Effect of amygdaloid lesions in a fear conditioning situation not involving instrumental learning

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Twelve amygdaloid lesioned and 18 control rats received 200 5-sec shocks in either the black or white side of a two-compartment box. Ss spent an equal length of time without punishment in the opposite colored compartment. The partition separating the two compartments was removed and the time Ss spent on each side in two 10-min test sessions was recorded. Control animals avoided the shock color by staying on the "safe" side approximately 80% of the time; in contrast, amygdaloid Ss spent scarcely half their time on the nonshock side, although they did display a highly significant preference for the black side regardless of whether or not they had been shocked there. The role of the amygdala in aversive conditioning situations was discussed.

Considerable evidence shows that amygdaloid lesions impair learning which is based on aversive motivation (e.g., King, 1958; Robinson, 1963; Horvath, 1963; Ursin, 1965; Pellegrino, 1968). The deficit is not due to sensory or motor dysfunction nor apparently to a lessening of general learning ability. Amygdalectomized animals display essentially normal unconditioned fear and motor reactions to the onset of electric shock, yet are slow to acquire the appropriate response (whether active or passive) in anticipation of the shock.

Avoidance learning can be thought to entail two separate conditionings (Mowrer, 1947)—one being the classical conditioning of an emotional response (fear) to the CS. The second factor is the instrumental avoidance response itself, which is elaborated as the escape response becomes conditioned to fear-produced stimuli and hence moves forward in time to antedate the US. Amygdaloid lesions could impair avoidance performance by interfering with fear conditioning or, alternatively, by preventing the attachment of the correct instrumental response to fear-produced stimuli. In the usual avoidance learning paradigm, these two conditionings are temporally overlapping. One cannot necessarily infer that because S fails to learn an avoidance task that he did not acquire the conditioned emotional response.

The purpose of the present study was to investigate the effect of amygdaloid lesions on conditioned fear in a situation which did not entail the acquisition of a new instrumental response. To this end, Ss were given a series of classical fear conditioning trials with no possibility of their escaping or avoiding shock, and tested later (without further shocks) in a simple choice procedure wherein they were allowed to choose between the stimulus which had been associated with punishment and a stimulus which had not been paired with shock.

METHOD

Subjects

The Ss were 30 Sprague-Dawley male albino rats who were approximately 120 days old at the start of the experiment. The animals were individually housed with food and water continuously available. Twelve animals received bilateral lesions of the amygdala, 12 were unoperated, and six received sham operations in which an electrode was lowered into the brain, but no current passed.

Surgery and Histology

Surgery was performed while Ss were under Nembutal anesthesia (60 mg/kg). Lesions were made by passing a 2.0 mA anodal current for 30 sec through a stainless steel electrode, insulated except for 1 mm at the tip. The electrode was stereotaxically aimed at the basolateral amygdaloid complex. Holes were drilled in the skull 1.3 mm posterior to bregma, 3 mm lateral to the midline, and the electrode was angled in so that at target the tip would be at lateral 5.0 mm at a depth of 9.3 mm below bregma. Ss were given at least two weeks to recover from surgery before training began. At the conclusion of the experiment the animals were sacrificed with ether and their brains removed and fixed in formalin. Subsequently, the brains were sectioned on a freezing microtome at 50 μ. In the area of the lesion every fifth section was photographed and enlarged for analysis. Examination of the histological material revealed damage to the basolateral amygdala in each experimental animal. Of other areas which sustained damage, the corticomedial amygdaloid nuclei and pyriform cortex were most frequently involved. There was no discernible relationship between the extent of amygdaloid destruction nor of insult to extra-amygdaloid areas and performance during the tests.

Apparatus and Procedure

The apparatus was a 24 x 8 x 7 in. plywood box, divided by a removable center partition into two equal-sized compartments. The roof of the box was Plexiglas and its floor was a grid made of ¼-in. diam steel rods, separated at their centers by ½ in. One compartment was painted black, the other was white. Electric shock could be delivered to the grid through a Variac. Shock duration and intershock interval were automatically controlled by electric timers.

During the fear conditioning phase of the experiment Ss received eight sessions of shock trials (S) in a distinctively colored compartment and eight sessions of no-shock experience (NS) in the opposite colored compartment. Half the Ss were shocked in black, half in white. A shock session consisted of 25 5-sec shocks separated by 20-sec intershock intervals. Shock level was adjusted for each S so as to produce moderate "dancing" and squeaking behavior, but averaged about 1.0 mA. On nonshock days S was simply placed in the appropriate compartment for 625 sec. Shock and no-shock trials were administered in the following sequence: S, NS, NS, S, S, NS, S, NS, NS, S, NS, S, S, NS, NS, S. Experimental sessions were spaced 48 h apart.

The strength of fear conditioning was assessed by placing S in the apparatus for 10 min with the center partition removed. Electric timers recorded the time S spent on the black and white sides. Ss were given two such preference periods, separated by 48 h. Half the animals were initially placed in the shock color, half in the safe color; for the second test they started in the opposite colored compartment.

RESULTS AND DISCUSSION

There was no significant difference between the performance of sham and nonoperated Ss, hence their data were combined. Also because of lack of a significant difference, results of the two test sessions were combined. Control animals showed a marked preference for the nonshock side, where they spent 79.51% of their test time. In contrast, amygdaloid Ss spent barely half (50.23%) of the preference period in the nonshock compartment, although they by no means chose sides randomly. Overall, the operated Ss spent 73.46% of the test time on the black side (71.72% for those who had been shocked in white and 75.55% for those shocked in black). For each S, time spent in the shock color was subtracted from time in the nonshock compartment. A two-way analysis of variance was performed on these

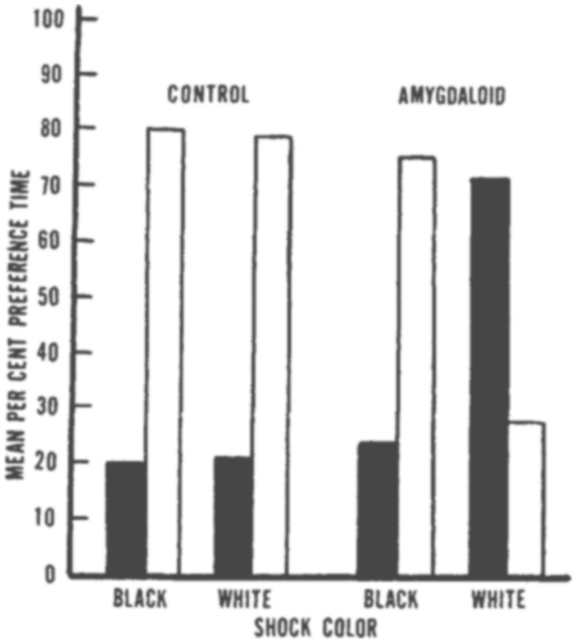

Fig. 1. Mean per cent time spent in nonshock (nonshaded bars) and shock (shaded bars) color compartments during preference testing. To illustrate a Lesion by Color interaction, results are presented separately for subgroups who were shocked on the black and white sides.

difference scores, with Lesion as one factor and Color as the other. The Lesion effect was highly significant ($F = 14.62$, $df = 1/26$, $p < .001$). Due to the strong color preference of amygdaloid animals, the effect of compartment Color was significant ($F = 7.16$, $df = 1/26$, $p < .02$), as was the Lesion by Color interaction ($F = 10.97$, $df = 1/26$, $p < .01$).

Goddard (1964) suggested that amygdaloid lesions impair the mechanism by which fear becomes conditioned to stimuli which precede punishment; Horvath (1963) felt that the avoidance decrement was due to loss of a more complex integrative function. The present findings indicate that amygdaloid lesions can produce inappropriate behavior in an aversive conditioning situation which is so simple as not to require learning of a new instrumental response. That the operated Ss could discriminate between the two compartments is evident from the fact that they significantly preferred the black side. Pellegrino (1968) has reviewed evidence showing that amygdaloid lesions impair the inhibition of learned responses. Since rats have a natural preference for dark places, it is possible that the amygdala is also involved in the suppression of unlearned response tendencies. Although the data offer no contradiction of the view that the amygdala is basic to the process of fear conditioning, our observations of operated Ss caused us to reject so simple an hypothesis. These animals appeared to be, if anything, more frightened during testing than control Ss. The deficit seemed to involve less the lack of conditioned fear than their inability to utilize fear as the cue for choice.

A not infrequent observation in neuropsychological investigations has been that by some criteria an animal appears to be normally motivated, yet by others not. According to Miller (1959), drives are defined by three distinct properties: they have nonspecific energizing effects; they have a cue or steering function; and, finally, drive reduction is reinforcing. We would speculate that in an amygdalectomized animal a stimulus, after pairing with shock, comes to elicit a nondiscriminated aversive emotional response—a "sham" fear whose stimulus consequences do not readily become conditioned to or elicit appropriate motor activities. Other possibilities are that amygdaloid Ss display supernormal generalization of fear (or fail to extinguish such generalized fear) or that they are deficient in the mechanism by which fear reduction is reinforcing.

REFERENCES

GODDARD, G. V. Functions of the amygdala. Psychological Bulletin, 1964, 62, 89-109.

HORVATH, F. E. Effect of basolateral amygdalectomy on three types of avoidance behavior in cats. Journal of Comparative & Physiological Psychology, 1963, 56, 380-389.

KING, F. A. Effect of septal and amygdaloid lesions on emotional behavior and conditioned avoidance responses in the rat. Journal of Nervous & Mental Diseases, 1958, 126, 57-63.

MILLER, N. E. Liberalization of basic S-R concepts: Extensions to conflict behavior, motivation, and social learning. In S. Koch (Ed.), *Psychology: A study of a science.* Vol. 2. New York: McGraw-Hill, 1959.

MOWRER, O. H. On the dual nature of learning—a reinterpretation of "conditioning" and "problem solving." Harvard Educational Review, 1947, 17, 102-148.

PELLEGRINO, L. Amygdaloid lesions and behavioral inhibition in the rat. Journal of Comparative & Physiological Psychology, 1963, 65, 483-491.

ROBINSON, E. The effect of amygdalectomy on fear-motivated behavior in rats. Journal of Comparative & Physiological Psychology, 1963, 56, 814-820.