Experiential Deprivation and Later Behavior

Stress of emergence is postulated as the basis for behavioral deficits seen in dogs following isolation.

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Deprivation of sensory and motor experience during early life has been blamed for a considerable portion of mental retardation and social inadequacy in man. A controversy exists between proponents of the developmental interpretation and proponents of the defect interpretation of such inadequacies (*1*). In animals the relationship between experiential deprivation and behavioral development has been widely studied and reviewed (*2–4*). Other experiments have dealt with the effects of an enriched environment (5). These two types of investigation are fundamentally similar except for reversal of the designation of experimental and control groups.

Techniques and duration of deprivation vary widely in experimental studies, as do the criteria by which the results of deprivation are evaluated. King (*6*) has called for more parametric studies in this area, but relatively few have been performed, possibly because of the potential magnitude and complexity of such investigations. By imposing different types of deprivation which are primarily either (i) sensory or (ii) motor or social, attempts have been made to determine which aspects of experience are most critical in behavioral development. Evidence exists that an organism is most vulnerable to deprivation or stimulation at certain ages (critical periods), though this interpretation has been questioned (7).

The interpretation of the deprivation experiment has been debated. Hunt (*2*) opposes strongly the idea that behavior is genetically programmed and unfolds along with morphological growth and differentiation. Lorenz (*4*) believes that the appearance of species-specific patterns in organisms deprived of ordinary prior experience is evidence for the intrinsic determination of much behavior. Despite funereal pronouncements, the nature-nurture issue seems still a lively corpse. Most present-day psychologists and biologists are middle-of-the-roaders in this matter; they speak of behavior as the outcome of an interaction or coaction of heredity and environment.

This article is largely concerned with the effects of experiential deprivation in dogs. In the 1950's, McGill University was a center for such studies; the subjects were Scottish terriers. Excessive exploratory activity, whirling, immaturity of emotional responses, and deficiencies of response to pain were recorded as outcomes of severe or moderate restriction (*8–10*). The deficits were interpreted in terms of Hebb's (*11*) theory of the need for a long period of "perceptual learning" for organization of the nervous system. Isolation is primarily passive withholding of essential information. Fisher (*12*) reported similar results and interpreted them similarly, but emphasized the reversibility of isolation effects to a greater extent than the McGill group did.

More recently the Hebbian interpretation of the effects of isolation has been challenged by Lessac (*13*), who proposes that the inappropriate behavior of dogs after isolation is due to destructive or interfering effects upon previously organized processes. He provides evidence that, following isolation, dogs often perform more poorly than they did before isolation.

A third view, defended in this article, also emphasizes the active rather than the passive role of experiential deprivation, but considers that behavioral deficits following isolation result more from competing emotional responses than from failure of behavioral organization during isolation or from loss of established patterns (*14*). Actually, this view is compatible with Lessac's view (*13*) that isolated animals become habituated to a very low average level of stimulation and respond to moderate stimulation as normally reared animals respond to violent stimulation.

Programmed Life Histories

The Jackson Laboratory program on experiential deprivation in dogs was initiated as a series of studies on the persistent effects of modified early experience. In all the experiments we have used the same basic isolation procedure. Puppies are removed from their mother at the age of 21 days, when they can for the first time survive independently without special handling. They are placed in cages about 60 centimeters square which permit feeding, watering, and removal of wastes without physical or visual contact with a human being. The cages are furnished with a one-way observation window, are kept constantly lighted at a low level of illumination, and are ventilated by a blower, which provides some masking of external sounds. Upon the monotonous background we can impose procedures such as removal of the puppies from the cage for varying periods at selected ages, provision of playthings, provision of opportunities for visual exploration, or rearing with another puppy. The technique permits rather precise programming of all aspects of a subject's early life history.

In all experiments the effects of isolation have been evaluated by means of an arena test, and some subjects have been tested for discrimination learning in a modified Wisconsin general test apparatus. The arena test includes 7½ minutes of observation of the subject's responses to a human handler, to toys, and to another puppy of the same age. The arena is 3½ meters square and is surrounded by an opaque barrier 1 meter high. The floor is divided by painted lines into nine equal squares. The procedure has been essentially constant over the series of experiments, but the scoring system has been radically altered. I shall not describe our original scoring procedure, except to indicate that it yields measures of orientation and of

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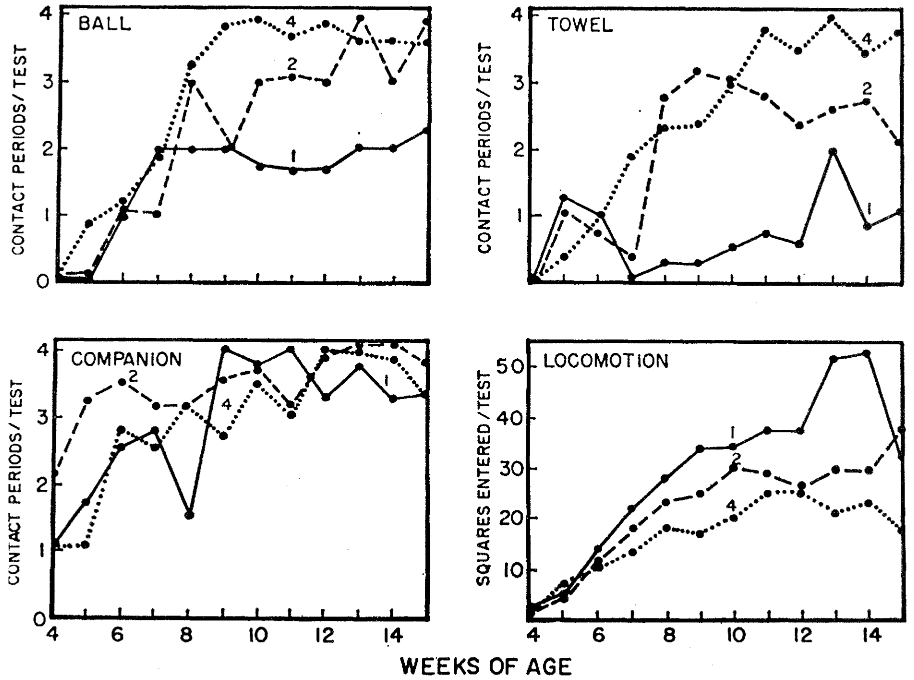


Fig. 1. Average number of observation periods, per test, in which contacts were made with a ball (top left), a companion puppy (bottom left), and a towel (top right) for dogs removed from isolation one, two, or four times per week from age 4 weeks through 15 weeks. (Bottom right) Average number of times per test that subjects crossed between nine squares marked on the arena floor. $N = 4$ per group.

contacts with a human handler, with toys, and with a companion puppy as well as counts of squares entered—a measure of locomotion (*15*). More recently we have developed the "code for observational description" (COFOD) technique, in which observers record a subject's behavior at regular intervals as a series of five-letter words, each word providing a "snapshot" of the subject at an instant in time (*14*).

Letter 1 of each COFOD word denotes the stimulus toward which the subject is responding; letter 2 describes the nature of the response. Location in the testing area is indicated by letter 3, and type and level of activity by letter 4. Letter 5 denotes any one of various miscellaneous indicators of emotional arousal. For example, HMAJT describes a dog "manipulating" (M = pawing or mouthing) the handler (H). The dog is in the arena (A) jumping (J) up and down and wagging its tail (T).

A useful feature of COFOD is a numerical transformation for letters 2 and 4. Response intensities are graded from orientation through approach, investigation, contact, and manipulation. Adding the numerical values of these letters for each test provides a response index (RI) which is a measure of the average intensity of responses directed toward identifiable stimuli. Response indexes can also be calculated for individual stimuli. Similarly, numerical equivalents of letter 4 increase with increase in level of activity, from lying down through sitting, standing, walking, running, and jumping. The sum of these numerical equivalents yields an activity index (AI). Practiced observers obtain rank order correlation coefficients of about .90 on ratings of RI and AI. Observing is easier and agreement is better when subjects make relatively stereotyped responses, but satisfactory records can be obtained from all subjects.

Varying "Dosages" of Experience

Experiential deprivation is not an all-or-nothing matter. One approach to quantification is to rear animals under different regimens which can be ranked in terms of complexity or some similar dimension. We chose, instead, to rear dogs under a regimen which provided experience, in varying proportions, of standardized restricted and free environments. Two questions were posed: (i) How much (or how little) free-environment experience suffices to stimulate and sustain normal behavioral development? (ii) Does the effectiveness of free-environment experience vary with the age of the subject? The second question is more difficult to answer than the first because one cannot alter the age at which free-environment experience is allowed without changing the duration of prior isolation.

In one experiment (*16*) ten beagles and ten wirehaired terriers were reared on five different schedules, which provided different degrees of experience, to the age of 16 weeks. During weeks 16 to 19 each animal was given 16 arena tests. Prior to week 16, all subjects had been kept in isolation cages from the time they were 3 weeks old, with interruptions as follows: groups 1, 2, and 4 were given one, two, or four arena tests per week during weeks 4 through 15; and group 2′ was observed biweekly during weeks 10 through 15. Group K was continuously isolated during weeks 4 through 15. Since the rate of acquiring experience, the age at which it is acquired, the amount of experience acquired, and the age at time of observation all vary in this study [such variation is inevitable in developmental experiments (*17*)], comparisons must be made among specific sets of data.

For example, groups 1, 2, and 4, given different amounts of experience in the arena, can be compared at the same ages. Puppies whose isolation is broken only once a week played with a ball about half as much as puppies given two or four isolation breaks (Fig. 1, top left). The numbers of contacts between companions were essentially equal for the three groups (Fig. 1, bottom left). However, these contacts were less intense in the one-break-per-week group, as evidenced by the low towel-contact scores, which measure intrapair competitions (Fig. 1, top right). The groups score in reverse order on locomotor activity (Fig. 1, bottom right). The age at which group differences appeared varied with the nature of the measurement.

The same puppies were also compared after being given comparable amounts of experience in the arena. The results were highly consistent for most measures. Rate of change in behavior *per test* was at first more rapid in the groups given fewer tests per week—that is, in groups of puppies which were older when they were placed in the arena. Until a degree of biological maturity had been attained, the puppies appeared not to benefit from additional experience.

Still another mode of comparison is that between groups given experience at the same rate but at different ages. No differences were found in stimulus-contact scores for puppies tested biweekly from ages 4 through 9 weeks (group 2) and those tested similarly from ages 10 through 15 weeks (group 2′). Groups 4 and K, tested four times a week from age 4 weeks and 16 weeks, respectively, made, on comparable tests, about the same number of stimulus contacts, but contacts of group K, whose training had been delayed, were less intense. Delayed onset of experience was clearly associated with increased locomotor scores for groups 2′ and K, as compared with groups 1, 2, and 4.

An analysis of scores for the final week of arena tests allows comparison of the two breeds at the same age after the five groups (1, 2, 4, 2′, and K) had been reared according to five different schedules of experience. Table 1 indicates that breed and schedule affected some, but not all, scores. In general, delaying experience (and restricting the amount) affected the intensity of contacts more than their number. Breed differences were demonstrated only on measures which were also modified by experiential programming, a fact which suggested that behavior most modifiable by variation in experience may also be particularly sensitive to genetic variation.

Table 1. Significance levels for effect of schedules of experience (S) and breed (B), based on analysis of variance of scores for week 19. *NS*, no significance.

Measure	S	B
All contacts, handler	.05	NS
Strong contacts, handler	.01	.01
Contacts, pendulum	.05	NS
Contacts, ball	NS	NS
Contacts, companion	NS	NS
Contacts, towel (competition)	.05	.01
Arena squares entered	.01	.01

Experience did make a difference, but the amount of experience required to make the puppies behave essentially like ordinary laboratory-reared animals was on the order of 20 minutes per week. Group averages conceal conspicuous individual differences in the persistence of postisolation deficits. Since some animals reared under conditions of severe restriction performed so well, I began to suspect that the postisolation syndrome was not simply the result of withholding critical information during a biologically critical period. Experiments were designed therefore to modify conditions of emergence into the arena, and conditions of isolation.

Emergence as a Stress

If isolation involves more than the withholding of information, what might this something else be? Behavioral organization could be deteriorating, as suggested by Lessac, but the schedules-of-experience results did not support this idea. On the contrary, there was even an indication of progressive behavioral organization during isolation. A third explanation emphasizes the contrast between the isolation cage and the arena and views the postisolation syndrome as dependent upon a prolonged "irrational fear" (*18*) of space and novel environment. Such fear is not seen in normally reared puppies because the environment opens up gradually to a growing puppy as its motor and sensory capacities carry it out of the nest into the world. When the transition must be accomplished in an instant, adaptive mechanisms are overstrained. It follows that cushioning the shock of emergence should lessen the symptoms.

In several experiments we sought to reduce the stress of emergence by stroking and handling the puppies before or after testing in the arena and by administering chlorpromazine before the tests. The effect of stroking and handling by a human being is clear. Animals thus handled made more contacts, and more intense contacts, with humans and toys (and usually with other dogs) than did animals required to emerge unassisted from a transport cage into the arena (*14*). The case for a favorable effect of chlorpromazine is more complex. In two experiments we showed that administering the drug with food just prior to the first few arena tests reduced the incidence of bizarre behavior and made puppies reared in isolation appear much more like normally reared puppies. In particularly favorable cases (*19*), puppies removed from isolation while drugged played vigorously with toys, followed the experimenter about the arena, and approached him on call at the first opportunity. These animals had no more experience than other puppies reared in isolation, who froze or struggled, howled and defecated, and made no directed responses to stimuli which attract dogs reared as pets in home or laboratory. We concluded that the postisolation syndrome could not be explained as a simple experiential deficit. Simple approach and "manipulative" behavior, including species-specific social patterns, had developed in an extremely barren environment and appeared promptly when adequate eliciting stimuli were presented and when the suppressive effects of fear were attenuated by chlorpromazine.

In our first experiments of this series it appeared that chlorpromazine benefited only animals which simultaneously received extra handling from the experimenters. Little effect was noted in nonhandled animals required to move from a transport cage into the arena under their own power. An experiment was designed to test further the relationship between handling and drug administration. All subjects (16 beagle puppies) were allowed to emerge spontaneously into the arena. At the end of each arena test one member of each pair was handled for 5 minutes, the other was allowed 5 minutes in an open transport cage from which it could enter the arena freely. Half the pairs received chlorpromazine in spansule form (10 to 12 milligrams per kilogram) 30 to 60 minutes before each test commenced.

Figure 2 illustrates the most important finding. As the series of tests proceeded, handled puppies emerged sooner and spent more time in the arena; in these puppies no effect of chlorpromazine is discernible. In nonhandled puppies there is a strong chlorpromazine effect which reinforces rather than counteracts the effect of lack of handling. We tentatively explain the contradiction between this finding and results of the earlier study which showed favorable effects of the drug in terms of the difference in the tasks required of the puppies in the two experiments. With no handling, the tranquilized puppy simply stays in a familiar environment. In the first study, the moderate amount of handling was more reinforcing to the drugged than to the undrugged subject, but, in the second study, the larger amounts of handling were sufficient in themselves and the drug effect was superfluous.

Another way to cushion the shock of emergence into the arena is to modify the isolation environment in such a way that the transition from the cage to the arena is less abrupt. Puppies reared with toys and with a companion (paired isolates) behave very much like those raised under the most extreme conditions of deprivation (*20*). The behavior of puppies reared in cages with a window looking out onto a laboratory was intermediate between that of true isolates and that of puppies reared as pets. We concluded that space itself—the absence of the familiar cage walls—is more important in the etiology of the postisolation syndrome than lack of familiarity with specific stimuli used in the arena test.

Breed Variation in Vulnerability

Two breeds, beagles and wirehaired terriers, were used in several of our experiments. In the laboratory, beagles are characteristically less active and less aggressive than terriers. After emergence into the arena, beagles showed persistent depression of directed responses; terriers seemed to recover more rapidly. To test this somewhat subjective impression, puppies reared as pets and puppies reared in isolation, of both breeds, were compared in the standard arena test. Several modifications of the isolation environment were employed, but these had such small effects that, for the purpose of this article, it is legitimate to group all isolates.

Figure 3 shows the average activity indices for the four groups during the series of 20 tests. Terriers were consistently more active than beagles. From the third week of testing, terriers reared in isolation were more active ($P < .05$) than those reared as pets. Throughout the tests, beagles reared in isolation were less active than those reared as pets. Thus it appears that isolation magnifies the breed differences in activity seen in dogs reared in standard fashion. The descriptive terms at the right in Fig. 3 provide a guide to the actual observations, but it must be noted that a mean value of 2.0 does not indicate continuous walking but indicates a mix of standing, walking, jumping, and so on, in varied proportions.

Similarly, we may compare the response indices for the four groups (Fig. 4). Here the curves for terriers and beagles reared as pets do not differ. But, after isolation, terriers consistently responded more intensely than beagles to the arena stimuli, and, from the second week of testing, their responses were indistinguishable from those of their pet-reared litter mates. The beagles raised in isolation had not come close to responding as freely as their pet-reared litter mates by the end of the experiment. By this measure, too, isolation enhanced the difference between the two breeds.

It is apparent, therefore, that genotype is one determinant of the direc-

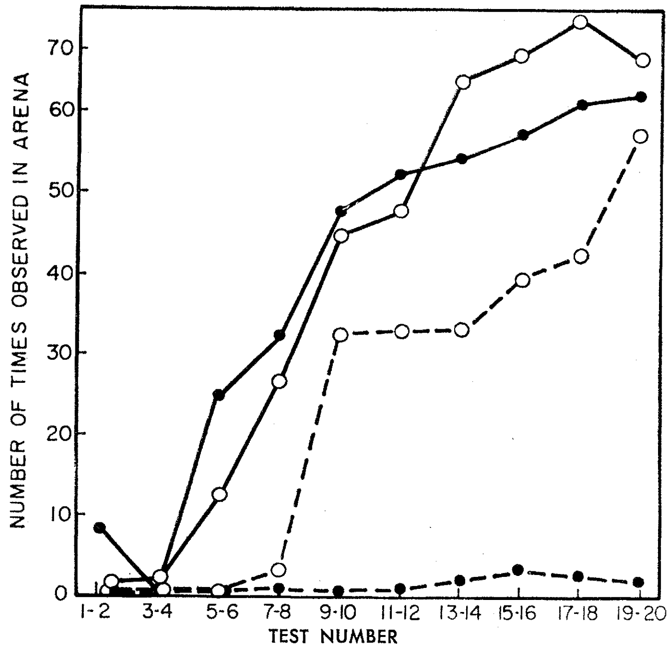
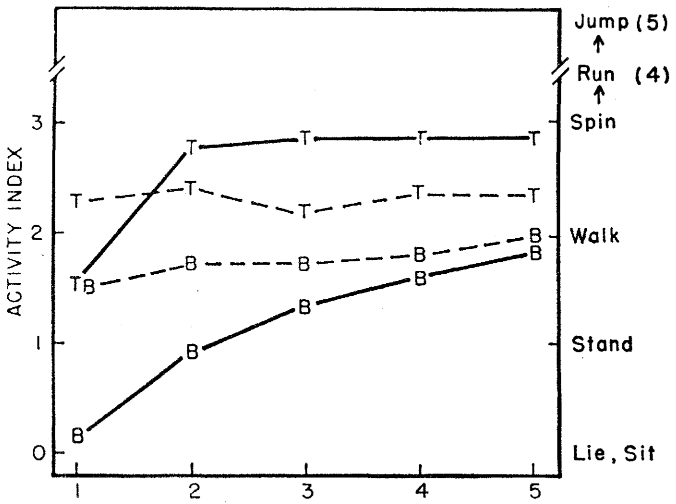
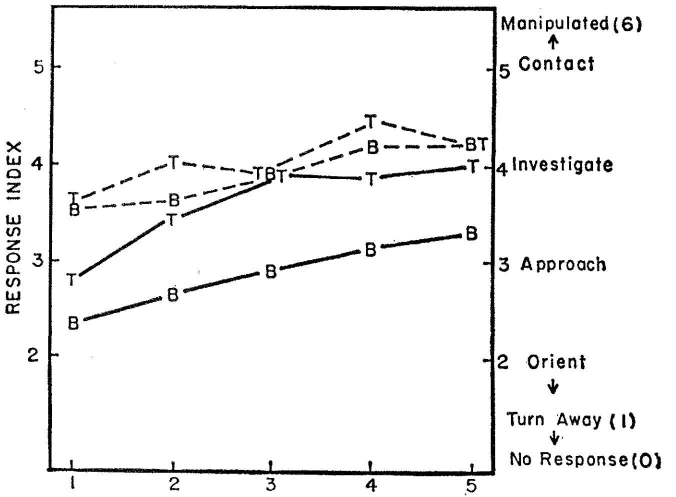


Fig. 2 (left). The effect of posttest handling and administration of chlorpromazine upon emergence into the arena from a transport cage similar to the isolation cages. $N = 4$ per group. (Open circles, solid line) No drug, handled; (open circles, dashed line) no drug, not handled; (solid circles, solid line) drug, handled; (solid circles, dashed line) drug, not handled.

Fig. 3 (bottom left). Average activity indices for beagles (*B*) and wirehaired terriers (*T*): (solid lines) isolates ($N = 24$); (dashed lines) pet-reared ($N = 8$). Each block includes four tests given during 1 week (at age 16 to 20 weeks). Numbers in parentheses indicate degrees of activity.

Fig. 4 (bottom right). Average response indices for beagles (*B*) and terriers (*T*). Each block includes four tests given during 1 week (at age 16 to 20 weeks). Numbers in parentheses indicate degrees of activity.





tion, duration, and intensity of the isolation effect. If living in a more open environment, typified by the arena, is taken as a desideratum, beagles would appear to be more vulnerable than terriers to the disruptive effects of isolation. One could, however, argue that beagles are better adjusted to life in a cell—perhaps the reason experimental biologists favor them for laboratory use. However, basing the argument that terriers are better adapted to an open environment upon the arena test alone is risky. Under other circumstances beagles seem better adapted to a free environment than terriers. Groups of litter-mate terriers must usually be split up in order to prevent gang attack upon subordinate members; litter-mate beagles seldom behave in this way (*21*). Observations such as these provide strong support for Hirsch's (*22*) assertion that "the effects of experience are conditioned by the genotype," but do not indicate which genotype is more adaptive. Clearly, investigators of experiential deprivation should be careful in generalizing from species to species, since breeds within a species can differ so widely. The results should also make behavior geneticists cautious about generalizing behavioral phenotypes from situation to situation. Beagles and terriers raised in isolation will not show the same kinds of difference they would show if they were reared as pets, and analogies can probably be drawn for mice or men.

Learning Ability of Postisolates

The arena test is highly sensitive to the effects of isolation, but it makes minimal demands upon the learning ability of the puppy. The bulk of the evidence summarized by Hunt (*2*) indicates a decrement in measured intelligence following early experiential deprivation. Thompson's and Heron's (*8*) isolated Scottish terriers performed less well than controls on an orientation test and on a delayed-response test which required the animals to locate food on the basis of cues which were withdrawn before the response was initiated. Melzack's (*9*) isolated beagles were less efficient than controls in following reversals of a visual cue associated with food reward. On the other side, Harlow (*23*) states that learning ability of macaques is apparently little impaired by early experiential deprivation—perhaps not at all if sufficient time is allowed for recovery. Similar findings are reported by Angermeier, Phelps, and Reynolds (*24*). In our studies of postisolation learning ability we have used a modified version of the Wisconsin general test apparatus. Dishes containing a preferred food were covered by slides on which card holders were mounted. In the visual task, black and white cards were used as the discriminative stimuli: pushing against the correct card uncovered the food; pushing against the incorrect slide did not. The position of the correct stimulus was varied in a complex predetermined order. For the spatial task, gray cards were placed on both slides. One side was consistently rewarded until ten consecutive correct responses had been made. The sides were then reversed. On both tasks, efficiency of learning was measured by the number of errors the dog made before attaining the criterion.

Individual variability in learning ability is great even among dogs of the same breed and rearing. It has proved more difficult to draw conclusions regarding effects of isolation upon learning than to draw conclusions regarding the effects upon social and manipulative behavior. The clearest finding is that 12 weeks of isolation do not necessarily impair reversal learning on the spatial task (*25*). Sixteen previously isolated dogs which had been observed for 5 weeks in the arena were trained. As each subject met criterion the position of the food was changed, and this procedure was continued until 12 complete series had been run. Six puppies reared as pets were tested in the same way.

On a spatial reversal problem the first trial of each new series is ordinarily nonreinforced. A well-trained subject may thereafter respond correctly, though typically some errors are made. In this study errors were scored from the second trial on. Figure 5 gives the result of the experiment. The values along the ordinate denote errors plus 1, in order that zero scores may be represented on a logarithmic scale. Mean values for errors show that the previously isolated dogs were consistently poorer learners than the pets. However, great variation was found within both groups, and the difference between the two groups reached statistical significance ($P < .05$, Mann-Whitney U test) only on series 2, the first reversal. Figure 5 also shows the errors made by the best and the poorest performers of each group. The values for the poorest performers among the pets were similar to those for the average performers among the isolates. On all but one series, however, the best performance for an isolate was equal to or better than the best for a pet.

Visual discrimination was measured in a separate group of 16 beagles, half of them reared in full isolation from week 4 through week 15 and half reared as "semi-pets" (with about one-third the handling provided in our standard pet-rearing procedure). As anticipated, visual discrimination (discrimination between black and white cards) proved to be more difficult than the spatial task—so difficult that one subject from each group failed to meet the criterion even once. The other subjects were tested on three series (two reversal series), the results of which are shown in Table 2. The data are much like those obtained on the spatial task; the dogs reared as pets showed superior performance only on the reversal problems. However, the differences do not reach conventional levels of significance (max $P = .104$ on the Mann-Whitney U test, one-tailed, for series 3). It would be unwise to conclude from these data that isolation had not impaired the capacity for discrimination reversal in some individuals, but the data show that the effect was not consistent.

Another group of eight beagles and eight terriers, all reared in isolation, was divided into two equal subgroups, given either spatial or discrimination reversal tests. No pet-reared controls were included in this experiment, as the major objective was a comparison of the two breeds after experiential deprivation. This set of animals performed less well than any other group we have trained. On the simpler spatial task (Table 3) one terrier failed to meet criterion and one beagle and one terrier developed phobic reactions and stopped working after a few series. On the visual task only one of the eight subjects met criterion on any reversal series. Though this experiment demonstrated that the breed difference in the effect of isolation upon performance in the arena test did not carry over into a learning task, the interpretation is clouded by the poor performance of all subjects, which suggests that testing conditions were not optimum. In retrospect, it appears that inclusion of a pet-reared group in this experiment might have helped to explain the results, but none was avail-

Table 2. Mean errors to criterion on successive black-white discrimination reversal tests.

Rearing	No. of subjects	Series		
		1	2	3
Semi-pets	7	60.1	86.0	86.6
Isolates	7	71.1	120.0	118.0

able at the time. Since then Ebel and Werboff (*26*) have shown that normally reared dogs perform as well as primates on the Wisconsin apparatus. It is thus probable that early isolation does have persistent detrimental effects on performance on the more complex visual reversal problem, but additional experiments are needed to resolve the question.

Theories and Generalizations

This series of studies has demonstrated marked individual differences in the disruption of behavior following early experiential deprivation. Isolation effects are modified by conditions of emergence into the arena, and differ for beagles and wirehaired terriers. Whether the effects are measured by problem-solving tests or by observation of the number and intensity of directed responses, it is found that a few subjects appear essentially unscathed by prior experiential deprivation. Isolation is necessary but not sufficient for the commonly observed reduction in directed responses and appearance of unusual behavior. A satisfactory theory must account for these findings.

As stated above, the major theories are the stimulus-deprivation theory of Thompson and Heron (*8*), based largely upon Hebb's (*11*) concept of a need for perceptual learning; the deterioration theory of Lessac (*13*); and the emergence-stress theory of Fuller and Clark (*14*). The predicted consequences of each of these models are shown in Fig. 6. I believe the emergence-stress theory provides the most satisfactory explanation of our data.

The deterioration theory is supported by evidence that young dogs that had been kept in isolation performed more poorly on several tests than they had before being isolated (*13*). Thus, isolation is more than simply the withholding of opportunity for perceptual learning. In our arena experiments the behavior patterns which were measured following isolation do not appear in young puppies prior to isolation; hence the fact that some dogs do not show these behavior patterns after isolation cannot be ascribed to deterioration. A more telling argument against the deterioration model is the fact that puppies removed from isolation at 16 weeks usually acquire social and manipulative behavior in the arena *more* rapidly than 4-week-old puppies do (*16*). Instead of deterioration one finds evidence for continued perceptual and motor development under conditions of relatively severe restriction.

There are two major arguments against the model which postulates that stimulus deprivation causes failure of perceptual learning. One is the "instantaneous" appearance of simple orientation, approach, and manipulative behavior patterns in a few puppies when given their first arena test (*14, 19*). The other is the finding that experiential deprivation produces many poor learners but is compatible in other subjects with excellent learning (*25*). Neither argument is conclusive, and it is possible to express the deprivation theory in a form that accommodates the findings, but, in my view, at the sacrifice of the principle of parsimony. The persistent decrement in learning ability shown by the McGill isolates (*8–10*) might be considered evidence that something was fundamentally wrong with their neural organization. Learning was still impaired after overt emotional disturbance had subsided. These older animals had, however, a long history of failure on many tasks, and it is difficult to extricate the effects of their remote isolation experience from their more immediate experience of failure.

In the emergence-stress model, excessive arousal in an organism exposed to a myriad of unfamiliar stimuli is assumed to produce overload in the neural systems underlying many forms of behavior. One role of early experience is that of allowing the organism to become habituated to multitudinous stimuli, so that it can direct its responses to one or a few which are significant. Habituation plays a similar part in Harlow's (*27*) hypothesis of learning. Acquiring a complex discrimination, for example, always involves elimination of responses to nonpertinent features of the environment. Lessac (*13*) also stresses the importance of habituation to particular levels of stimulus intensity. That part of his interpretation of postisolation behavior which emphasizes interference with adjustive patterns in overly aroused animals is compatible with the emergence-stress hypothesis. The difference lies in our nonacceptance of the concept of deterioration.

Table 3. Individual performances of beagles and terriers tested, after isolation, on spatial and visual reversal tests. Testing was discontinued when the subject failed to reach criterion within 300 trials or failed to approach the goal for 5 consecutive days.

Breed	No. of subjects	Series completed*
	Spatial test	
Beagles	4	2, 12, 12, 12
Terriers	4	0, 3, 12, 12
	Visual test	
Beagles	4	0, 0, 1, 2
Terriers	4	0, 1, 1, 1

* Maximum number of series, 12.

The difference between the 16-week isolate entering the arena for the first time and its litter mate who has visited the arena for extremely brief periods weekly is that the litter mate has received experience in small doses and has gradually become habituated to the entire complex. Its immaturity during early visits to the arena restricted sensory input to a manageable level, and overload did not occur at any stage.

Variation in vulnerability to postisolation disturbance of behavior could be primarily variation in the reaction to input overload. Habituation can occur later in life than is usual, but perhaps later habituation is less efficient. One would predict that, for a dog reared in isolation, the arena might serve as a fear-arousing stimulus in somewhat the way that an opening umbrella produced aversion in Mahut's (*28*) home-reared dogs. The behavioral effect of increased psychological arousal would vary with the complexity of the task, and it is conceivable that isolates might show superior performance on certain tasks. To accommodate breed differences, the emergence-stress model must assume inherited differences in the probability of substitutive responses—for example, "freezing" or spinning—on the part of dogs under stress. The emergence-stress model plays down the role of experience in guiding perceptual learning, though it does not deny the phenomenon. The theory also places more emphasis on intrinsic forces in behavioral development than accords with much current psychological thought.

The obverse of the arena test of dogs reared in isolation is the confinement of puppies reared in a free environment (*29*). Such puppies are disturbed and attempt to escape from a small cage, which isolates would prefer to a free environment. The emergence-stress model can be converted to a confinement-stress model for puppies habituated to a different world.

Does the theory proposed to explain the effects of isolation upon dogs bear upon the effects of experiential impoverishment upon children? The essential features of the emergence-stress model—exposure of an experientially deprived and neurologically well-developed organism to a complex alien environment—are to be found in many groups of children. It may be harder for children to become habituated to the new environment than it is for dogs, because of greater self-percep-

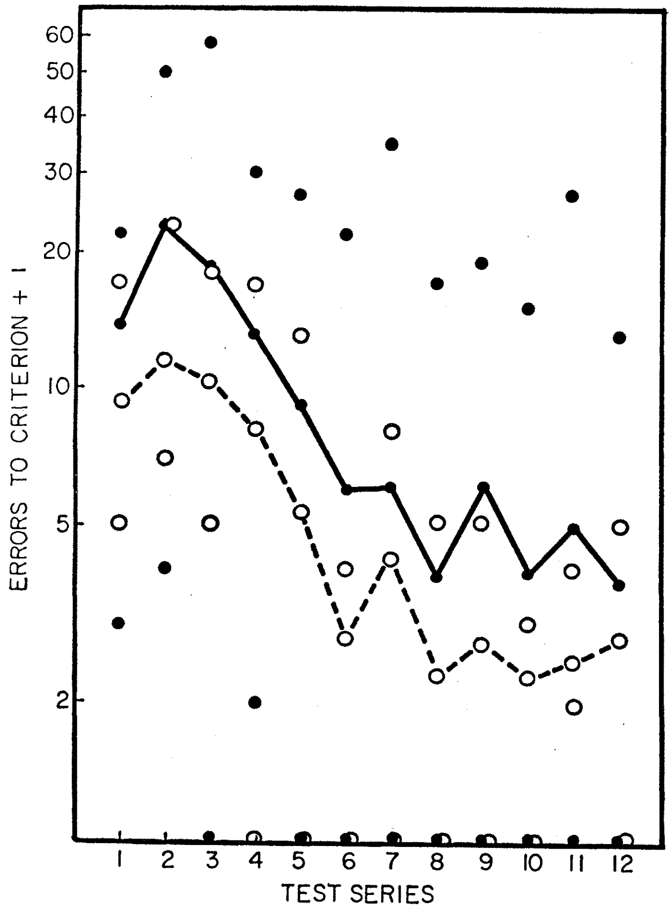


Fig. 5 (above). Average number of errors plus 1 before the subject attains criterion for the spatial task with reversal at each series. (Solid line, solid circles) Isolates ($N = 16$); (dashed line, open circles) dogs reared as pets ($N = 6$). In addition to the averages, the best and poorest performances in both groups are shown.

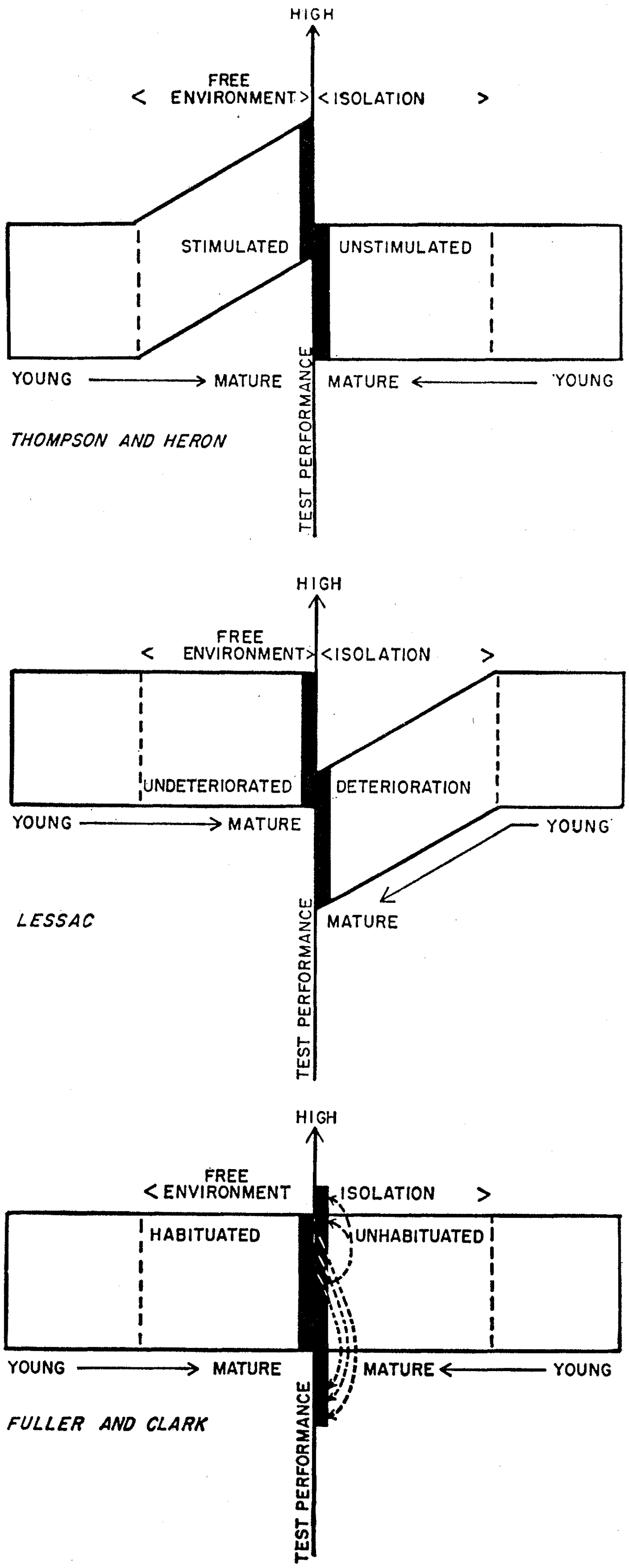


Fig. 6 (right). Diagrammatic representation of three theories for the effects of experiential deprivation upon test performance. All are based upon interpretations of experiments with dogs. (Top) Unstimulated isolates fail to develop perceptual mechanisms; hence they rate lower on test performance than animals reared in a free environment. (Middle) Deterioration of established mechanisms occurs during isolation. This model yields a prediction similar to that of the stimulation, perceptual-learning model for postisolation group comparisons between subjects raised in isolation and subjects raised in a free environment. However, preisolation-postisolation changes within the two groups differ. A combination of the two models is logically admissible. (Bottom) Perceptual and motor development are assumed to proceed similarly in isolation and in a free environment. When confronted by a test situation, usually in an open space, unhabituated dogs reared in isolation are highly aroused and, in general, perform poorly. High arousal can facilitate some performances—for example, locomotor activity in some breeds of dogs.

tion in the child. A 16-week-old dog is not embarrassed while acquiring ball-playing or social responses ordinarily acquired by 6-week-old puppies. A 16-year-old boy in a remedial-reading class is aware that the tasks set for him are appropriate for 6-year-olds. Such particularly human dimensions must be kept in mind in generalizing the emergence-stress model. Provided this is done, the hypothesis can be applied and tested with other species, including man. The search for an explanation of the lasting effects of early experiential deprivation is more than academic. Whether the effect of isolation is primarily deprivation, deterioration, or nonhabituation has implications for correction of the deficits produced. The emergence-stress model offers, perhaps, a little more hope for rehabilitation than the other two models do.

Summary

Our experiments on the effects of experiential deprivation upon later behavior of dogs have dealt with four major areas. The programming of life histories has involved the scheduling of breaks in isolation and the introduction of specific stimuli to isolation cages. Biweekly breaks, of less than 10 minutes each, largely counteract the effects of isolation. An opportunity for the animal to look out of the isolation cage has some counteracting effect, but the presence of playthings or rearing with a companion does not.

Another series of experiments has centered on the circumstances of emergence from isolation. Special handling and administration of a tranquilizing drug at this time were effective in reducing the usual postisolation symptoms.

Genetic variation in reaction to early isolation has been observed in comparative experiments with beagles and wirehaired terriers. Genotype may modify the magnitude, the duration, and even the direction of effect. Behavioral phenotypes readily changed by varying the schedules of experience tend to be those for which the greatest differences are observed from breed to breed.

Observations of the effects of experiential deprivation upon problem solving (intelligence) are inconsistent. Some dogs raised in isolation perform very well, but many are poor performers. Deprivation does not necessarily, therefore, prevent normal development of intelligent behavior, but it appears to interfere with performance in vulnerable subjects.

The two major theories in the field have considered isolation effects to be primarily the result of deprivation of information necessary for perceptual development, or, alternatively, the result of deterioration of patterns of response through disuse. The series of studies described here suggests that major attention should be given to the circumstances of emergence from isolation and subsequent testing. Isolation may simply prevent organisms from becoming habituated to stimulus complexes, so that attending to pertinent components while disregarding others is made difficult. The stimulus overload would be particularly severe when the organism emerged from isolation. Genetic factors might play a major role in determining whether the response to the stress of emergence were withdrawal (beagle-type response) or hyperactivity (terrier-type response). Genetic and other factors affecting the persistence of the stress response could tilt the balance toward delayed but satisfactory behavioral adjustment or toward permanent retardation.

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