

no significant effect on any of these variables.

The second experiment was performed to determine if these changes would occur (i) in the familiar environment of the home cage nest, (ii) without any alteration in litter size, and (iii) if weight loss and dehydration were prevented by supplying milk through gastric intubation. Eighteen pups, six from each of three litters, were studied. Each litter was left intact in its home cage nest after removal of the mother. Temperature was maintained in the litter by a thermostatically controlled heating pad placed under the aquarium floor. An equal number of pups from each of the three litters were treated as follows: one-third of the pups were left undisturbed throughout the experiment, another one-third were intubated by hand and fed 0.8 ml of reconstituted condensed milk every 4 hours by the method used successfully by Thoman to nourish rats raised from birth without their mothers (5), and one-third were intubated by hand but were returned to the litter in the home cage without feeding. Recordings were made $\frac{1}{2}$ hour after separation and every 8 hours thereafter for 24 hours, always just prior to the next intubation.

All three groups showed significant decreases in cardiac and respiratory rates; these decreases were not quite so rapid as when the pups were placed in unfamiliar surroundings, but they reached approximately the same low levels by 16 hours (see Fig. 2). Again, activity measures showed no trend. The three groups did not differ significantly in any of the measures employed at any of the times of recording with the exception of the inactive heart rate of the intubated and fed group at 24 hours, which was slightly higher than the other two groups ($.05 > P > .01$). Litter temperature varied little throughout the experiment ($+0.8^{\circ}$ to -1.0°C , median -0.2°C). All pups in the fed group gained weight ($+0.5$ to $+1.2$ g, median $+0.9$ g or $+4$ percent of body weight in 24 hours). The intubated control group lost 2.4 g (median) over the 24 hours. These results showed that the physiologic changes following separation from the mother were not dependent upon starvation and dehydration or upon an unfamiliar environment.

A physiological readjustment has been found to occur in 2-week-old rat pups after separation from their mothers. These physiological changes

resemble the changes that occur during the initiation of hibernation, when decreases of cardiac and respiratory rate actually precede the drop in body temperature (6). Rat pups of this age are known to be incompletely homeothermic (7), and their body temperature will approach room temperature unless heat is supplied by the mother or by artificial means. With reduced core temperatures, cardiac and respiratory rates are further depressed, and spontaneous movements appear sluggish.

These experiments indicate that this response is elicited simply by removing the mother from the home cage, without otherwise disturbing the pups and despite provision of warmth and sufficient nutrition to allow a substantial weight gain. Whether there is a single essential aspect of the mother-pup interaction, the absence of which elicits this response, is unknown. Such factors as the olfactory and tactile stimulation provided by the mother's attention to the pups, the consummatory experience of suckling and receiving milk, and even the possibility of a maternal hormonal factor transmitted in the rat mother's milk must be considered. Finally, the frequency, route, amount,

and composition of nutrient may be crucial. The rat mother normally provides some milk every hour, and at this age daily weight gains of 2 g are common, in contrast to the 1-g weight gain achieved by the five tube feedings over 24 hours. An opportunity is present in this model system to clarify some of the basic principles governing the biological effects of early deprivation.

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Fixation Produced by Conflict

Abstract. *All rats given a choice between a rewarded alternative and a conflict alternative (rewarded and punished) developed position fixations when the position of the alternatives was reversed. In contrast, all animals given one rewarded alternative and another nonrewarded (or punished and nonrewarded) alternative learned to choose the rewarded side during 25 successive reversals.*

Punishment is a complex process. It can either facilitate or retard the performance of a learned response, depending on how it is used in a particular situation (1). The administration of punishment has been criticized as being ineffective (2) and, more seriously, as producing deleterious side effects—particularly stereotyped or neurotic behavior (3). Solomon (4) has pointed out that unfortunate consequences usually follow when instinctive, rather than learned, behavior is punished. In support of this argument, much evidence in recent years has shown that punishment can be used effectively to suppress learned behavior without any obvious concomitant, disadvantageous reactions (5).

In this report I present an instance of perseverative behavior developed by laboratory rats as a consequence of punish-

ment combined with reward in a learning situation. An experiment shows fixated behavior resulting from conflict used in two-choice reversal learning. The new feature of this experiment involves training rats to choose between two alternatives (A and B), both of which are rewarded by food but one (A) is also punished by electric shock. At first, the rat learns to choose the unpunished alternative (B). The next step in the reversal learning procedure is to switch the punishment from alternative A to B (with both alternatives still rewarded). Now the rat should learn to switch all its responses from choice B (now punished) back to A (now unpunished). When no punishment is involved in reversal learning, a rat is quite capable of learning to reverse its choice of two alternatives, as in the standard situation in which first A is rewarded

while B is not and, subsequently, B is rewarded while A is not. The ordinary reversal procedure can be repeated many times, and rats not only learn to reverse their choice but actually improve their performance (make fewer errors) in later reversals (6). In contrast, the conflict-reversal situation reported here causes rats to fixate on one alternative and to continue to choose it during successive reversals, regardless of whether it is punished or not. Thus, a peculiar pattern of stereotyped behavior occurs.

Three groups of subjects were used. The response consisted of choosing one of two similar levers (presented simultaneously) and of pressing it once. The correct response was always rewarded by food, but the consequence of the incorrect response differed for the three groups. The incorrect response was followed by neither reward nor punishment in the extinction (E) group, by punishment but no reward in the punishment-extinction (PE) group, and by both punishment and reward in the conflict (C) group.

Animals were run while hungry (80 percent of normal body weight) in experimental boxes with two retractable levers (7). Reward consisted of immediate delivery of one 45-mg food pellet; punishment was a brief (0.15 second) electric shock of moderate intensity (85 volts), which was delivered to the rat's feet via the grid floor immediately after the incorrect bar was pressed. The subjects, 40 adult male rats, were first trained to depress either of two levers (presented one at a time) to receive food and were then randomly assigned to each of the three groups described above. They were then given the first problem (original learning) with bar 1 negative and bar 2 positive. Sufficient training was given (110 trials) so that all animals learned to select the positive lever (bar 2) when presented with both bars. A trial consisted in presentation of both bars and either depression of one bar by the rat within 60 seconds or no response after the passage of 60 seconds. In the first reversal session there were 10 trials of original learning (bar 1 negative, bar 2 positive) followed by 50 reversal trials (bar 2 negative, bar 1 positive). Subsequent reversals followed the same procedure, with each daily reversal session containing 10 initial warm-up trials under the same condition as the previous day, followed by 50 reversal trials. In all, there were 25 reversals, with 60 trials per reversal.

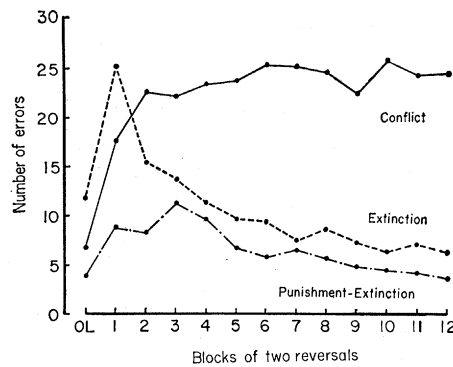


Fig. 1. Mean number of errors per problem during original learning (OL) and 24 reversals (averaged for pairs of reversals) for three experimental groups.

The main response measure was the bar chosen, with choices of the negative bar designated as errors.

The most striking finding was that the conflict animals did not reverse their choice at all, although both other groups reversed. Instead, they fixated on one bar and continued to choose it, regardless of whether it was the positive or the negative bar in a particular condition. Most conflict animals maintained a preference for the bar that was positive in original learning (bar 2). The position preference is indicated by the error scores, which were much higher for group C than for the other two groups. Figure 1 shows the mean number of errors for each group, averaged over pairs of reversals. The 50 percent error rate for the conflict group (25 out of a possible 50) was caused by averaging alternate 100 percent and zero errors for individual animals as conditions changed but their choice remained stable. Because of this fixated behavior, all animals in group C made far more errors than any animal in the other two groups; that is, there was no overlap in the scores either for total errors (on all reversals) or for errors on the last four reversals.

In contrast to the conflict group, both group E and group PE learned and reversed rapidly, with performance improving on successive reversals (see Fig. 1). In fact, the punishment-extinction group learned and reversed faster than the extinction group. This was true in terms of errors on all reversals ($P < .001$) and of errors on the last four reversals only ($P < .05$). The increased effectiveness of punishment extinction, as compared with extinction without shock, has been previously found for a single reversal (8).

To show more clearly that animals

in the conflict condition were fixating on one bar, a fixation index was computed. This fixation score was the proportion of choices made to the preferred bar by each animal, and it was computed for all groups. The possible range of the fixation score was from 0.50 (showing no fixation—that is, equal choice of both levers) to 1.00 (showing complete fixation—that is, 100 percent choice of one lever). The mean fixation score (0.907) on reversals 1 to 20 for group C showed almost total fixation. Comparable mean fixation scores for group E (0.525) and group PE (0.539) showed no fixation. When individual fixation scores were considered, there was no overlap between the conflict group and the other two groups. The fixation scores in both group E and group PE were mostly between 0.50 and 0.60, which indicates no difference in fixation for the extinction and punishment-extinction conditions. In contrast, the conflict group's fixation scores were mostly above 0.85.

Fixation is a term used by Maier (3) to describe a similar perseverative position response, which resulted from very different experimental conditions. Maier's rats were given an insoluble problem, and they developed position responses that later prevented the solution of a soluble problem. Maier proposed that this stereotyped position response was an abnormal fixation due to the frustration generated by the insoluble problem with unavoidable punishment.

The present situation is quite different from the one used by Maier (3). The strong frustration or anxiety, which characterized that situation and which presumably caused the perseverative behavior, is absent in choice reversal. Here, the animal is faced with a free choice between two responses: one (correct) results in food reward, and the second (incorrect) produces both food and shock. The logical preference appears to be the consistent choice of the unpunished, rewarded lever. The fact that all conflict animals did learn to choose this unpunished lever during the first problem demonstrates that the punishing shock is aversive enough to be avoided and that the rats are capable of learning to avoid it. However, not one conflict subject learned to choose the unpunished bar when its position was changed during many successive reversal sessions. Instead, all the conflict rats developed strong position prefer-

ences, as if they were indifferent to the occurrence of shock. This behavior contrasted sharply with that of animals in the other two groups: every rat easily learned to reverse its choice as the conditions changed.

Since rats are known to have position preferences in many choice situations, a nonreversal control group was added to determine the extent of position preference (fixation) in the present apparatus. Nine rats were given 25 choice sessions corresponding to the 25 reversal days. These rats chose between two equally rewarded levers. They were never exposed to conflict or to shock. Under these conditions, a few rats developed position preferences, but only two rats showed extreme preference; a majority continued to choose both levers. The average fixation for this food-food control group (0.749) was significantly less than the fixation found in the conflict reversal group (0.907) ($t = 2.81$, $P < .02$), and the distributions of scores in these two groups were noticeably different.

Thus, the occurrence of fixated behavior in the conflict-reversal situation is considerably greater than the position preference that would occur without punishment. Further, the extremely fixated behavior must be considered as a direct result of the conflict situation, since other groups reversed normally. Evidence of stereotyped responding was observed in earlier experiments that used the conflict procedure with a single response (9). This latest indication of response fixation is a much more striking instance of strange behavior. Animals choose to endure conflict and punishment when they could easily avoid it by choosing a rewarded alternative, which is always available. This peculiar fixated behavior is not predicted by current reinforcement or conflict theories (10).

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Brood Care in Halictid Bees

Knerer (1) found that mature larvae of the social halictine bee, *Evylaeus malachurus*, weighed 60 percent more than provisions bearing eggs. He suggested that this weight gain was due to progressive provisioning by the adult bees, although such behavior apparently was not observed.

We report a similar gain in total weight of cell contents during the larval growth of the solitary halictid *Notomia melanderi*, the adults of which have no contact with healthy larvae (2). This weight gain is evidently due to the intake of atmospheric water by the provisions. The hygroscopic nature of honey and of the provisions of several species of wild bees is known (3).

Cell contents of *N. melanderi* changed in total weight with larval development as follows: cell contents, placed in sealed tared vials in the field, after initial weighing were oven-dried at 100°C to a constant weight to determine free water content. Tabulation of results showed:

1) Egg or small larva with provisions: $N = 48$; live weight mean ($\bar{X}$), 0.1369 [range (R), 0.0866 to 0.1777] g; dry weight $\bar{X}$, 0.0829 (R , 0.0606 to 0.0942) g; water content 39.5 percent.

2) Half-grown larva with provisions: $N = 24$; live weight $\bar{X}$, 0.2131 (R , 0.1897 to 0.2548) g; dry weight $\bar{X}$, 0.0724 (R , 0.0615 to 0.0881) g; water content 66.0 percent.

3) Mature larva before defecating, all provisions consumed: $N = 40$; live weight $\bar{X}$, 0.2342 (R , 0.1883 to 0.2695) g; dry weight $\bar{X}$, 0.0661 (R , 0.0442 to 0.0743) g; water content 71.8 percent.

Mature larvae of *N. melanderi* weighed 58.5 percent more than provisions bearing eggs. There was an average gain in live weight of 0.0973 g

during larval growth, but there was a mean loss in dry weight of 0.0168 g, perhaps due to respiration.

Although a species of social halictine has been seen touching provisions bearing eggs with its glossa, this possible provisioning behavior occurred rarely and several other social halictines did not do this (4). The large size of the mature larvae of these and other halictine bees relative to the size of the provisions (5) is probably due to the hygroscopic nature of the provisions as in *N. melanderi* and probably is not due to any significant amount of progressive provisioning.

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Interaction of Plant Hormones: Absciscic and Gibberellic Acids

Drury has recently proposed that the definition of interaction used by statisticians should be used to describe results of physiological experiments (1) but states it in a restricted form. The statistical definition he quotes confines the term interaction to a numerical value which is the difference between a measurement (R) of the response of a system to the action of two factors (A and B) applied together, when compared with the sum of the measurements of responses (R_A , R_B) to the two factors applied separately; the interaction (I_{AB}) is defined by the equation:

$$R = R_A + R_B + I_{AB} \quad (1)$$

Defined in this way, interaction has a precise meaning for the statistical analysis of received measurements and has been fully discussed by Lockhart (2). Drury's application of this statistical definition of interaction to physiological phenomena is, however, oversimplified. This is because the statistical operations generally work with the data on the scales in which they are pre-