The partial-reinforcement extinction effect in 4-5-day-old guinea pigs

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The partial-reinforcement extinction effect was demonstrated at 4-5 days of age in the precocial guinea pig and was related to the appearance of this effect at 12-14 days in the altricial rat. We suggest that the maturity of the septohippocampal system at birth in the guinea pig, relative to the immaturity of this system in the rat, is a possible basis for this difference.

In recent years, we have been examining the ontogeny of a number of related reinforcement effects to which we have applied the term "paradoxical" (see Amsel & Stanton, 1980, for a review). One of these effects, the one most thoroughly investigated over the past 40 years, is the partial-reinforcement extinction effect (PREE). This term describes the fact that instrumental training under a schedule of intermittent (often 50%) reinforcement results in greater resistance to subsequent extinction than does training under continuous (100%) reinforcement. The phenomenon is robust and, to our knowledge occurs in adults in every mammalian species that has been tested. Ontogenetic investigation of this effect in laboratory rats has shown that the PREE is not present in 11-day-old pups but can be shown to exist in pups 1 to 3 days older (Chen & Amsel, 1980a, 1980b; Letz, Burdette, Gregg, Kittrell, & Amsel, 1978).

Unlike the altricial rat, the precocial guinea pig is relatively mature at birth. Its brain and sensory systems function at or near adult levels (Tilney & Kubie, 1931). The development that occurs in the first 3 weeks of life in the rat has already occurred in the guinea pig by the time of birth, and the guinea pig's neonatal brain is said to be roughly equivalent to the 40-50-day-old rat's brain (Dobbing & Sands, 1970).

This early CNS maturity in the neonatal guinea pig is paralleled by behavior that in the rat has a much later development. In the guinea pig, but not in the rat, there is little variation in behavioral arousal from 5 to 100 days of age (Campbell & Mabry, 1972), and there is no difference in the acquisition or retention of an escape or a passive-avoidance response between infancy (5 days old) and adulthood (100 days old) (Campbell, Misanin, White, Lytle, 1974). Spontaneous alternation, which is first displayed in the rat at about 27-28 days, appears 3 weeks earlier in the

guinea pig (Douglas, Peterson, & Douglas, 1973). Lesions of the septohippocampal system appear to reduce or eliminate spontaneous alternation (e.g., Douglas & Isaacson, 1964; Roberts, Dember, & Brodwick, 1962), while lesions of amygdala, cingulate gyrus, and various cortical areas are ineffective in this regard (Douglas, Kowal, & Clark, Note 1).

Virtually the same statements can be made for response persistence in extinction, including the PREE, which is reduced or eliminated in adult rats by lesions of the septum but not of the amygdala (Henke, 1974, 1977), by lesions of the hippocampus (Amsel, Glazer, Lakey, McCuller, & Wong, 1973; Rawlins, Feldon, & Gray, 1980), by blocking of the hippocampal theta rhythm by septal stimulation (Gray, Araujo-Silva, & Quintao, 1972), and by administration of amobarbital (Gray & Ball, 1970).

All of this suggests that the PREE that appears between Day 12 and Day 14 in the rat should occur much earlier in the guinea pig. We conducted an experiment to test this hypothesis.

METHOD

Subjects

The subjects were 16 4-day-old guinea pigs born in our laboratory to mothers obtained during the last month of pregnancy from the University's Animal Resource Center. Each experimental group contained no more than two subjects from the same litter, and each litter contributed at least one subject to each group. Each group was approximately counterbalanced for sex. Age was determined by checking for births every morning and evening and designating the day of birth as Day 0. Litters were housed in 48 × 48 × 20 cm plastic cages that contained pine shavings and a continuous supply of tap water and Purina guinea pig food. The room was illuminated from 0800 to 2200 h, and the pups were run during this part of the light-dark cycle.

Apparatus

The apparatus was a small Plexiglas runway with a 13 × 17.5 × 10 cm startbox, a 32 × 7.5 × 10 cm alley, and a 17 × 25 × 10 cm goalbox. The startbox and goalbox had manually operated sliding doors made of opaque Plexiglas. An electric timer was activated by the raising of the startbox door and was stopped when the subject broke a photobeam at the entrance to the goalbox. This yielded a

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Guinea pigs trained and tested at 4-5 days of age show a clear PREE despite interpolated CRF trials between training and extinction. In the rat, the effect first appears between 12 and 14 days. We have proposed elsewhere (Amsel & Stanton, 1980) that the emergence of the PREE and other paradoxical reinforcement effects depends upon some level of functional maturity in the septohippocampal system. The present result is consistent with this position insofar as, in the rat but not in the guinea pig, (1) the hippocampus is not functionally mature until at least 30 days of age—the number of granule cells in the dentate gyrus shows its greatest development in the 2nd week of life and increases sixfold by adulthood (Altman & Das, 1965), and (2) the theta rhythm that has been linked to the PREE in the rat (Gray et al.,

1972) is first seen in the rat at 12 days of age but is present in the guinea pig from birth (Gillespie, 1974).

A caveat is necessary here. Guinea pigs are notoriously difficult to train, and our infant guinea pig preparation compounded this problem. We were, therefore, forced to devise special procedures to get these infants to run, so there are a large number of specific procedural factors that differ between our infant guinea pigs and infant rats, which are also not easy to train. One obvious factor is the nature of the reward. Our operating principle with infants of both species has been to devise procedures of deprivation, reward, and pretraining that will get these animals to approach the goal consistently on the first few training trials. In the case of the infant rat, as in the goalbox placements in the guinea pig, for example, we always give "priming" trials in which the pup is placed directly on the nipple of the anesthetized dam in the goalbox to facilitate later training to approach.

In addition to the reported running time differences, we also have observed a striking difference in the vocalizations in the CRF and PRF groups, which, unfortunately, we did not anticipate and record. Specifically, early in acquisition the guinea pigs in the PRF group would squeak repeatedly upon encountering the empty food dish on the early nonreward trials. (This vocalization early in PRF acquisition on nonreward trials was apparently an indicant of frustration related to the strong reward expectancy generated by the many goalbox placements and priming trials that were required to get the guinea pig pups to run in the alley. And this heightened frustrative emotionality might have been the cause of the more vigorous performance in the PRF than in the CRF subjects early in training.) The vocalization gradually diminished, so that by the end of acquisition, the PRF animals were quiet on both reward and nonreward trials. In contrast, the CRF subjects were quiet throughout acquisition. In extinction, whereas the PRF subjects were relatively quiet, the CRF subjects began to vocalize vigorously in the goalbox.

These observations parallel findings of two earlier experiments. In one, involving the precocial domestic chick (Amsel, Wong, & Scull, 1971), distress calling recorded in the goalbox was greater early in acquisition in the PRF than in the CRF groups, declined to zero in both groups by the end of training, and was intense early in extinction in the CRF but not the PRF group. In another, involving 11-day-old rats (Amsel, Radek, Graham, & Letz, 1977), ultrasounding that had virtually disappeared during the acquisition of an approach-to-dam response increased approximately 20-fold over the course of extinction. The pattern of vocalization in all of these experiments is thought to reflect the emotional response of primary frustration to nonreward, which is either not present in CRF or is reduced in PRF acquisition and reap-

pears in extinction, particularly under CRF conditions.

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