vs control)	1	124.04	124.04	0.17 **
AB	1	1250.25	1250.25	1.75 **
Error	54	38536.00	713.63	
Total	57	45724.59		

* $p < 0.01$, two-tailed test.

** Not significant.

APPENDIX B

ANALYSIS OF VARIANCE SUMMARY TABLE OF PRETEST DATA PRESENTED IN TABLE 15

Source	df	SS	MS	F
Factor A (manipulation)	2	1902.56	951.28	2.89 *
Error	51	16814.75	329.70	
Total	53	18717.31		

* Not significant.

APPENDIX C

ANALYSIS OF VARIANCE SUMMARY TABLE FOR PRETEST DATA PRESENTED IN TABLE 17

Source	df	SS	MS	F
Factor A (manipulation)	2	916.8	458.4	2.41 *
Error	15	2854.8	190.3	
Total	17	3371.6		

* Not significant.

APPENDIX D

Although it might be argued that rearing in a tunnel, with its three-dimensional substrate, would provide experience to the young gerbil involving descent from a high exposed place to a lower, protected area and that the visual-cliff test is, therefore, confounded with rearing environment as is the shelter-field test, there is reason to believe that such a response-transfer interpretation of the data presented in Chapter IX is not appropriate. First, as can be seen in Table 26, the percentage of subjects descending from the visual-cliff platform in environments which provide shelter but no experience with a cliff (House) does not differ from that of subjects descending in environments which provide shelter and experience with a cliff (Cliff-House). Second, data to be presented elsewhere, revealed that subjects reared in cage conditions providing experience with a cliff but no experience with a shelter (Cliff-open) make fewer descents from the visual cliff platform that do subjects which have a shelter present in the rearing environment.