

alanine] (25 to 35 mg/kg) in two pretrigeminal preparations from cats with midbrain hemisection, the EEG asymmetry was replaced by a bilateral symmetrical activation and the acetylcholine content of the two sides showed only small differences (Table 2). The arousing effect of DL-Dopa has been attributed to a stimulating action on the reticular activating system (6). The last experiment as well as preliminary assays of the cholinesterase activity of the cortex (7) seem to rule out the possibility that the increase of cortical acetylcholine following the hemisection is due to vascular damage or to a decrease of acetylcholinesterase activity.

Our results suggest that the amount of cortical acetylcholine in the cortex may be related to the degree of activity of the reticular activating system. The EEG activated pattern of the pretrigeminal preparation is maintained by a tonic barrage of impulses arising in the rostral portion of the pons (2). The midbrain hemisection would produce ipsilateral sleep by the decrease of the number of activating impulses impinging upon the cerebral cortex (3). Several data support the suggestion that part of the fibers ascending to the cortex are cholinergic (8). It is conceivable that the resting state of ascending fibers during the EEG synchronization leads to accumulation of acetylcholine in their endings or in the cortical neurons or in both.

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Method for Discriminative Avoidance Training

Abstract. Experiments were performed in which the typical procedure for obtaining discriminated avoidance behavior with rats in a lever-pressing apparatus was compared with a new procedure which allowed only avoidance but not escape from the shock. When either escape or avoidance is possible, the rats make a majority of escape responses, but where escape is impossible avoidance behavior is rapidly established.

Discriminative avoidance procedures are used extensively in studies of the effect of drugs, brain stimulation, and other variables of interest to the medical and behavioral sciences. In such a procedure an animal is trained to perform a response in the presence of a stimulus which signals the occurrence of a noxious stimulus, such as shock, strong light, or intense sound. The response, which usually consists of pressing a lever or of running from one side of an alley to the other, terminates the signal and prevents the advent of such noxious stimulation. However, the reported difficulty of establishing a discriminative avoidance habit with rats in a lever-pressing apparatus (1) severely limits the use of this much favored experimental situation and raises several problems of a theoretical nature. This report describes a procedure in which these difficulties were overcome and which resulted in the acquisition of the required behavior.

The apparatus consisted of a metal chamber fitted with a grid floor which could be electrified. A lever, requiring a downward pressure of 10 g, was fixed at one end of the chamber, and a 6-volt lamp was placed at ceiling height immediately above the lever. Electric shock (0.6 ma) was supplied by a constant current source and was delivered through a scrambling unit which successively reversed the polarity of each rod of the grid floor, thereby making it impossible for the animal to avoid shock by locating a safe standing place.

The main feature of the procedure was that the warning signal, once presented, continued until a press on the lever was made. During presentation of the signal the noxious stimulus—shock—was given at regular intervals but did not last long enough to give the

animal an opportunity of escaping from it. In the two experiments reported here the interval between the onset of the signal and the first shock was 7.5 seconds. The interval between successive shocks in the presence of the signal was varied so as to occur, on the average, every 13 seconds. A total of 13 2-hour sessions was given, with intervals of 22 hours between each session. In the first experiment, rats were exposed to the procedure described above. In the second experiment a procedure was adopted which is commonly claimed to yield negative results.

In experiment 1, three male hooded rats, about 120 days old, were used. In each of the 13 2-hour sessions the following procedure was used. Shortly after the subject was placed in the chamber a signal (light) was presented, and unless the lever was pressed within 7.5 seconds of signal onset the first of a series of brief shocks (0.2 seconds) was delivered. These shocks occurred at irregular intervals, on the average once every 13 seconds. As soon as the lever was pressed the signal terminated and the shock series was suspended. After a variable in-

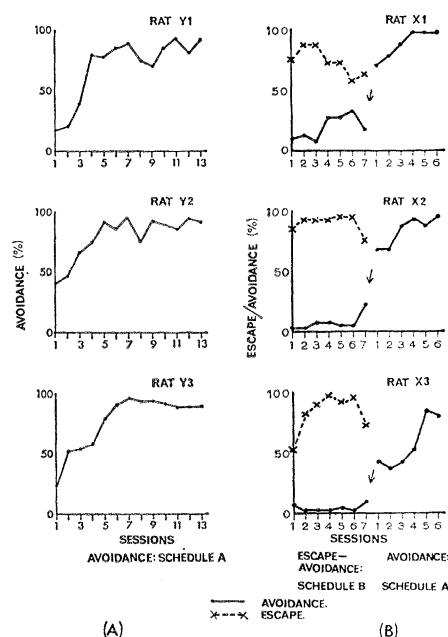


Fig. 1. (A) avoidance (percentage) as a function of the sessions conducted according to a procedure which allowed only avoidance but not escape. (B) Escape and avoidance (percentages) as functions of sessions conducted according to a procedure which allowed escape as well as avoidance. The procedure was changed after seven sessions to that used for (A).

interval (mean, 13 seconds) the signal and shock series was again introduced.

The results of this procedure are shown in Fig. 1A. All the subjects acquired the avoidance response—that is, they responded during the interval between signal onset and the first shock. This result could have been obtained if the procedure merely generated a high rate of response and had not established stimulus control over the lever-pressing habit. However, the fact that the ratio of the number of responses to the number of signal presentations tended to 1 supports a discrimination-learning interpretation.

Experiment 2 was designed so that the effects of the conventional training procedure, in which training occurs under an escape-avoidance contingency, could be examined. Three male hooded rats, approximately 120 days old, were used. The experiment was run in two phases. In phase 1, which lasted for seven 2-hour sessions, an escape-avoidance procedure was used; in phase 2, which lasted for six 2-hour sessions, the avoidance procedure outlined for experiment 1 was used.

The escape-avoidance procedure during phase 1 was as follows. Shortly after a rat was placed in the chamber, the warning signal was presented; 7.5 seconds later a shock was given which lasted for 10 seconds. If the rat pressed the lever during the interval between the onset of the signal and the onset of the shock, the signal was terminated and the shock was avoided. If the response occurred after the shock had started, the shock and signal were terminated and the response was scored as escape. The interval between successive signal-shock presentations was varied, the mean being 13 seconds. The procedure adopted for the second phase has already been described.

The results are shown in Fig. 1B. For each subject the percentage of escape and avoidance responses during phase 1 of the experiment and the percentage of the avoidance responses during phase 2 are given. The rats which were subjected to an escape-avoidance contingency primarily made escape responses. When the procedure was changed so as to eliminate the possibility of escape from ongoing shock, avoidance behavior was firmly and rapidly established. All three subjects avoided shock and reached an avoidance criterion of more than 85 percent.

The discriminative avoidance procedure described here has been used successfully to detect the effects of administering different, small doses of 5-hydroxytryptophan which had not been detectable by other behavioral methods (2).

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Effects of Cutaneous and Muscle Sensory Nerve Volleys in Awake Cats: A Study in Perception

Abstract. *The hypothesis that discharges from afferent nerves from muscle stretch receptors do not participate in kinesthesia has been substantiated by test of discrimination thresholds. In awake, unrestrained cats, nerve stimulation activating group I and most group II sensory fibers (from muscle spindles and Golgi tendon organs) in pure muscular nerves failed to evoke sensory discrimination. Cutaneous nerve stimulation in the same animals produced sensory discrimination even below intensities required to elicit detectable nerve thresholds.*

Afferent groups Ia, Ib, and II from stretch receptors in striated musculature have often been implicated in kinesthesia (1). Recent evidence in the anesthetized cat suggests that thalamic and cortical areas receive little, if any, functional contributions from Ia and Ib afferent nerves (2). Analysis of unit firing patterns to graded somesthetic stimuli, moreover, reveal extensive areas of the reticular formation and red nucleus unresponsive to the influence of low-threshold group I sensory fibers (3). Stimulation of cutaneous nerves produced pronounced effects in these same areas with very weak volleys. The absence of evoked response activity with low-threshold muscle afferent volleys implies that subjective discriminations, such as perception of limb position or muscle tension, may not be subserved

by afferent discharges from the Golgi tendon organ or muscle spindle. To test this hypothesis, experiments were performed in awake, freely moving cats with electrodes implanted on peripheral nerves.

Previous work on similar preparations has shown that group I afferent volleys in awake, unrestrained cats failed to elicit either responses in the electroencephalogram or behavioral reactions, whereas weak cutaneous volleys succeeded in eliciting orienting responses. This indicated indirectly that weak cutaneous volleys evoked conscious sensations whereas weak muscular volleys apparently did not (4, 5). Since these experiments depended upon a passive reaction on the part of the animal, it cannot be ruled out that group I sensory fibers elicited subjective sensations which were weaker in comparison with cutaneous fibers, and thereby failed to effect the electroencephalographic or behavioral activity to a degree sufficient to be noted. A more direct and accurate test of discrimination thresholds to weak somesthetic volleys was obtained by training animals to respond actively to direct stimulation of a peripheral nerve so as to indicate perception of sensory volleys.

Six cats were trained to press a bar for food rewards during a period when a signal light, or auditory click (four clicks per second), was presented. Rewards could be obtained only during these "on" periods. Bar-pressing was discouraged during "off" periods by withholding presentation of the "on" period until the animal had not pressed the pedal for at least 30 seconds. Those animals tending to press the bar in spite of continued withholding of the "on" periods learned to stop pressing during "off" periods after receiving a mild shock (0.1 ma) from the lever. Before the electrodes were implanted, training proceeded until bar-pressing performance was almost exclusively restricted to "on" periods.

Under barbiturate anesthesia electrodes for stimulating the peripheral nerves were implanted surgically on nerves in both forelimbs, a cutaneous nerve (superficial radial) on one side, and a muscular nerve (deep radial) on the other side, according to methods described elsewhere (4). In some cats the hamstring nerve of the hindlimb carried an electrode instead of the deep radial nerve. Both muscle nerves are believed to contain proportionate num-