Self-stimulation in pigeons: The problem of "priming"

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In an experiment designed to investigate the roles of deprivation and priming in self-stimulation in pigeons, two of eight birds for which electrical stimulation of the brain (ESB) had previously been shown to be rewarding self-stimulated at good rates irrespective of state of deprivation or priming. The other six birds responded poorly whether satiated, hungry, or thirsty, despite the delivery of externally-paced priming shocks. It is concluded that self-delivered ESB is more effective than externally-paced ESB in initiating self-stimulation; this is taken to be a consequence of the interaction of rewarding and aversive effects of ESB.

In a study of rewarding and punishing systems in pigeon brain (Macphail, 1966), it was shown that ESB at certain forebrain sites could sustain responding in hungry pigeons when given for each response during extinction periods (in which no food rewards were given) following acquisition periods in which wheat was delivered for every tenth response, and ESB for each response. Where ESB was shown to have this effect, it was taken to be rewarding; however, subsequent results showed that many of the Ss for which ESB had been classified as rewarding would no longer self-stimulate when satiated. The most likely explanations of this failure to respond appeared to be either that ESB is rewarding only when delivered to deprived Ss or that Ss need to be "primed" to respond, and that this was accomplished in the original experiment by the ESB delivered during acquisition periods.

The present experiment was designed in an effort to separate out the effects, if any, of deprivation and priming, and to see whether any effects attributable to deprivation were peculiar to food deprivation.

Method

A pair of bipolar electrodes was implanted in the brains of 10 adult pigeons (*Columba livia*). ESB delivered to eight of the Ss (the experimental group) had been classified as rewarding by the test described above, and ESB delivered to the two control Ss had been shown to have no effect on either acquisition or extinction period responding, and was classified as neutral.

Ss were tested in the Skinner box in which the food-reinforced acquisition and extinction sessions had been run; the food tray was removed from the apparatus to minimize food directed responding.

Experimental group. The procedure on each day of the experiment was the same, only the state of deprivation of the Ss being varied.

Basically, the design was as follows: each bird was placed in the box for 15 min., and allowed free access to the response key throughout that time. Each key-pecking response resulted in the delivery to the S of an 0.4 sec. train of ESB at an intensity previously shown to sustain extinction period responding. During the middle 5 min. of the 15 min. period, the experimenter delivered 10 0.4 sec. trains of ESB every 30 sec., making 100 "free" shocks in all. Each series of 10 shocks was evenly spaced over a period of approximately 7 sec.

This sequence was, however, interrupted if an S made more than 10 spontaneous responses in the period of access; in this case, the num-

ber of responses made in the minute in which the tenth response occurred was recorded, and the bird was allowed a further 9 min. free access to the key, responses during that time being counted. No free shocks were administered after a bird had made its tenth response.

Hence, if a bird made less than 10 responses, it was in the box for 15 min., and received 100 free shocks; a bird that made 10 or more responses could be in the box from 10 to 24 min., and receive anything from 0 to 100 free shocks, according to the minute in which it made its tenth response.

There was one session per day, and there were nine days testing. On the first two days, Ss were satiated with food and water; on the third, fourth, and fifth days, they were deprived of water 24, 48, and 72 hr. respectively. Ss were allowed five days to recover from the water deprivation, during which time they were given food and water ad lib, and were, on the last four days of testing, 24, 48, 72, and 96 hr. food deprived.

Control group. The procedure for the controls was identical, except that no ESB was delivered at any stage.

Histological verification of the loci of electrode tips has been obtained for all Ss. Placements were as follows: No. 13, No. 31— anterior lateral hypothalamus; No. 15, No. 22—neostriatum; No. 18—ecto-striatum; No. 17, No. 24—paleostriatum; No. 9—septal area, midway between the medial and lateral forebrain bundles; No. 36, No. 38—optic tract.

Results

The results are summarized in Table 1, in which the scores shown are the number of responses in either the entire 15 min. period, where less than 10 responses were made, or the 10 min. period including the minute in which the tenth response was made.

Only two Ss, No. 15 and No. 17, responded at rates comparable to those achieved in extinction periods following withdrawal of food reward. Neither control S responded at all until 48 hr. food deprived.

There was no evidence that the free shocks had any effect; of the Ss that did respond regularly, No. 17 was given no free shocks on any occasion, No. 15 received shocks on only one, and No. 13, on two days. As for the other experimental Ss, on nine of the 12 occasions on which any of these Ss exceeded 25 responses, no free shocks had been delivered.

Table 1.

S	Mean number of responses when satiated	Mean number of responses when water deprived	Mean number of responses when food deprived
Experimental group			
9	0	0	2
13	46	82	67
15	100	386	282
17	376	364	618
18	26	19	77
22	0	14	18
24	0	0	65
31	0	16	38
Control group			
36	0	0	2
38	0	0	34

Owing to the poor responding obtained in this experiment, little information on the effect of deprivation could be gained. There is a suggestion, in the scores of No. 15 and No. 17, that there may be some significant link between self-stimulation and states of deprivation, since both these birds responded more on all four days of food-deprivation than on the two days satiation testing; No. 15 responded rather more under conditions of water than food-deprivation, whereas No. 17 showed the reverse effect.

Discussion

The fact that six of the experimental Ss performed poorly irrespective of their state of deprivation indicates that, for these Ss, the presence of acquisition periods was an important factor in the ESB sustained responding obtained in the earlier experiment. The failure of the free shocks delivered in the present experiment to initiate responding raises the question whether the acquisition periods played some function other than that of priming Ss; for example, it might be argued that ESB was merely disrupting the learning processes that normally lead to extinction. This proposal clearly cannot explain the behavior of birds No. 15 and No. 17, for which the conclusion that ESB is rewarding seems inescapable. A more economical account of these results may be sought in an explanation of the failure of the free shocks to prime Ss in this experiment.

Priming has been shown to be an important factor in self-stimulation in rats (Wetzel, 1963), and two explanations of its significance have been advanced. The first (Wetzel, 1963) proposes that the need for priming reflects the interaction of rewarding and aversive effects of ESB, the second (Deutsch, 1963), that it is due to the fact that the "drive" for ESB is generated by the ESB itself. Deutsch's proposal suffers from the difficulty that not all Ss require priming (Wetzel, 1963); the present results confirm that in pigeons, also, priming is not a necessary requisite of self-stimulation.

The adoption of Wetzel's account allows a tentative explanation of the failure of free shocks to prime Ss in this experiment; for if it is assumed that priming alters the balance of rewarding and aversive effects of ESB, two differences between ESB received during acquisition periods, delivery of which is determined by the S, and externally paced free shocks assume significance. The first is that self-delivered shocks may be patterned by Ss to optimize any change in the balance of rewarding and aversive effects, the second, that the time of arrival of self-delivered shocks is "known" to the Ss. That either or both of these factors may be of importance

is indicated by two experiments on rats: Meyers & Valenstein (1964) found that, as the intensity of brain-shock was raised, thus increasing the probability of recruiting aversive fibers, so did rats' preference for self-delivered over externally-paced shock. Lockard (1963) showed that rats in a two-compartment box would choose the compartment in which a warning signal preceded unavoidable foot-shock in preference to one in which the same physical stimulus was presented, but not correlated with foot-shock. This finding may be taken to indicate that the strength of aversive stimulation may be reduced through foreknowledge of its time of arrival, perhaps through some anticipatory defensive response.

The possibility that ESB is disturbing extinction in some Ss cannot be ruled out on the basis of this experiment, but the account proposed here is the most economical available, with the further assumption that the interactions suggested are the consequence of the simultaneous activation of anatomically contiguous rewarding and punishing fibers; for it has been shown (Macphail, 1966) that there are aversive sites in the avian fore-brain, and that "ambivalent" behavior is obtained in areas where it seems likely on anatomical grounds that rewarding and punishing fibers are being simultaneously stimulated. Subsequent work, (Macphail, in preparation) has shown that, in a different situation, ESB does not disrupt extinction, and that it can reinforce learning of a discrimination in an apparatus not previously associated with conventional reward.

References

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