Avoidance behavior in the rat following insular cortical lesions

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Rats with insular neocortical lesions were trained on three passive-avoidance problems. Two of these problems included a food incentive, while the third problem was devoid of any food incentive. Animals with insular lesions showed a deficit in acquiring the passive-avoidance response on the food-related problems but quickly adopted the avoidance response on the problem without the food incentive. Results are interpreted in terms of consummatory response inhibition.

Rats with bilateral lesions of the insular cortical area do not readily inhibit a previously dominant motor response (Kaada, Rasmussen, & Kveim, 1962; Paré & Dumas, 1965). These animals are deficient in adopting a passive-avoidance response. This notion is further supported by the fact that stimulation of the orbito-insulo-temporal cortex exerts strong inhibition on somatomotor activities (Kaada, 1960). Therefore, for animals subjected to a passive-avoidance procedure, the insular cortical lesions represent a release phenomenon (Kaada, 1951; Kaada et al, 1962).

An alternative explanation would consider the possibility that the insular region is also concerned with the mediation of consummatory behaviors in addition to the inhibition of somatomotor responses. The author (Paré & Dumas, 1965) previously observed that rats with insular cortical lesions were deficient in acquiring a passive-avoidance response but readily adopted an active-avoidance response. Whereas both tasks required an avoidance response to shock, the passive-avoidance task required the animal to inhibit an approach response to food in order to avoid shock. The shuttlebox was the basis for the active-avoidance problem. The learning deficit manifested on the passive-avoidance problem may have been attributable to the inability of these rats to inhibit ongoing behavior, as suggested earlier. Another explanation considers the fact that a food incentive contributed to the motivational complex of the passive-avoidance problem and was absent from the active-avoidance task. This point is especially relevant, since it has been postulated that insular cortical lesions involve neural structures concerned with food and self-preservation. The insular cortex of the rat is the homologue of the posterior orbital, anterior insular, and temporal polar cortex of primates, which Pribram & Bagshaw (1953)

define as the frontotemporal cortex; they relate the function of taste to the insular portion. MacLean (1958) concludes that the frontotemporal cortex is concerned with survival mechanisms involved in obtaining and assimilating food. The present study was designed to explore the extent to which a food incentive influences the passive-avoidance deficit of insular lesioned rats. The effect of insular lesions was observed on three passive-avoidance problems. Two of these problems included food-reinforced responses, whereas the third problem did not involve a food incentive. It was hypothesized that rats with insular lesions would manifest an avoidance learning deficit on food-related problems but would readily acquire the avoidance response in the problem that was devoid of a food incentive.

EXPERIMENT 1

Method

Forty-nine male Long-Evans rats were used in all three experiments. These animals were approximately 92 days old at the beginning of the study. Rats were assigned randomly to three treatment groups: an insular neocortical group (N = 26), an operated control group (N = 12), and a normal control group (N = 11).

Surgery was performed under Nembutal anesthesia (40 mg/kg). Ablations were performed while the animal's head was held in a stereotaxic instrument, and tissue was aspirated with a micropipette. Operated control Ss received the same treatment minus the aspiration of cortical tissue. Twenty days postoperatively, Ss received training on the first passive-avoidance problem.

The apparatus in the first experiment consisted of a runway, 54 x 4 x 9½ in. high. A guillotine door was situated 11 in. from the starting end and formed the startbox. Another guillotine door separated the goalbox from the runway. A foodcup was situated in the far wall of the goalbox. The runway had a wood floor; the goalbox floor consisted of brass rods spaced ½ in. apart.

All animals were maintained at 80% of their ad lib body weights. For 5 days all rats received 10 acquisition trials each day in the runway. A trial consisted of placing the animal in the startbox and opening the guillotine door. After the animal had entered the goalbox and consumed the two 45-mg food pellets, it was returned to the

Fig. 1. Mean running time in seconds for the three treatment groups. The shock trial was presented on the fourth trial on the sixth day.

Fig. 2. Mean inflection ratios for the three treatment conditions. A value at, or near, .00 indicates little or no change in response rate during the CS-tone interval. A + value indicates an increase in response rate, and a - value denotes a suppression in response rate during the tone period.

startbox. Running time was recorded for each trial. On the fourth trial of the 6th day, the S received a 2-sec 0.5-mA grid shock when the food pellet was collected. Subsequent trials on that day and for 2 more days were run without shock and were identical to those trials administered during the first 5 days. A passive-avoidance response was manifested by remaining in the startbox subsequent to the shock trial.

Results

On the postshock trials, control animals showed a marked increase in running-time scores (see Fig. 1). Insular neocortical rats showed a temporary increase in running time after shock but quickly returned to the preshock level on Days 7 and 8. Animals with insular lesions manifested a significant deficiency in acquiring the passive-avoidance response, as indicated by running-time scores ($F = 81.92, p < .001$).

EXPERIMENT 2

Experimental animals failed to adopt the avoidance response, which involved a food incentive in Experiment 1. This phenomenon was also investigated in a second study, wherein the S was required to inhibit a response instrumental in the acquisition of a food reward.

Method

The experimental apparatus consisted of a typical operant-conditioning chamber, 9 x 11 x 8 in. high. A manipulandum

was located 2 in. above the grid floor.

All rats, still maintained at 80% of their body weights, were trained to depress the manipulandum in order to obtain a 45-mg food pellet. After a stable response rate had been established, all Ss received one conditioned emotional response (CER) trial daily for 8 days. A CER trial involved the introduction of a "beeping" tone for a 3-min period, followed immediately by a 1-sec 0.5-mA shock via the grid floor. The number of responses emitted during the 3-min periods before and during the tone were recorded. A passive-avoidance response was characterized by a reduction of barpressing responses during the tone period.

Results

During CER trials the control Ss readily suppressed the operant response. Experimental animals failed to manifest a response suppression. This effect is illustrated by the inflection ratio, $B - A/A$, where A represents the number of responses occurring during the 3-min period before the tone and B represents the number of responses occurring during the 3-min tone period. Mean inflection ratio values for the three treatment groups are shown in Fig. 2. Normal control and operated control animals manifested a gradual suppression, whereas insular neocortical animals kept responding at the same pretone levels.

EXPERIMENT 3

A third experiment was performed in order to observe a passive-avoidance response that did not involve a food incentive. For this study all animals were returned to their ad lib body weights.

Method

The apparatus consisted of a 6 x 6 in. platform, mounted 2 in. above the floor and located inside an enclosed area which measured 20 x 20 in., with 18-in.-high walls. The floor consisted of a wire grid with wires spaced $\frac{1}{2}$ in. apart.

Rats received one trial daily for 4 days. A trial consisted of placing the rat on the platform. The high-probability response was for the rat to quickly step off the platform onto the wire grid floor. The time interval between platform placement and the step-off response was automatically recorded and constituted the response latency measure. After 30 sec in the apparatus, the rat was returned to its home cage. On Day 3 the animal received a 1-sec 0.5-mA shock upon stepping from the platform to the grid floor. A passive-avoidance response was manifested on Day 4 by remaining on the platform for the duration of the trial.

Results

All Ss showed a very short step-off latency on the two preshock trials. Latency scores averaged less than 4 sec for the preshock trials (see Fig. 3). However, on the postshock trial the average latency scores were approximately 20 sec. A

Fig. 3. Mean step-off response latency scores for preshock trials and the postshock trial.

Fig. 4. Reconstruction of lesions of a representative group of animals from the experimental group.

Kruskal-Wallis analysis of the step-off latency scores for the postshock trial failed to reveal significant differences between treatment groups.

Histological evaluation of brain tissue revealed that the bilateral ablations involved areas along the rhinal fissure. This included Areas 13 and 20, according to Krieg's (1946) designation, and is referred to as insular cortex by Krieg (1946) and Kuhlenbeck, Szekeley, & Spuler (1960). The ventral portion of this *regio insularis* overlies the claustrum. Figure 4 shows the brain reconstructions of representative animals from the experimental group.

DISCUSSION

These experiments would indicate that animals with bilateral insular cortical lesions are deficient in learning a passive-avoidance response in a problem situation that involves food seeking, but readily adopt the passive-avoidance response in a problem situation that does not require food seeking. The insular cortex may be concerned with mechanisms that are involved in obtaining and assimilating food and thereby essential to self-preservation. However, there are certain aspects of the present study that should be

discussed first, before the above interpretation is accepted.

There is some question as to whether the CER task actually involves a true passive-avoidance response. Although the typical response suppression manifested by most animals in this situation represents an inhibition of the previously dominant approach response to food, the passive response of not barpressing does not result in shock avoidance, since shock is stimulus contingent and not response contingent. This slight modification in the passive-avoidance procedure may introduce additional dimensions to the problem that are not accounted for here.

Another consideration is the problem sequence. The runway problem was followed by the CER problem, which in turn was followed by the platform problem. Since the task presentations were not counterbalanced for different groups of animals, it is impossible to partial out the possible cumulative training effects inherent in this design. This is an important consideration, especially since the least difficult problem (i.e., the platform problem) was presented last. The training on the first two

problems may have obscured possible differences between groups on the last problem.

An alternative explanation for the present results could include the possibility that animals with insular lesions were less sensitive to grid shock and, therefore, were not motivated to inhibit the approach response. The lack of differences between treatment groups on the platform experiment in this report and the fact that insular animals learn a shock-motivated active-avoidance response as well as controls (Paré & Dumas, 1965) would argue against this explanation.

Response inhibition appears to be the most reasonable explanation at this time, especially if inhibition is concerned with responses directed to the acquisition and assimilation of food. This interpretation receives further support from the fact that the cortical areas in question have demonstrated somatomotor inhibitory functions and have been implicated in the processes of searching, sniffing, and tasting food.

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