then for each eye separately. Two vertical and two horizontal maps were made for each of these conditions. During a vertical map, for example, the spot was moved with constant speed of 10 deg/sec from bottom to top and top to bottom; 50 such scans covered the field. Data were collected separately for upward and downward motion of the spot to provide the two vertical maps. Horizontal maps were also obtained in this fashion.

Currently, a total of 50 units from five animals have been mapped in detail. Receptive fields of all units were in the lower half of the visual field. All maps were examined, but categorization of the units was based largely on the receptive field map obtained with the spot moving in the direction which elicited the strongest response from the unit (*4*). Units encountered during the recording were classified as either diffuse or elongated. Diffuse receptive fields have no clearly defined boundaries, and the units responded to stimulation over a wide portion of the visual field. Twenty-seven units were of this type (Fig. 1).

Receptive fields from 23 units were categorized as elongated. Their shapes ranged from somewhat elliptic to clearly edge- or bar-shaped in correspondence with elongated receptive fields described by others. Whereas normal kittens have a full complement of receptive field orientations at birth (*13*) all of the elongated fields found in our animals were oriented either vertically or horizontally (Fig. 2). Since diagonally oriented receptive fields have been mapped in normal animals with our recording procedure [figure 7 in (*4*)], their absence here is not an artifact.

Three characteristics of these elongated receptive fields are striking when compared to elongated receptive fields found in normal cats. First, 21 of the 23 units with elongated receptive fields were predominantly or exclusively activated by only one eye, whereas normally only 10 to 20 percent of the units in the visual cortex of the cat respond to just one eye (*3*, *4*). The discordant stimulation of the two eyes might have produced this loss in binocularity (*14*). The remaining two units were lost before we could determine whether they were also monocular. Second, a particular eye could activate cortical units with receptive fields of only one orientation, either vertical or horizontal, although in the normal cat receptive fields of all orientations can be activated by both eyes. Furthermore, in 20 of these 21 monocular units, the receptive field orientation corresponded to the orientation of the lines to which the eye that activated the unit had been exposed during rearing. Figure 2, rows 3 and 4, for example, shows elongated receptive fields recorded from two units found in the same cat—one unit was activated only by the eye exposed to horizontal lines, and the other only by the eye exposed to vertical lines. Third, some of the elongated receptive fields were considerably larger than those present in normal cats (*3*, *4*).

The change in the distribution of orientations of cortical unit receptive fields that we found when kittens were raised with both eyes viewing different patterns demonstrates that functional neural connections can be selectively and predictably modified by environmental stimulation. Whether the discordant stimulation is a necessary condition is not known. A final aspect of our technique is that we succeeded in reviving our animals after the electrophysiological recording. Therefore, we can test the performance of these same cats in the discrimination of patterns and determine the behavioral effects of the physiological manipulation.

HELMUT V. B. HIRSCH*
Department of Psychology, Stanford University, Stanford, California 94305
D. N. SPINELLI
Department of Psychiatry, Stanford University

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* Address after 15 June 1970: Department of Biophysics, Johns Hopkins University, Baltimore, Maryland.

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Physiological Responses of Infant Rats to Separation from Their Mothers

Abstract. *Decreases of 40 percent in cardiac and respiratory rates occur during the first 12 to 16 hours after 2-week-old rat pups are separated from their mothers. These rates decrease without significant alteration in activity level and despite maintenance of body temperature, of nutrition by intubation, of an intact litter, and of the home cage nest.*

There is increasing experimental evidence that immediate and prolonged behavioral responses occur in infant monkeys after interruption of the mother-infant relationship at certain early periods of development (*1*). Less obvious behavioral changes have been described after early separation in dogs and cats (*2*), but little attention has been paid to the possibility of separation responses occurring in mammals below this phylogenetic level. Few studies of early maternal deprivation have included physiological measurements; thus, the dimensions of the biological impact of such experiences are as yet unknown, although some interesting endocrine abnormalities have recently been reported in a clinical study of emotionally deprived human infants (*3*).

An earlier study from this laboratory on the development of cardiac rate regulation in rats prior to weaning (*4*) demonstrated a phase from day 7 to day 16 of postnatal life when resting heart rates in the home cage litter were maintained at relatively high levels compared with rates at 3 weeks of age or in adulthood. The present experi-

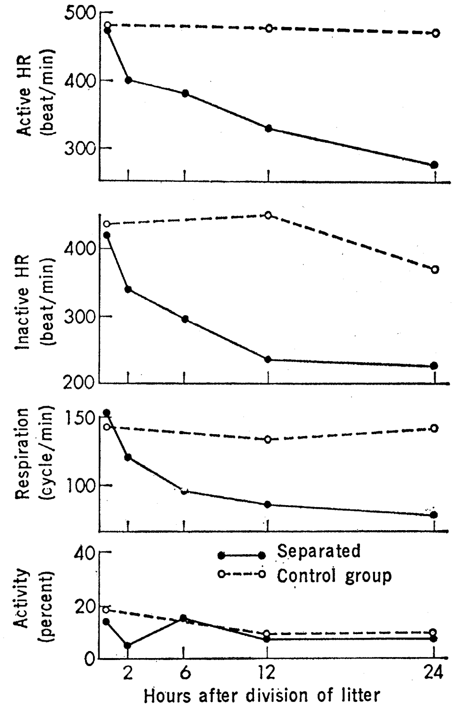

Fig. 1. Cardiac rates during spontaneous activity and inactivity, basal respiratory rates, and activity levels of 14-day-old rat pups separated from their mothers in a temperature-controlled incubator compared with the control group of littermates who were left with their mothers. *HR*, heart rate.

ments examine the acute cardiorespiratory and behavioral effects of separation of 14-day-old pups from their mothers by two different experiments involving controls for factors of temperature, diurnal rhythm, nutrition, and litter size.

Wistar rat litters born and maintained in our laboratory on reversed day-night cycle were culled to eight to ten pups on the second day of life, housed in 6-gallon aquaria, and implanted with 30-gauge silver wire electrodes at least 24 hours before recording. Implantation was done under light ether anesthesia. One 5- to 7-mm subcutaneous loop was placed dorsally at the level of the forelegs and over the right posterior thorax; the second over the left flank, just anterior to the hind legs. The twisted ends (3 to 5 mm in length) emerged above the spine and lay along the back in the same direction as the body hair. A small drop of collodion at the point of emergence prevented electrode movement artifact. The pups were then replaced with their mothers and were found to gain weight normally during the next 24 hours until testing.

With this period allowed for adaptation between implantation and testing, little or no behavior was directed at the electrodes during recording, and lightweight leads could be attached by tiny spring clips without disturbing the resting pups at this age. Impedance pneumograph, electrocardiograph-electromyograph, and cardiotachometer channels were recorded by Grass model 7 polygraph from unrestrained pups. Thirty pups from five different litters were utilized in these experiments. Two-minute recordings were taken at each time interval during the 24 hours following separation. The initiation of activity was determined from the polygraph record by the simultaneous onset of high-frequency spiking in the EMG (electromyogram) and movement artifact in the impedance channel; its termination coincided with a return to the pattern of inactivity with the disappearance of EMG and the resumption of a pattern of regular respiration in the impedance pneumograph channel. Activity was measured as percent of total sample time spent active. Cardiac rate was sampled from the cardiotachometer channel at the peak of each spontaneous activity period and at the lowest point during inactivity for each half-minute of recording. Medians of these values constituted an individual subject's active heart rate and inactive heart rate for each time period. Respiratory rate was calculated from a 6-second sample taken at the period of slowest regular respiration during inactivity.

In the first experiment, mothers were removed from their home cage for ½ hour before heart rates were taken of the undisturbed litter in the home cage. Then half the pups of each litter were placed as a group in a plastic tray in an incubator maintained at 32° to 34°C while the mother was returned to the remainder of the litter, which served as the control group. Twelve pups, six from each of two different litters and evenly balanced as to sex, were used. The separated pups were recorded at 2-, 6-, 12-, and 24-hour intervals from initial separation, and the control group was recorded at 12 and 24 hours. Temperature was measured in each group at the time of recordings, and readings did not differ consistently or vary more than 1.0°C. During the 24 hours, weights of the separated pups fell 1.1 g and weights of the control group rose 3.5 g.

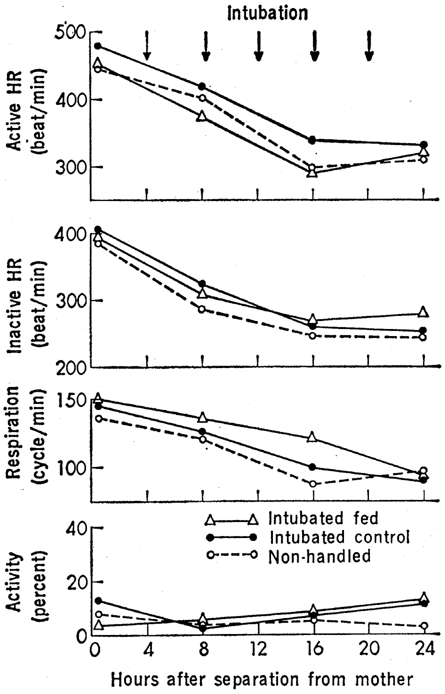

Fig. 2. Cardiorespiratory and activity measures on 14-day-old rat pups left in their home cages after removal of their mothers. A group given supplemental nutrition by tube feeding every 4 hours is compared with the control group of littermates who received similar stimulation without feeding and with others who were left undisturbed. *HR*, heart rate.

Both active and inactive heart rates and respiration decreased substantially in the separated pups during the first 12 hours after transfer to the incubator (see Fig. 1). Median active heart rates fell 145 beat/min (range: −110 to −260, $P < .01$), and inactive heart rates fell 185 beat/min (range: −150 to −230, $P < .01$). Respiration also decreased 70 cycle/min (range: −30 to −80, $P < .01$), but activity percent showed no clear-cut trend (range: +10 to −20, $P > .2$). Heart and respiratory rates thus became different in the two groups of litter mates, although the percentage of time active was almost identical in each group. These divergent trends continued during the next 12 hours.

The data from this experiment indicated the following results. When half the litter was separated from its mother and placed as a group into a strange environment without nutrition but with controlled temperature, there was a reliable decline of nearly 50 percent magnitude in heart and respiration rates in the separated group, irrespective of the pups' activity. In the control group of pups left with their mothers, the reduction of litter size by one-half had 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 ½ 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° 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.

MYRON A. HOFER
Department of Psychiatry,
Albert Einstein College of
Medicine at Montefiore Hospital,
Bronx, New York 10467

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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 punishment 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