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## EXTERNAL STIMULUS CONTROL OF SELF-STIMULATION BEHAVIOR

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Abstract. Dogs with electrodes implanted in the anterior forebrain region were successfully trained to leverpress for brain stimulation reward upon the presentation of a 1,000 Hz tonal conditioned stimulus and to withhold responding during its absence and upon a 2,000 Hz tonal discriminative stimulus. The conditioned response extinguished upon removal of reward and was promptly restored when reward became again available. The results are discussed in terms of a conditioned drive induced by the action of the cue. It is proposed that environmental factors play an important role in the initiation and maintenance of self-stimulation behavior. Brain stimulation reward may serve as reinforcer of conditioned instrumental reflexes in an essentially similar way as natural rewards.

Self-stimulation is commonly regarded as a kind of operant behavior in which both reinforcement and drive are produced by the same electric stimulus delivered to the brain reward system through chronically indwelling electrodes. Due to this dual action of brain stimulation, the animal's working for electrical reward differs essentially from behaviors reinforced with natural rewards since the required level of motivation for the latter is achieved by controlled food (or water) deprivation prior to each experimental session.

The lack of enduring humorally induced motivation is believed to account for several pecularities of self-stimulation. For more details see Trowill et al. (24). First, self-stimulation, compared to behaviors reinforced with natural rewards, appears extremely sensitive to non-reinforcement. Extinction develops promptly already after a few leverpresses or other learned movements which are not followed by brain stimulation. Second, Howarth and Deutsch (8) found that rats would fail to resume pressing for brain reward if their access to the manipulandum was hindered for a period of a few seconds. This phenomenon, termed extinction without responding, gave support to the suggestion that extinction in self-stimulation is not a function of the number of nonreinforced responses but of the time elapsing from the last brain stimulation. Third, rats when put on partial reinforcement schedule cease responding for brain stimulation sonner than for a natural reward. This is clearly evidenced when the ratio of the number of responses to the number of stimulations is gradually increased. Although rats make a remarkable number of presses for one food pellet they will stop working already at a few responses for one train of electric pulses (24).

Also, according to some data, the self-stimulating animal is to some extent "inattentive" to external stimuli. In this way Brady (6) tried to explain the lack of suppression of self-stimulation by an external stimulus which was earlier paired with a foot shock. The conditioned emotional response could be easily demonstrated when water was used as reinforcer. A similar mechanism may account for the difficulty to obtain a secondary reinforcement effect with brain stimulation reward. In the case of natural rewards, this effect develops if the animal's operant, besides causing reward (which is a primary reinforcer), also activates an external signal. The reinforcing property of the latter is evidenced as a delay of extinction when the animal's responses no longer produce reward but further switch on this signal. Another method to investigate this process is a two-lever situation, in which one of the levers activates a tone earlier associated with brain stimulation, in addition to the actual reward, and the other produces reward without the tone. The animals will press more frequently on the first lever. There is some controversy about the possibility to reproduce the secondary reinforcement effect using brain stimulation as a primary reinforcer. Positive results have been reported by Stein (21), Knott and Clayton (10), Trowill and Hynek (23) and Beninger and Milner (2), but Seward et al. (20) and Mogenson (15) obtained negative data.

Many of these patterns of self-stimulation fit well into the drivedecay theory proposed by Deutsch and Howarth (7) which claims that the electric stimulus simultaneously activates motivating and reinforcing pathways. Whereas the reinforcing effect is limited to the duration of the stimulating train, the motivating effect outlasts it for a short time and instigates the animal to perform the next response. This response triggers a new train which provides reinforcement and reactivates the drive for the subsequent response, and so forth. Nevertheless, the results of some investigations suggest that another process may be also involved in the mechanism of self-stimulation. First, if self-stimulation is based only on the positive feedback as postulated by the drive-decay theory (7), it should be necessary to administer at least one brain stimulation at the onset of each experimental session in order to make the animal start pressing. This experimenter — produced stimulation, commonly termed priming, is really needed at the beginning of training, but subsequently many animals approach the lever as soon as they are placed in the experimental situation. This last phenomenon is particularly demonstrative in dogs that tend to press the lever even before being connected to the stimulator (18) or make a considerable number of responses without any reward (19). Second, self-stimulation in some placements does not proceed regularly, but is organized in bouts. Although consecutive responses within each bout are repeated at a frequency which permits to assume their dependence on the drive in terms of the Deutsch-Howarth theory, the intervals between bouts exceed the proposed decay time of this drive. Therefore, a different mechanism must be accepted for the first response in each bout. Third, incompatible with the drive-decay theory is the remarkable resistance to extinction seen in some dogs (19). In addition, extinction without responding was absent in these dogs, because despite their not being allowed to press for one min or longer, they consistently approached the manipulandum as soon as it became again available.

These observations support the incentive-motivational model of self-stimulation (24) which posits that cues associated with rewarding brain stimulation acquire motivational properties and instigate the animal to perform for further reward. Accordingly, it is the experimental environment which plays the role of a complex conditioned motivational stimulus.

More information about the conditioning mechanisms in self-stimulation comes from studies where animals learned to press for brain stimulation reward upon a specific cue. Keesey (9) and Terman and Kling (22) investigated this problem in a two-lever situation. Which of the manipulanda delivered brain stimulation reward was signalled by the intensity of light over each lever. Moreover, in order to switch on the lamps the animal had to break a photobeam at the rear of the cage, otherwise reward was not available.

Lenzer and Frommer (13, 14) demonstrated that rats will easily learn to leverpress upon presentation of a sporadic cue and to withhold their performance in the absence of the signal. Only single investigations in other species were reported. Anschel and Anschel (1) trained nine monkeys to press upon a green light and to suspend pressing during presentation of white light. Four animals acquired complete discrimination mastery whereas five others continuously explored the lever and responded as on a mixed schedule of reinforcement without external cues. A no-cue situation was not used in that study. The first investigation where dogs learned to press upon a sound was published by Perez-Cruet et al. (17). In their study, however, this behavior was established only for the practical purpose of comparing vegetative phenomena during self-stimulation and at rest. More extensive observations were reported by Paylova et al. (16) who used a procedure resembling Type II conditioned motor reflexes with food reward described by Konorski and Miller (12). The dogs were presented with a tone signalling the availability of reward. Their pressing was reinforced only during the tone, but not during intertrial intervals which lasted several times longer than the signal. As the animals learned to approach the lever upon the tone and to withhold from pressing between the trials, another tone was introduced, and during its presentation the pressing was not effective. This paradigm resembles the procedure of differentiation in Type II motor conditioned reflexes (11) or go-no go discrimination learning. Finally the conditioned response was extinguished and subsequently restored. The results of this research will be summarized below.

Six dogs were used. All had electrodes chronically implanted into the rostral forebrain region comprising the septum, the preoptic area, the nucleus accumbens and related structures. The animals were screened for selt-stimulation and the best electrodes were qualified for further study. The sessions were conducted in a sound-attenuating chamber where the animals were partially restrained on a Pavlov stand. In front of the dog was an easily accessible lever activating a stimulator which delivered 0.5 s train of 240 Hz sine wave after each leverpress. The stimulator was also connected to a key operated by the experimenter carefully observing the animal's behavior through a window.

During the first session the experimenter stimulated the dog's brain successively through all 4 to 6 implanted electrodes until the indices of positive reinforcement appeared such as closing of the mouth, sniffing and exploration of the environment (see 18). The placements where these phenomena appeared at the lowest current were selected for further self-stimulation training which proceeded according to a shaping procedure. At the beginning of training the dogs were given motivating stimulations at the time they were inactive, and all searching movements incidentally directed to the lever were reinforced with the same

stimuli. Gradually the lever became a goal intensively explored by the dog and touched with his nose or foreleg. The experimenter was more and more stringent in evaluating the correctness of the movements and reinforced only definite contacts of the animal with the manipulandum. A crucial moment in the acquisition of the task was when the animal for the first time touched the lever strongly enough to activate the stimulation circuit without the aid of the experimenter. Several sessions with a continuous reinforcement schedule were needed to stabilize performance. The animals were then trained to leverpress for brain stimulation reward upon a specific cue, and to withhold responding in its absence and during presentation of a discriminative cue.

During acquisition of the conditioned response the dog obtained brain stimulation reward only when his leverpressings were contingent upon a 1,000 Hz tone termed a conditioned stimulus. In the initial stage of training the tone was activated for 15–60 s at varying intervals to resemble an intermittent reinforcement schedule. Four dogs repeatedly returned to the lever, so that their leverpresses occurring during the cue were reinforced. The two other dogs reacted to this intermittent reinforcement with suppression of responding and abandoned the lever. They failed to resume pressing unless stimulated *gratis* by the experimenter.

The pairing of a rewarding brain stimulation with a neutral stimulus prior to the execution of an instrumental act causes that this stimulus acquires conditioned motivational properties (3). Bindra and Campbell (4) associated a metronome with rewarding hypothalamic stimulation and noticed that after this procedure the sound produced a marked increase in perambulation scores. The same phenomenon was observed when a natural reward (water given to thirsty rats) was used instead of brain stimulation (5). These results led to a general conclusion that neutral stimuli associated with a reinforcer (the unconditioned stimulus) acquire, through classical conditioning, incentive motivational properties and promote the animal to respond for further reward.

Our results with dogs support this conclusion only partially, in that repeated pairing of a neutral stimulus with the electrically produced reward according to principles of classical conditioning causes this stimulus to enhance the animal's general motor activity. In our experiments this finding was manifested by the animal's restlessness or arousal. We assume that the restlessness displayed by our dogs reflected a motivational state created by the external stimulus through a conditioning process. Nevertheless, this central motivational state is by itself not sufficient to promote the animal to perform the instrumental act that earlier resulted in brain stimulation reward. This is particularly

evident in dog 1 that despite about 140 pairings of the tone with experimenter — produced brain stimulation and the subsequent self-stimulation, failed to approach the lever upon the cue (see Fig. 2). Acquisition of the task was achieved only with the use of a special reinforcement strategy requiring the animal to perform a definite goal-directed movement before the experimenter activated the stimulator. At the beginning of conditioning any behavior which occurred upon the tone onsets such as an orienting response or turning of the head toward the lever, was reinforced, but later on more and more adequate movements were required to produce reward. As during initial stage of self-stimulation training, the animal's first effective leverpress, now made upon presentation of the cue, was a crucial point in the process of

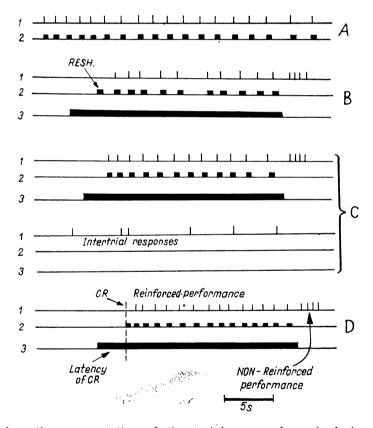


Fig. 1. Schematic representation of the training procedure. 1, dog's responses; 2, brain stimulations; 3, conditioned stimulus, A, self-stimulation without external cue; B, initial stage of training; C, advanced stage of training; D, fully developed response to the conditioned stimulus. Resh., reshaping stimulation administered by the experimenter. CR, conditioned response.

acquiring the task. Brain stimulation according to this procedure was termed reshaping, in order to distinguish it from priming where no attention is paid to the animal's behavior.

Figure 1 summarizes the steps by which external stimulus control of self-stimulation was achieved. The fully developed response is shown in part D of this figure. The dog which is standing quietly on the stand and making no or negligible intertrial responses, upon tone onset approaches the lever and presses it. The first press in each trial is believed to be executed under the conditioned motivation induced by the cue, and therefore is regarded as a conditioned response. The mechanism of subsequent presses in the trial is the same as during self-stimulation not controlled externally, each press being a consequence of preceding reinforcement. Together with the end of the tone the current is cut off. Those presses appearing during the 5 s after the tone reflect the animal's reaction to a sudden removal of reinforcement and are not regarded as intertrial responses. Often, particularly in initial acquisition sessions, their rate exceeds the reinforced leverpressing rate which resembles the pattern seen at the begining of extinction.

Parts B and C of Fig. 1 show successive stages of the acquisistion of the task. After having been reshaped for self-stimulation upon the tone the dog started to "examine" the lever both during the cue and in its absence. At this stage there is still no reason for regarding the approach to the lever upon the tone as a conditioned response. Rather, this behavior resembles the pattern of responding on a partial reinforcement schedule, with intermittent availability of reward. In the course of further training intertrial responses decreased or disappeared, and the latency of the animal's first press on the lever upon the cue (i.e., the latency of the conditioned response) shortened and stabilized. Behaviorally, the dogs reacted to each presentation of the cue with a closing of the mouth, turning of the head to the lever and an approach reaction. Stabilization of this pattern was achieved during several sessions where 20 s presentations of the cue were separated by variable intertrial intervals.

Figure 2 illustrates the acquisition of the task by all six dogs. Dogs 1 and 3 required reshaping. This procedure was also occasionally used in other animals. Five dogs fulfilled the acquisition criteria which consisted of high percentage of conditioned responses and substantial decrease in intertrial responses. However, in dog 5 the conditioned responses were unstable, therefore this animal was excluded from further discrimination training. Dog 6 was also eliminated due to an enormous amount of intertrial responses which did not decrease.

The stages of acquisition of the conditioning task by our dogs led

us to a conclusion that besides a central motivational state created by the pairing of a neutral stimulus with reward, an instrumental strengthening of a particular movement is needed in order to transform the latter into a purposeful response emitted upon the cue. In other words, in order to acquire the task the dog had to perform the given response actively during presentation of the conditioned stimulus. The necessity of this active performance was also stressed by Konorski (12) with respect to food rewarded instrumental conditioned reflexes.

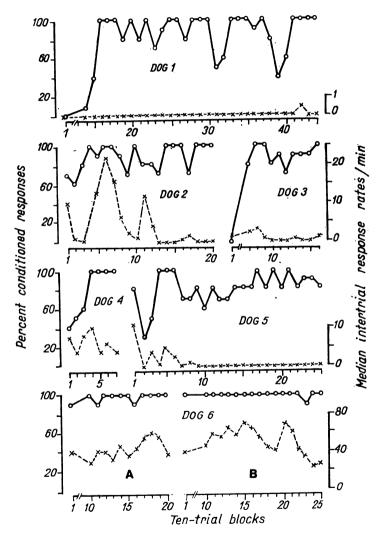


Fig. 2. Acquisition of the conditioned response. In dog 6 two electrodes (A and B) were used to sustain self-stimulation. White circles, conditioned responses; crosses intertrial responses.

Figure 3 illustrates discrimination learning in 4 dogs. The animals were presented with two cues: a 1,000 Hz tone signalled, as previously, the availability of reward, and a 2,000 Hz tone was a discriminative stimulus. Leverpressings which occurred during presentation of the latter were not rewarded. In each session the animals were presented with 20 conditioned and 10 discriminative stimuli. Each stimulus lasted 20 s and was preceded by a variable intertrial interval. As seen from

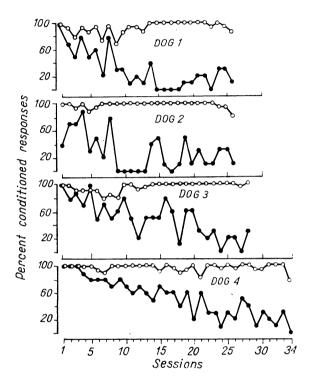


Fig. 3. Discrimination learning. White circles, percent of conditioned responses upon the conditioned stimulus; black circles, upon the discriminative stimulus.

the figure, all dogs learned to discriminate the two cues, although a persistent 100% discrimination was not reached. Intertrial responses were absent or scarce during the entire discrimination training.

Extinction of the conditioned response is shown in Fig. 4. The dogs were presented with 20 conditioned stimuli during each session, but leverpressing was not reinforced. Although the conditioned response extinguished promptly in a single session, it reappeared again in an overnight session. Therefore, several sessions were needed to achieve a chronic extinction.

At the beginning of the first restoration session the dogs were given

a priming stimulation and allowed to self-stimulate for a short period without an external cue. Thereafter they were presented with the conditioned stimulus, and their pressing during the action of the latter

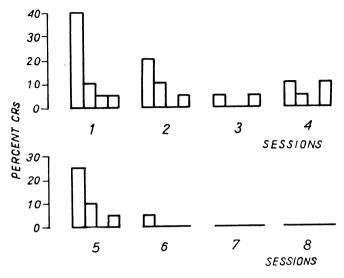


Fig. 4. Combined data showing extinction of the conditioned responses in all four dogs tested. Each session consisted of 20 presentations of the conditioned stimulus. The animals' leverpressing was not reinforced. Bars represent successive blocks of 5 trials.

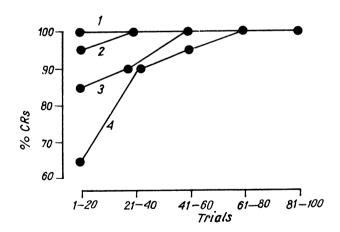


Fig. 5. Restoration of the conditioned response. At the beginning of the first session each dog obtained a priming (experimenter—produced) brain stimulation and was allowed short self-stimulation without external cue. Then the conditioned stimulus was presented 20 times in each session, and the dog's responses during its action were reinforced in the usual way. The numbers close to the solid lines refer to individual animals.

was again reinforced. As shown in Fig. 5, the conditioned response was promptly restored in all the dogs.

The intrinsic process of the conditioning mechanism in self-stimulation is far from being elucidated. There are some indications that it may be related to the function of the catecholaminergic pathways. Wauquier et al. (25) studied the action of apomorphine, a dopaminergic agonist, on conditioned reflexes with brain stimulation reward established in dogs according to the same procedure as in the present study. At a certain dose a dramatic increase in intertrial responses was noted. By this pattern the dogs behaved as our dog 6 or the five monkeys of Anschel and Anschel (1) which did not acquire the discrimination mastery. The effect of apomorphine was counteracted by haloperidol, a dopaminergic blocker.

As shown by our data, brain stimulation may be successfully used as reinforcer of instrumental learning controlled by external signals, and by this does not differ essentially from natural rewards. The lack of humorally produced drive may be easily compensated by a motivational state induced through the action of environmental factors acting as a complex conditioned stimulus.

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