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ELABORATION OF CONDITIONED ALIMENTARY REFLEXES HAVING DIFFERENT PROBABILITIES OF REINFORCEMENT IN RATS WITH HIPPOCAMPAL LESIONS

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Abstract. A motor alimentary conditioned reflex was elaborated in hippocampectomized and intact albino rats. Food reinforcement followed 100%, 50%, 33% or 25% of conditional stimulus presentations (click from a rotating food box). No differences were found in the rate of conditioned alimentary reflex elaboration between the hippocampectomized and control rats at 100% and 50% reinforcement, although the time-courses of formation of the conditioned reflex connection differed substantially. With low reinforcement probabilities (33% and 25%) the operated rats, unlike the intact ones, exhibited no adequate responses throughout the 10 experimental days. The results obtained corroborate an earlier suggestion that the hippocampus is involved in the organization of behavior the reinforcement probability of which is unknown or relatively low.

INTRODUCTION

In recent years, an increasing number of investigators have been become interested in the mechanisms involved in the evaluating probabilistic properties of the environment by man and animals (2, 14). Lesions of certain areas of the neocortex have been shown to impair the ability to develop adequate probabilistic responses (4, 13).

A large body of evidence reported suggests that the hippocampus belongs to the system involved in assessing the informational properties of the environment. This is indicated, in particular, by strong hippocampal involvement in the initial period of conditioned reflex (CR) elaboration (5), when the probability of reinforcement is still unknown to the animal; by the absence of an effect of hippocampal lesions when the CR has consolidated (6, 11); and by behavioral disturbances in hippocampectomized rats following a change from constant to partial reinforcement (1, 21).

At the same time the fact that the data available in the literature on the role of hippocampus in CR activity are often extremely contradictory, indicates that the procedures employed to study this problem have been inadequate. As confirmed in subsequent experiments, it seemed that a valuable tool for the neurophysiological study of CR's might be a model of conditioned switching which has been comprehensively investigated in Asratyan's laboratories. It has been found that a tonic (switching) stimulus may bring about functional changes not only in cortical elements of the temporary connection (20) but also in the hippocampus (19).

The present experiments have shown that the switching of the alimentary and defense CR's to the same stimulus (bell ring or light) is elaborated much faster in rats with hippocampal lesions than in intact rats or in control rats with destruction of parietal cortex (Fig. 1). Similar results have been obtained when different types of switching were used such as time of the day or flickering light, as well as when use was made of a more complex simultaneous switching of the alimentary and defensive CR's, a switching which intact rats are essentially unable to perform (18) (Fig. 2 and 3). Additional experiments have demonstrated further that the acceleration of switching cannot be explained either by specifics of the defense reflex, or by a weakening of the emotional response of fright, or by the memory disturbances.

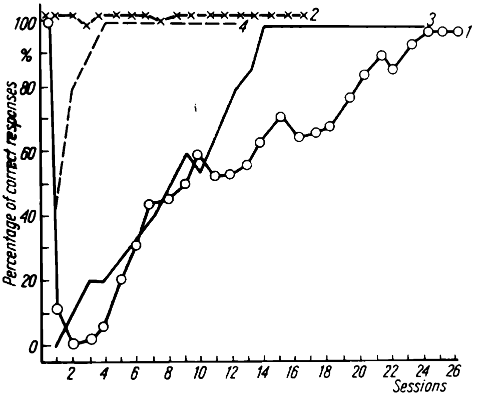

Fig. 1. Percentage of correct alimentary CR's in morning sessions in intact (*1*) and hippocampectomized (*2*) rats and of defensive responses in afternoon sessions in intact (*3*) and hippocampectomized rats.

When interpreting the accelerated elaboration of CR in hippocampectomized rats (16, 17, 22), it has been concluded that in the integrative activity of the brain, the hippocampus appears to enable the animal to respond to those signals the reinforcement probability of which in unknown or very low. The behavior of hippocampectomized rats in CR switching is oriented to signals from events that are highly probable in a given situation and is no longer complicated by low-probability events,

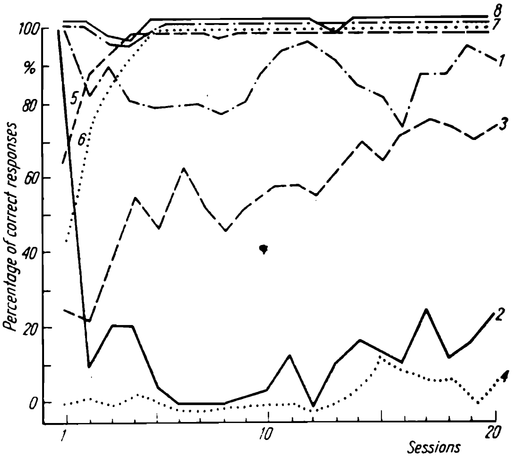

Fig. 2. Percentage of correct responses in sessions during elaboration of double switching-over. Designations for intact rats: defensive (*1*) and alimentary (*2*) CR's for morning sessions and defensive (*3*) and alimentary (*4*) CR's for afternoon sessions; for hippocampectomized rats: defensive (*7*) and alimentary (*8*) CR's for morning sessions and defensive (*5*) and alimentary (*6*) CR's for afternoon sessions.

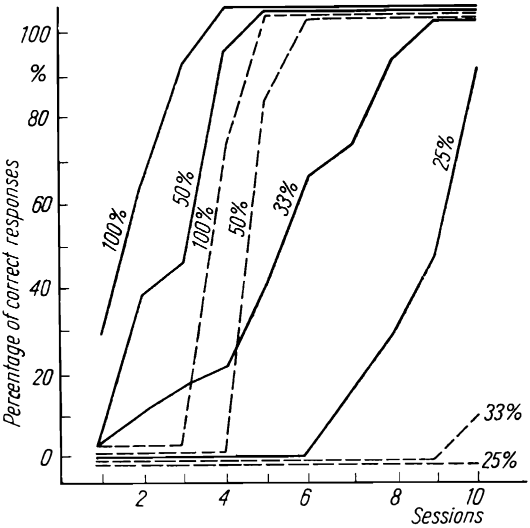

Fig. 3. Time-course of alimentary CR elaboration in intact (solid line) and hippocampectomized (broken line) rats at different probabilities of reinforcement.

such, for example, as the possibility of painful stimulation in an alimentary situation. Hippocampal lesions thus reduce the emotional tension which is particularly characteristic for the switching of heterogeneous CR's (23).

This conclusion was in need of direct proof; that is it was necessary to obtain more precise information about the effect of hippocampal lesions on the formation of temporary connections at relatively low probability of reinforcement. The interpretation of the data available (1, 2) is complicated by the effect of perseveration following hippocampal lesions an effect which is usually considered to result from impairment of the inhibitory process (7, 8).

METHODS

Adult male albino rats were used. Ten days prior to the experiment, in 20 rats the hippocampus was bilaterally damaged by electroagulation with a special electrode according to the method of Mering (15); 20 other rats were used as non-operated controls.

CR was elaborated in a chamber 30 x 50 cm. In the center of the chamber was a food box with 50 compartments into which food (white bread) was placed before the experiment. The CR was a click from the rotating food box. In term of reinforcement, there were four groups of rats with 100%, 50%, 33% and 25% reinforcement, respectively; that is food accompanied each food box rotation or on a half, a third or a fourth of rotations. Each group thus included 5 intact and 5 operated rats. The sequence of reinforcement was determined from a table of random numbers. There was also the following limitation: no more then three empty compartments could be presented in a row. Ten to 15 CRs were presented at intervals of 1–3 min per ssesion. The latent period's of the responses and the interstimulus approaches to the food box were recorded. The motor activity of the animals was judged from the number of times a rat moved from the right to left of the chamber corner and vice versa during the first 10 min of the session. The CR was elaborated for a period of 10 days after which the rats were sacrificed. Histological analysis of the brain was made on sections stained by the Nissl technique. Data were analysed statistically using Student's test.

RESULTS

Figure 3 shows the mean values reflecting the time-course of CR elaboration at different probabilities of reinforcement in intact and hippocampectomized rats.

With 100⁰/₀ reinforcement, intact rats developed the CR for two to three sessions. Even in the first session, correct responses with a latent period of 7.51 ± 1.66 sec were observed. The motor activity of intact rats during the first two sessions was at a low level; they spent most of the time in the corner where they ate the food taken from the food box (Fig. 4). It was only on the 2nd–3rd day that the rats made a large number of interstimulus approaches to the food box and began to explore the chamber more intensively (Fig. 5). In the 3rd session, the latent period of the CRs decreased to 3.33 ± 1.06 sec, and was progressively reduced subsequently. The number of interstimulus approaches decreased, although it strongly varied in different rats. Motor activity remained low throughout the session because the rats mostly moved within a small area from the corner to the food box and vice versa (Fig. 4 and 5). During the first three to four sessions with 100⁰/₀ reinforcement, the operated rats exhibited increased motor activity; they intensively explored the chamber, stood up on their hindlegs and sniffed around. However they showed no adequate responses to food-box rotation despite high alimentary excitation which was evident in their immediate eating food placed before them. From time to time they also ate food from the food box although more often the food there remained untouched and they ran past it or over it without looking inside. During the 4th session, all rats of this group began to exhibit adequate responses to food-

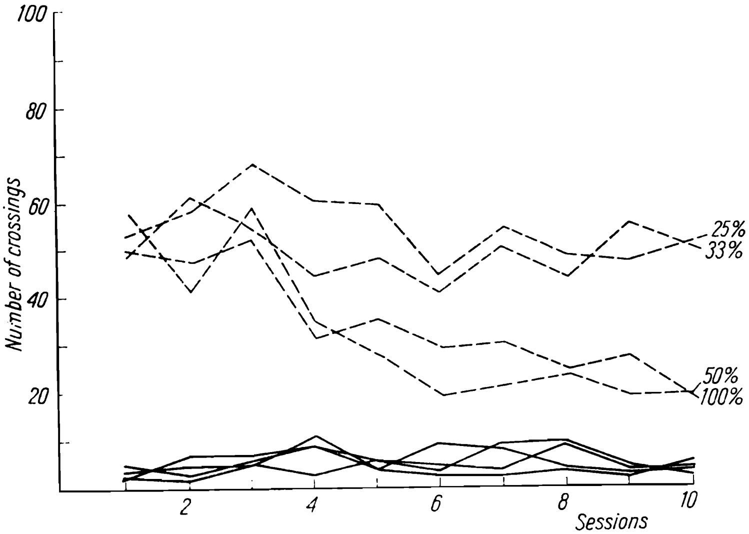

Fig. 4. Motor activity of intact (solid line) and hippocampectomized (broken line) rats during elaboration of alimentary CR.

box clicks as well as a large number of interstimulus responses (Fig. 5). On the 4th day, the latent period of the CR was 4.96 ± 1.42 sec, and on the 5th day, 3.24 ± 1.11 sec. Motor activity after four to five sessions noticeably decreased in all operated rats (Fig. 4).

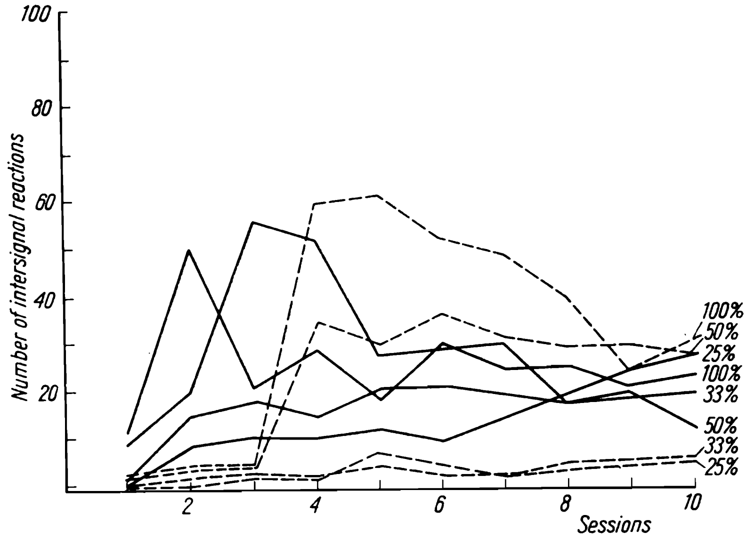

Fig. 5. Mean number of interstimulus responses in intact (solid line) and hippocampectomized (broken line) rats during elaboration of alimentary CR.

When 50% of the food-box rotations were reinforced, the intact rats approached the food box only a few (three to six) times per session, eating food 20–30 sec after the CS. Motor activity was low, as a rule. Adequate responses were observed on the 2nd day, and the latent period of responses in the second half of the 2nd session was 1.62 ± 0.36 sec.

With 50% reinforcement probability, the operated rats first showed adequate responses only on the 5th session, that is after 50–62 presentations of the CS. The percentage of correct responses during the 5th session varied from 60 to 100%, and the mean latent period was 3.01 ± 2.34 sec. In the 6th session, the rats ran to the food box on the CS 100% of the time, and the mean latent period was 1.93 ± 0.59 sec. As the CR stabilized, the motor activity somewhat decreased and interstimulus responses became fewer.

With 33% reinforcement, the rate of CR elaboration was slowed in intact rats, although adequate responses were occasionally observed in the 2nd session. The 50% level of correct responses was surpassed by all rats only on the 6th day, and the 100% level was attained on the 8th day (Fig. 3). Concurrently, the latent period decreased from 9.45 ± 2.01 to 2.13 ± 1.10 sec.

With 33% reinforcement, as well as with 25% reinforcement, the operated rats showed a high level of motor activity. They intensively explored the chamber throughout the sessions and sometimes ate bread from the food box, but a CR could not be elaborated in any of them over the 10 experimental days (150–200 presentations of the CS) (Fig. 3 and 4).

With the low reinforcement probability, intact rats likewise showed no adequate responses during the first six sessions. Their behavior, however, strongly differed from that of the operated animals as judged by motor and interstimulus activities. Motor activity was enhanced in them only during the first minutes of the session, after which they spent most of the time in the corner of the chamber washing themselves, although they made more interstimulus approaches to the food box than the operated rats (Fig. 4 and 5). After the 6th session, the percentage of correct responses progressively increased and the latent periods decreased.

For a further analysis of these results, experiments were carried out with amphetamine injection which enhances some types of motor activity in rats and speeds up the elaboration of the avoidance response (9, 10). It was of interest to compare the effects of amphetamine and hippocampectomy on reflex elaboration at different reinforcement probabilities.

Amphetamine was injected intraperitoneally in the dose of 1.0 mg/kg 30 min before the session for a total of 10 days. Otherwise, experimental conditions were the same as described above.

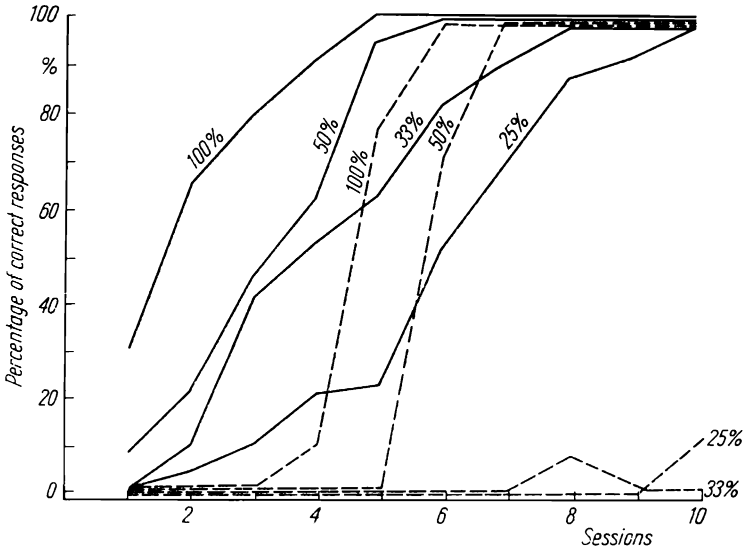

Fig. 6. Percentage of correct responses in intact (solid line) and hippocampectomized (broken line) rats following intraperitoneal injection of amphetamine (1.0 mg/kg).

Intact rats showed enhanced motor activity following amphetamine injection. Hippocampectomized rats likewise exhibited increased motor activity, though to a lesser degree (Fig. 6). The rate of CR elaboration changed slightly at 100% and 50% reinforcement in intact rats but showed a significant increase with 33% or 25% reinforcement (Fig. 7).

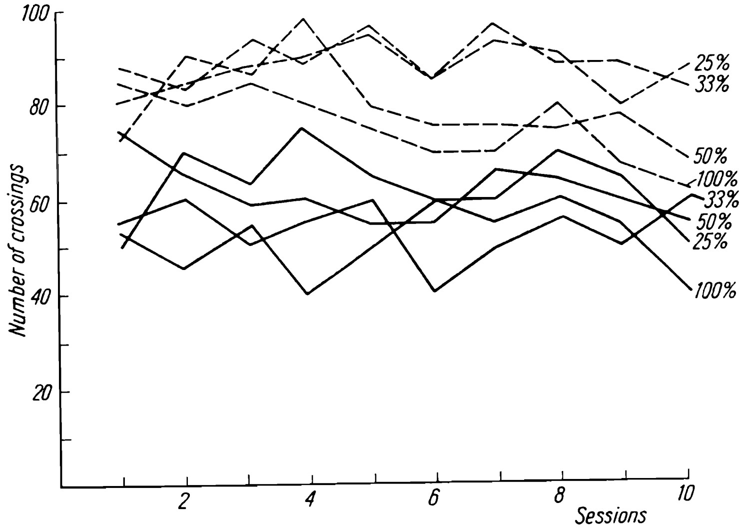

Fig. 7. Motor activity of intact (solid line) and hippocampectomized (broken line) rats following intraperitioneal injection of amphetamine (1.0 mg/kg).

Morphological controls revealed bilateral hippocampal lesions in all operated rats similar to those described previously (17). Extent of damage to the hippocampus ranged 55–90% to the structure. Neocortical damage as a rule was concerned with a trace of electrode, extrahippocampal subcortical structures were not damaged (Fig. 8).

DISCUSSION

Thus, with high probability of reinforcement, i.e., when each or a half of the presented stimuli was reinforced, intact and hippocampectomized rats showed only slight differences in the rate of CR elaboration to foodbox clicks. While the intact rats attained the 100% criterion on the 4th day with 100% reinforcement and on the 5th day with 50% reinforcement, the operated rats reached these levels on the 5th and 6th days respectively. This is consistent with the results reported by Clark and Isaacson (1) and by Frenchina and Brown (3) who found no differences in the rate of reflex formation between hippocampectomized and intact animals with 100% and 50% reinforcement. The procedure used in the present experiments, however, resulted in considerable differences in the time-courses of CR formation between these two groups of rats. Whereas the intact rats exhibited a progressive increase in the number of correct responses and a decrease of their latent periods, the hippocampectomized rats attained a high response level at once, following a complete absence of CRs for 3–4 sessions. On the following day, some rats showed a 100% incidence of responses with relatively short latent periods. With low reinforcement probability (33 and 25%), the differences between operated and intact rats were much greater. Unlike the intact rats, the operated rats showed no adequate responses throughout the 10 test days (150–200 presentations of the CS).

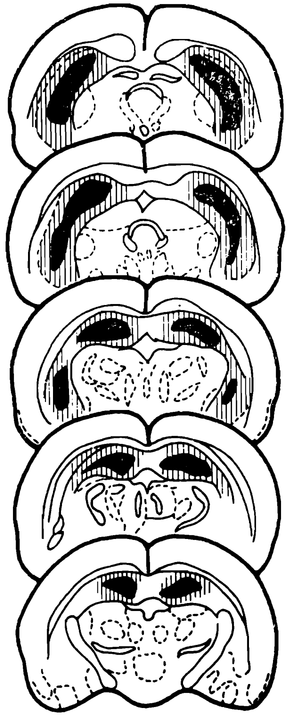

Fig. 8. Typical largest (hatching) and smallest (black) hippocampal lesions projected on diagrams of frontal section.

A noteworthy fact was hyperactivity of the operated rats which was particularly marked in the absence of CRs. As adequate responses appeared, the motor activity of such rats decreased.

There is a large number of facts in the literature indicating enhanced motor and exploratory activity in hippocampectomized animals (7, 12, and many others). The hyperactivity of hippocampectomized animals is in most cases regarded as resulting from enhanced orienting-exploratory activity rather than of general motor activity, associating it with slower habituation of animals to a novel environment (8).

In the present experiments, the motor activity of bilaterally hippocampectomized rats was essentially the same as that of amphetamine injected rats, although there were differences between these groups in the process of learning. Whereas hippocampectomy resulted in a complete failure to elaborate a reflex within the period studied when probability of reinforcement was low, amphetamine injection, on the contrary, augmented reflex formation with such reinforcement probability. The elaboration of the alimentary reflex in hippocampectomized rats receiving amphetamine remained essentially unchanged, although motor activity increased.

These results suggest that different mechanisms underlie the hyperactivity in hippocampectomized rats and in those receiving amphetamine. These results agree with the conclusion reached by Leaton (12) that hippocampectomized rats show an increase not of general motor activity but rather of the orienting-exploratory activity directly associated with learning.

Kimble et at. (7) believe that hyperactivity reflects a fall in the rate of information processing as a result of hippocampal lesions.

The learning rate of operated rats at high reinforcement probabilities differed but slightly from that of intact rats. A substantial behavioral defect was, however, observed in hippocampectomized rats with low reinforcement probabilities: none of the animals were capable of elaborating a CR when only a third or a fourth of the stimuli were reinforced.

Thus, these results support an earlier suggestion (22) that the hippocampus is involved in the organization of behavior the reinforcement probability of which is unknown or relatively low.

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