THE NEURAL BASIS OF GROOMING BEHAVIOR IN THE RAT

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By

DAVID ALAN HOPKINS, B.Sc., M.A.

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AUTHOR: David Alan Hopkins, B.Sc. (University of Alberta)
M.A. (McMaster University)

SUPERVISOR: C.H. Vanderwolf, Ph.D.

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SCOPE AND CONTENTS: Grooming was elicited by electrical stimulation of the midbrain tectum, the limbic system, and the medial anterior hypothalamus. Hypothalamic stimulation resulted in the more frequent occurrence of one class of components of grooming (face-washing, fur-licking, and biting), while another class (shaking and scratching) occurred more frequently in spontaneous grooming and during and following limbic system stimulation. Grooming elicited by anterior hypothalamic stimulation resembled thermoregulatory grooming in some respects, except that salivation and vasodilatation of the tail were absent. Components of both evoked grooming and spontaneous grooming occur in organized sequences, so that particular components tend to follow one another with a high probability. Self-stimulation did not generally occur at hypothalamic sites from which grooming was elicited.

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CHAPTER I

Introduction

Any animal shows certain patterns of behavior which are the same as those shown by other normal animals of the same species. Historically, considerable controversy was generated in attempts to explain this "species-typical" behavior (see Bindra, 1959, pp. 5-23). Species-typical behavior ranges from simple reflexes to complex sequences of activities in which the patterns are relatively stereotyped, occur apparently without specific learning, and have demonstrable neurological substrates. While the development and occurrence of species-typical activities depends upon many interacting factors (Hinde, 1959; Lehrman, 1953), the neural basis is essentially the same within and between species.

The concern of the present thesis is the neural basis of grooming, as a species-typical activity of the rat, with particular reference to grooming elicited by electrical stimulation of the brain. The pioneer work in eliciting species-typical activities by direct electrical stimulation of the brain was done by W. R. Hess at Zurich. Hess (1957) implanted chronically indwelling electrodes into various areas of the cat brain, passed weak currents through the electrodes, and observed the effects in cats which were unrestrained and free to move about. With this technique, he found that stimulation[1] of the

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[1] Stimulation means localized direct electrical stimulation of the brain unless otherwise specified.

diencephalon and midbrain elicited autonomic and somatic motor activity that was in many cases highly integrated and well coordinated. Subsequently, others have elaborated these findings in the cat (Delgado, 1952; Egger and Flynn, 1967; Fernandez de Molina and Hunsperger, 1962; Gloor, 1960; Hunter and Jasper, 1949; Skultety, 1962) and extended them to the chicken (von Holst and von St. Paul, 1962, 1963), rabbit (White and Himwhich, 1957), and monkey (Delgado, 1959, 1964, 1965). The rat has also been the subject of intensive study.

With few exceptions, most of the somato-motor behaviors evoked using electrical stimulation have been relatively simple locomotor responses, in the sense that the basic mechanisms are dependent on lower levels of the central nervous system (Denny-Brown, 1960; Ruch & Patton, 1965). Or, they have been more complex appetitive behaviors such as eating, drinking, sexual, aggressive, and exploratory behavior whose integrated performance depends on the higher levels of the neuraxis, although isolated reflexive components of the total acts may be carried out at a low level (Bard and Macht, 1958). Grooming, however, has received little systematic study although this activity is species-typical and occurs more frequently and under a greater variety of conditions than the more conventionally studied species-typical activities. Moreover, while the goal objects for activities like eating, drinking, fighting, and so on are apparent, it is much less obvious why animals groom so much since, except when animals groom one another, there is no external goal object.

It has been demonstrated previously that grooming can be elicited by stimulation of specific areas of the brain (MacLean, 1957b; Hopkins,

1967) and the research to be reported here was undertaken to further elucidate the neural basis of grooming elicited by stimulation of the brain of the rat. In order to place this research in context, experiments on the functional basis of grooming will first be summarized and then the present state of knowledge about the neural basis of grooming will be considered.

The Functional Basis of Grooming

In their home cages, male rats spend up to 40% of their waking time engaged in some form of grooming (Bolles, 1960). Face-washing, the first stereotyped component of grooming, appears as early as two days after birth and "by day 23 adult-like grooming sequences are quite common" (Bolles and Woods, 1964). These sequences, often several minutes in duration, typically begin with licking of the forepaws which are then brushed over the snout, whiskers, and ears. Subsequently, the animal licks and bites the fur on the back, flank, and ventral surface. Exposed skin on the scrotum, perineal region, and feet are usually licked. Scratching the body with a hind foot is also a common component of grooming.

The first and most obvious functional consideration in trying to account for these observations is that animals groom to keep their coats clean and free of debris, foreign objects, or parasites. However, it is unlikely that all grooming occurs simply for purposes of self-care, considering the amount of time a rat spends in what are usually clean living conditions like a laboratory cage. Moreover, the incidence of grooming can be altered by the administration of certain drugs (Bindra and Mendelson, 1963; Bindra and Spinner, 1958) and is decreased by food-or water-deprivation (Bolles, 1960, 1963). Thus, it has been a common conclusion that grooming occurs independently of any specific external stimulation. Extended further, this line of reasoning has led some investigators (Bolles, 1960; Doyle and Yule, 1959; O'Kelly, 1940; Robinson, 1963) to interpret the frequency of grooming as an "index of emotionality". However, the reported correlations between grooming and "emotionality" have been sometimes negative and sometimes positive (Fentress, 1968a). Fentress (1968a, p. 141) concluded that this apparent conflict of results might be resolved if "the relationship between grooming and factors such as 'emotionality' or 'arousal' is non-linear."

Leaving aside "emotionality" as an explanatory notion, ethologists (e.g., Tinbergen, 1951) have frequently interpreted the occurrence of grooming in unexpected situations as evidence for a "reservoir" theory of motivation. They have observed that when two mutually-exclusive or incompatible behaviors, such as attack and escape, are activated, and an animal alternates between them, the animal frequently eats, sleeps, or grooms within seconds (Zeigler, 1964). Tinbergen (1951) concluded that animals which behave this way are in a conflict situation where the conflicting tendencies are about equal and that the large amount of motivational energy so generated "sparked over" into "irrelevant" neural motor areas. In this way, Tinbergen interpreted grooming in conflict situations as evidence for his "reservoir" theory of motivation. The theory postulates that behavior patterns are represented in delimited areas in the brain which are continually primed and require only the proper releasing stimuli for a given behavior to occur. When the behavior is thwarted, as in conflict situations, the excess energy discharges through another anatomically proximal but functionally unrelated center.

Other investigators, however, have suggested that the occurrence of grooming in conflict situations can be accounted for in terms of: (1) the prepotency of grooming in the behavioral repertoire (Zeigler, 1964), or (2) the tendency of grooming to follow sequentially other activities (Bolles, 1960; Hughes, 1968), or (3) elicitation by specific internal or external stimuli (Andrew, 1956; Rowell, 1961). For example, autogenital licking, which almost invariably follows penis withdrawal during copulation (Beach, 1947), could be regarded as a displacement activity. However, this licking can be explained by any of these three interpretations. Whether autogenital licking serves some sexual function is unclear, but Stone (1927 cited by Beach, 1947) reported that the activity "is accompanied by distinct pelvic movements similar to those occurring during copulation."

Finally, grooming and saliva spreading are major heat loss mechanisms in the rat and other furred mammals (Hainsworth, 1967; Higginbotham and Koon, 1955; Robinson and Morrison, 1957; Stricker, Everett, and Porter, 1968). This behavioral thermoregulation serves very efficiently in the absence of panting and sweating in response to heat stress in the rat. The behavior is functional over a wide range of core temperatures (Hainsworth, 1967) which may be elevated by increased ambient temperatures or increased somato-motor activity. As ambient temperature and core temperature increase, the amount of salivation increases (Hainsworth and Epstein, 1966) and grooming and saliva spreading tend to be directed more to the scrotum, feet, and tail (Stricker et al., 1968). Evaporative heat loss is facilitated by vasodilatation in these areas of the body when the core temperature reaches a critical level (Grant, 1963; Thompson and Stevenson, 1965). Since core temperature may be elevated by increases in activity associated with "emotionality", and aggressive, escape, or sexual behaviors discussed above, the grooming in those situations may also be related to thermoregulatory behavior.

Thus, depending on the stimuli, grooming may manifest itself as a correlate or self-care, arousal, aggressive behavior, sexual behavior, or temperature regulating behavior.

Neural Mechanisms in Grooming

Neural mechanisms in grooming have been studied principally through observations of grooming acts elicited by direct electrical or chemical stimulation of specific loci in the brain or by warming local areas of the brain. Hess and Meyer (1956) indicated 19 electrode sites in the cat brain at which electrical stimulation reliably elicited grooming both during and immediately following the stimulation. Thirteen of the effective loci were in the septum pellucidum, near the columns of the fornix, and the other six loci were distributed widely throughout other parts of the limbic system. The grooming elicited by Hess and Meyer (1956) consisted mainly of rhythmical licking and biting of the fur all over the body, although some of the evoked grooming was restricted to relatively circumscribed areas, such as a small area on one shoulder.

Shortly afterwards, MacLean (1957b) reported that grooming could also be elicited by direct stimulation of loci within the hippocampus of both the cat and rat. In this case, stimulation with either electrical currents or cholinergic drugs injected directly into the brain was effective. Little grooming was observed during the stimulation, which was accompanied by abnormal patterns of electrical activity in the hippocampus, but grooming occurred frequently following stimulation when the abnormal high voltage discharges had stopped. Other investigators have also observed grooming following the termination of direct stimulation of various limbic structures (Altman, 1969; Miller, 1961).

Considered collectively, these reports indicate that coordinated sequences of grooming can be elicited by stimulation at several widely-separated points which lie within the Papez circuit in the limbic system, and that this evoked grooming coincides with the propagation of hippocampal afterdischarges. These conclusions are important in further interpretation of the neural mechanisms in grooming for two reasons. First, the occurrence of grooming as a sequel, rather than a concomitant, of hippocampal afterdischarges indicates that the grooming may actually be more directly related to neural activity in areas outside the limbic system. Second, the Papez circuit has also been implicated in the neural control of motivational activities like eating, drinking, copulation and defense-aggression, so that the occurrence of grooming may be functionally related to such activities.

Consider first the significance of grooming as a sequel to afterdischarges in the limbic system. In interpreting this finding, concepts from Jacksonian neurology are useful (see Taylor, 1958). Motor organization is viewed as being arranged in a number of levels in a hierarchical fashion. At the lowest level (e.g., bulbo-spinal level) simple reflexes are represented. At higher levels, there is a re-representation of lower levels and a more complex organization comprising motor sequences. At each level the elements of a lower level are combined to form a larger functional unity. Activity in the lower elements is governed by the higher levels and if the higher level is destroyed, the lower elements may appear more excitable (release phenomenon), less excitable, or simply disorganized. Returning to the experimental findings, electrical stimulation of the septal area produces in the hippocampus a pattern of seizures which is similar to the patterns of hippocampal electrical activity seen after direct stimulation of the hippocampus itself. Therefore, it is possible that the grooming following hippocampal stimulation (MacLean, 1957b) and the grooming during and following septal stimulation (Hess and Meyer, 1956) are "release" phenomena resulting from the depression or functional removal of the hippocampus which follows a seizure. This suggestion is supported by the observation that, although grooming occurred during septal stimulation, the latency of the grooming was frequently long (Hess and Meyer, 1956) during which time there may have been spreading of seizure activity to the hippocampus which would subsequently be depressed. Further support for the release hypothesis comes from Woods' (1964) observations which indicate that grooming can be functionally regulated by mesencephalic areas without the participation of limbic system structures. Woods decerebrated rats at the level of the superior colliculi with clear separation of the posterior hypothalamus and mesencephalon. Within a week following this decerebration, a drop or two of water anywhere on the body initiated vigorous and appropriate grooming, including sitting up, face-washing, and fur-licking. Within two to three weeks, grooming became sufficiently normal that manual cleaning of the rat by the investigator was no longer necessary.

There is, however, an alternative to the notion that the hippocampus is non-functional during a seizure. Since grooming does not occur unless afterdischarges are elicited (MacLean, 1957b), the evoked grooming may result from excitation produced by propagation of hippocampal seizure activity into brain stem structures "downstream" of the hippocampal area. There are, for example, strong direct projections along which activity might be propagated from the hippocampus to the rostral part of the central grey substance, and indirect hippocampal projections into the mesencephalic area via the median forebrain bundle and hypothalamus, fasciculus retroflexus and mammillotegmental tract (Nauta, 1958). Of course, at different stages of hippocampal seizure activity, release or excitation could be occurring. In either case, the evidence suggests that the grooming observed following stimulation of limbic areas is induced by mesencephalic activity, rather than by the limbic system activity itself.

When the brain stem is electrically stimulated, grooming may ensue, but there is some doubt whether this mesencephalic activity is sensory or motor in nature, or both. For example, electrical stimulation of the caudal thalamic region in the monkey induced grooming (which was mostly scratching), as well as ejaculation (MacLean, Dua, and Denniston, 1963). This stimulation probably induced grooming through sensory activity because (1) the caudal thalamic region receives the medial division of the spinothalamic tract, which carries "light touch fibres" and (2) the stimulated animals used either hand and avoided obstacles in order to groom. MacLean et al. also reported that most of the effective points of stimulation were in sensory pathways and, for these reasons, they suggested that the animals groomed because they felt itchy.

The observations of MacLean et al. (1963) can of course also be construed as further evidence that grooming is functionally related to brain stem activity, since the evoked grooming began shortly after the onset of stimulation. The joint occurrence of grooming and ejaculation as a result of electrical stimulation is also important, however, since it relates to the point made earlier that stimulation of loci in the Papez circuit may evoke motivational activities, as well as grooming. That is, direct stimulation which evokes grooming often evokes, at the same or other parameters of stimulation, activities such as eating, copulation, or defense-aggression from the same sites.

The overlap between areas at which stimulation elicits grooming and sexual activities is particularly consistent. These overlapping points have been found in the hypothalamus (Vaughan and Fisher, 1962; Roberts, Steinberg, and Means, 1967), thalamus (MacLean et al., 1963), hippocampus (MacLean, 1957b), and in the septal area MacLean and Ploog (1962) found that stimulation which elicited penile erection was followed by afterdischarges in the hippocampus. The functional relationship between grooming and sexual activities is, however, difficult to assess. For example, electrical stimulation of the lateral anterior hypothalamic area evoked a complete pattern of male copulatory behavior in three animals, with the singular exception, however, of post-intromission grooming. At the same time, stimulation of the same sites at lower intensities elicited grooming without any sexual activity (Vaughan and Fisher, 1962).

It is possible that, whatever the functional basis for the sexual activity, the grooming elicited by direct stimulation of hypothalamic areas has a thermoregulatory function. First, the lower intensity of hypothalamic stimulation which evoked grooming (Vaughan and Fisher, 1962) also evoked resting, and both grooming and resting dissipate heat from the body. Second, the anterior hypothalamus is intimately involved in a variety of mechanisms which produce a loss of body heat (Bligh, 1966). Finally, a thermoregulatory function has been shown for the grooming evoked by stimulation of the hypothalamus in the opossum (Roberts, Berquist, and Robinson, 1969). These authors found that warming the medial preoptic area and anterior hypothalamus between the anterior commissure and the optic chiasm with radiofrequency stimulation elicited grooming (as well as resting), although mating was not elicited. Thus, the thermoregulatory grooming elicited by stimulation of the hypothalamus, as well as the resting elicited concomitantly, appear to be unrelated to the functional basis of sexual activity which may be elicited by stimulation of the same area.

Although grooming is induced by increased body temperature, such grooming continues to occur whether or not it actually reduces body temperature. When animals recover from damage to the lateral hypothalamus, they perform normal grooming acts, including the movements involved in spreading saliva in response to increased body temperature and environmental temperature (Hainsworth and Epstein, 1966). However, hypothalamus damaged rats do not secrete saliva so that these grooming acts have no appreciable effect in actually reducing body temperature.

Other studies employing lesions also have found little or no effect on grooming or produce effects that could just as easily be attributed to secondary factors (Dirlam, 1969). For example, Jarrard (1968) observed the "behavior of hippocampal lesioned rats in home cage and novel situations." Time sampling observation revealed no differences in grooming among hippocampal lesioned, neocortical lesioned, and normal control animals. On the other hand, Kimble, Rogers, and Hendrickson (1967) found that "male and female hippocampal lesioned subjects displayed less self-care behavior than did normal subjects." The difference between the two studies is likely due to the fact that Kimble et al. (1967) observed their animals in a social situation composed of a male and an estrus female. In this situation, an effect of hippocampal lesions may have showed up not because the neural substrates of grooming have been damaged, but because the eliciting stimuli are different and their effectiveness may be reduced in the lesioned subjects.

In summary, grooming behavior has a high saliency in an animal's behavioral repertoire. Its incidence is affected by a wide variety of specific and non-specific stimuli. Heat stress, sexual activity, aggression, or conflict all lead to increases in grooming. In addition, the neural substrates for temperature regulation, sexual behavior, and affective defense overlap extensively in the hypothalamus where integrating functions are likely to occur. While both stimulation and lesion studies show that different levels of the neuraxis are involved in the control of grooming, the evidence comes from a number of different species and the behavior has not been studied extensively and in detail in any one species.

Objectives of the Research

The first objective of the research was to map the neural substrates of grooming at different levels of the neuraxis in the rat. Accomplishing this, it was then possible to consider the relationship between grooming elicited from different levels of the neuraxis with respect to components, sequential organization, and reinforcement.

The purpose in examining the relationship between evoked grooming and reinforcement, or reward, deserves elaboration because of its relevance to evidence suggesting that studies of motor performance provide clues to the physiological basis of reward. The essential concept relating motor performance and reinforcement is that reinforcement consists of the performance of a consummatory motor pattern. Response theories of reinforcement have been proposed by ethologists (e.g., Tinbergen, 1951) and psychologists (e.g., Premack, 1959, 1962; Sheffield, Wulff, and Backer, 1951). More recently, Glickman and Schiff (1967) have related ideas of this sort to neurophysiological studies. They argue that the sufficient condition for reinforcement is facilitation of neural activity in the pathways controlling "motor sequences already preformed in the brainstem." Specifically, using Schnierla's (1959) classification of behavior, they suggest that elicitation of approach behaviors is positively reinforcing and elicitation of withdrawal behaviors is negatively reinforcing. Empirically, one line of support for the theory comes from experiments demonstrating that animals will perform an operant response to receive brain stimulation that elicits species-typical and motivational behaviors. According to these views, stimulation of sites in the brain is reinforcing because it produces or facilitates activity in the neural substrates of a particular behavior. In the present context, it is predicted that stimulation of sites from which grooming can be elicited will also be rewarding as indicated by self-stimulation.

CHAPTER II

The Mapping Experiment:

Mechanisms of Grooming at Different Levels of the Neuraxis

In the mapping experiment, electrodes were implanted in paleocortical and subcortical structures. The neocortex was not explored because (1) movements elicited by stimulation of the neocortex tend to be relatively simple (e.g., Lilly, 1958), and (2) complex species-typical behavior often survives decortication or transection of the brain stem (Bard and Macht, 1958; Woods, 1964). Therefore, it is unlikely that the neocortex would be involved in grooming.

GENERAL METHODS

Subjects

The subjects in all experiments were male hooded rats purchased from Quebec Breeding Farms Incorporated, St. Eustache, Quebec. The 215 subjects, 190 of which underwent surgery, weighed 190 to 350 grams at the beginning of the experiments. Many of the subjects from the mapping experiment were also used in subsequent experiments.

Surgery

Using a stereotaxic technique, one to five bipolar electrodes were implanted while the subject was anaesthetized with sodium pentobarbital (40-60 mg/kg). Atropine sulphate (0.2 mg/kg) was injected intramuscularly at the start of the operation to inhibit mucous secretion in the respiratory pathway. The electrodes were embedded in a mound of dental cement moulded over stainless steel screws mounted in the skull. At the conclusion of the operation, penicillin G (100,000 I.U.) was injected intramuscularly. At least two weeks were allowed for recovery. A total of 263 sites in the striatum, diencephalon, midbrain, and hippocampal formation were explored.

Electrodes and Stimulation Parameters

The bipolar electrodes were made from twisted Nichrome wire 0.010 in. in diameter. Two types of electrode were used. Those made in the laboratory had male Amphenol or Winchester subminiature connectors soldered to the Nichrome wire. A dental cement body made the electrode assembly rigid. The commercial electrodes were made by Plastic Products Company, Roanoke, Virginia (MS-303-.010). Hippocampal electrodes were insulated to within 0.5 mm. of the tips. All the other electrodes were insulated completely except for the cross-sectional area of the tips. The tips were separated from 0.2 to 1.0 mm.

The stimulator was a Grass Model S4 set for biphasic "square wave" pulses of 0.1 or 0.2 msec. duration. Frequencies of 5, 20, and 200 pulses per second (pps) were used. At each frequency, voltages of 1.5, 3, 5, 7, and 9 volts were used. Occasionally, other voltages were also used. Stimulation was delivered through flexible wire leads that allowed the subjects maximum freedom of movement.

Histological Procedures

At the conclusion of the experiments, the subjects, while under deep barbiturate anaesthesia, were bled and perfused with normal saline followed by a 10% formalin solution. The brain was removed and stored in formalin for one week or more. Frozen sections of the brain were cut to a thickness of 40μ. Every second or third section through the electrode track was kept for staining. The sections were stained with either thionin or cresyl violet. The locations of the electrodes were verified independently on two or more occasions without knowledge of the behavioral effects obtained by stimulation of specific sites.

Behavior Testing

The apparatus that subjects were tested in was a plywood platform measuring 20 x 30 in. with walls 4 in. high. The floor was covered with sawdust.

A subject was placed on the test platform for 10 min. before stimulation was begun. Stimulation was then delivered in an ascending series of voltages (1.5, 3, 5, 7, and 9 volts) beginning with the stimulator set at a frequency of 5 pps. After this series, the same ascending series of voltages was administered at a frequency of 20 pps, and then 200 pps. Pulse trains were of 15 to 120 sec. duration with an interval of at least 60 sec. between pulse trains. Each site was stimulated at least twice at each frequency and voltage combination up to levels that produced escape from the testing platform or some strongly disorganized motor response. Currents producing behavioral effects generally ranged from 0.2 to 1.4 ma. Most animals were retested one or more times on subsequent weeks. Detailed written records were made of the evoked behavior and in some cases motion pictures were taken.

Using a Grass Model 7 electroencephalograph, cortical and hippocampal electrical activity was recorded from two rats following stimulation of the opposite hippocampal formation.

RESULTS

Electrical stimulation of the brain evoked behavior of one form or another from all the loci tested. Grooming was elicited by stimulation of the midbrain tectum, the hippocampal formation and related subcortical structures, and the medial anterior hypothalamus. Marked differences in the forms of the grooming elicited from each area suggested that different mechanisms were being activated by the stimulation. Thus, the results are presented in terms of the anatomical areas from which the different grooming sequences were obtained. Appendix A presents detailed descriptions of the various components of grooming.

The Midbrain Tectum

Stimulation of the lateral area of the stratum lemnisci of the superior colliculus elicited grooming of the contralateral back in four subjects. Figure 1 presents a photomicrograph of a site from which stimulation elicited back grooming. Figure 2 is a composite of the four positive sites and of negative sites from the same general levels.

In the normal animal, the basic posture for grooming the back consists of an erect trunk, support from the hind legs and tail, and turning of the head and shoulders to the side to be groomed. From this position, the rat bites and licks the fur of the back for several

Fig. 1. Photomicrograph of a site from which stimulation elicited grooming of the back (x 180).

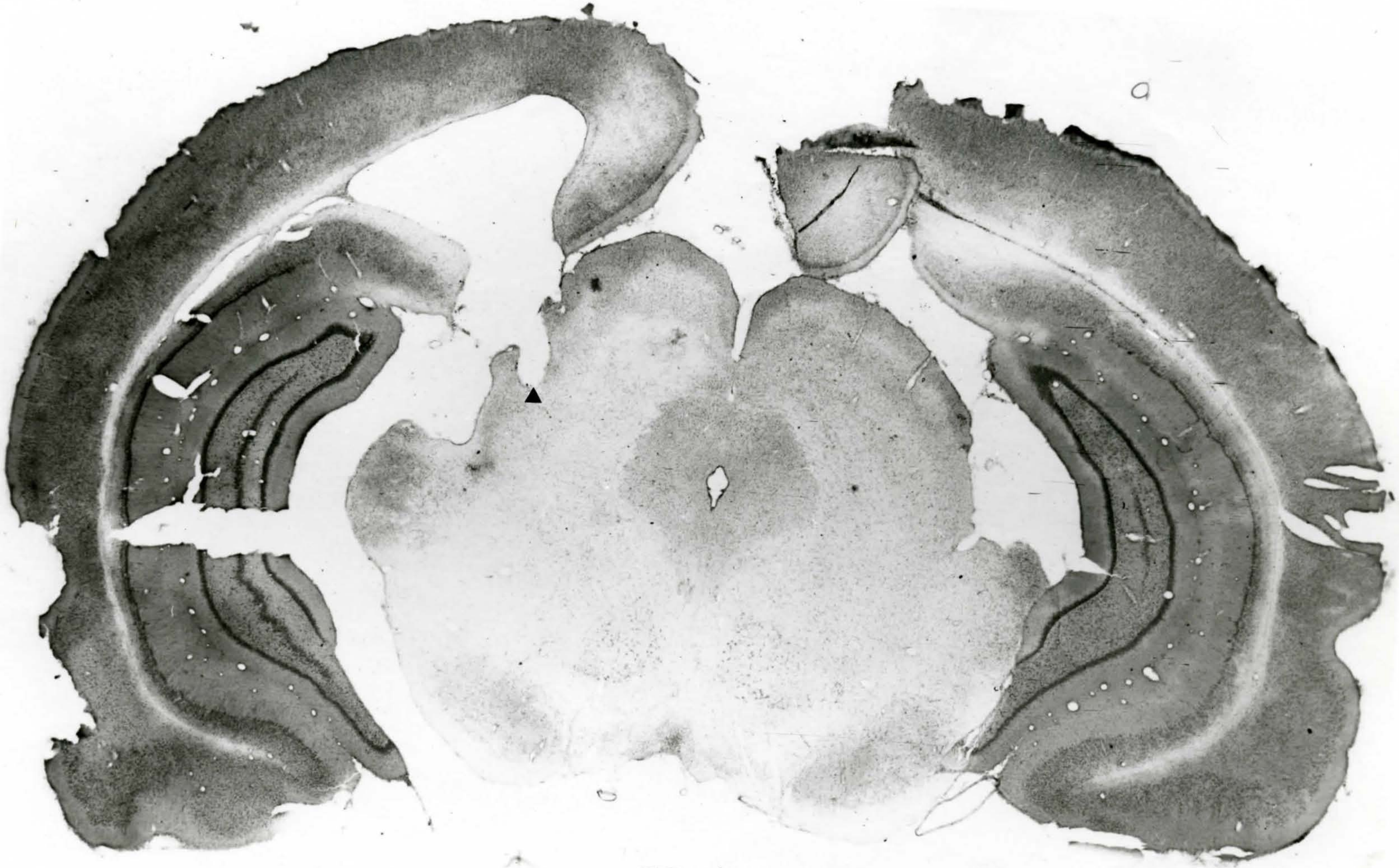
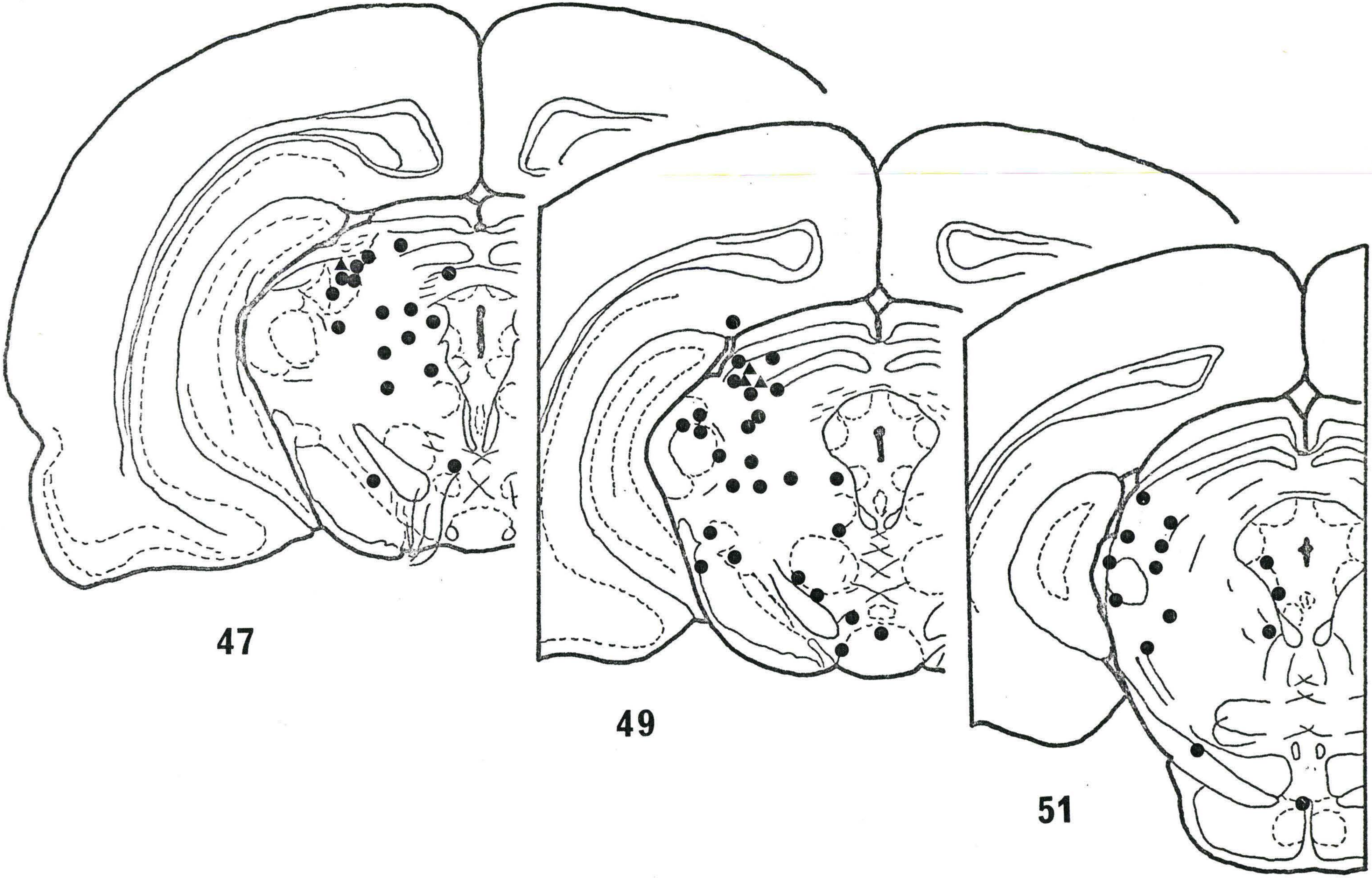


Fig. 2. Composite frontal diagram at the level of the midbrain tectum of sites from which stimulation elicited back grooming (▲) and sites from which stimulation did not elicit back grooming (●). The numbers below the drawings refer to the figure in Konig and Klippel (1963) on which each drawing is based.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seconds. The biting and licking usually start on the upper part of the back and proceed down the back towards the base of the tail.

The evoked response was virtually the same in all four subjects. It differed from the normal in that the grooming was directed to the middle part of the back, and the lower back and base of the tail were not groomed. Also, the phasic movements were not as rapid as normal and the response fatigued in approximately ten seconds. However, the response could be evoked again following a recovery period of less than 60 sec. In other aspects, the details of the evoked back grooming were very similar to spontaneous grooming of the back. Licking and phasic head and limb movements were directed toward the upper half of the back opposite the side of the brain being stimulated. Initially, the foreleg on the side being groomed was extended while the paw of the other foreleg grasped the fur of the extended leg as the animal turned its head and shoulders and licked the fur of the back. Often, with the licking movements continuing, the grasped foreleg was released and both forelegs brushed the fur of the back in the region where the licking movements were directed.

An interesting feature of this response was that if the animal was in the act of face-washing when stimulation was turned on, there was a ready transition to grooming of the back, as compared with the effect of stimulation applied when the animal was in a resting position with all four feet on the floor of the testing platform. Typically, in the latter case, the animal had difficulty assuming an adequate posture on its hind legs and often lost its balance (as normal rats will also do occasionally). This observation suggests that the stimulation activated the phasic components of back grooming but not the basic postural mechanisms for back grooming, i.e., assumption of rearing position with an upright trunk.

The Hippocampal Formation and Limbic System

Stimulation of the hippocampal formation and other limbic system structures shown in Figure 3 elicited shaking and brief face-washing followed by more normal appearing grooming (i.e., longer sequences of stereotyped grooming).

The principal evoked grooming response was a shaking or shuddering of the entire body from side to side. In the normal rat an identical response can be produced by sprinkling water or sawdust on its head and back. The response also occurs spontaneously in a variety of situations. This spontaneous response consists mainly of head shaking without much involvement of the rest of the body. Interestingly, the head shaking occurs at very high rates when animals are exploring an open field[2]. In contrast to spontaneous shaking, the response evoked by electrical stimulation was predominantly shaking of the entire body, and was much more vigorous. Brief bouts of face-washing lasting one or two seconds often occurred during the period when shaking was also occurring, but it was usually not until the shaking had stopped that some of the animals engaged in longer sequences of grooming the entire body. The shaking elicited by stimulation occurred during stimulation, but was most often an aftereffect occurring

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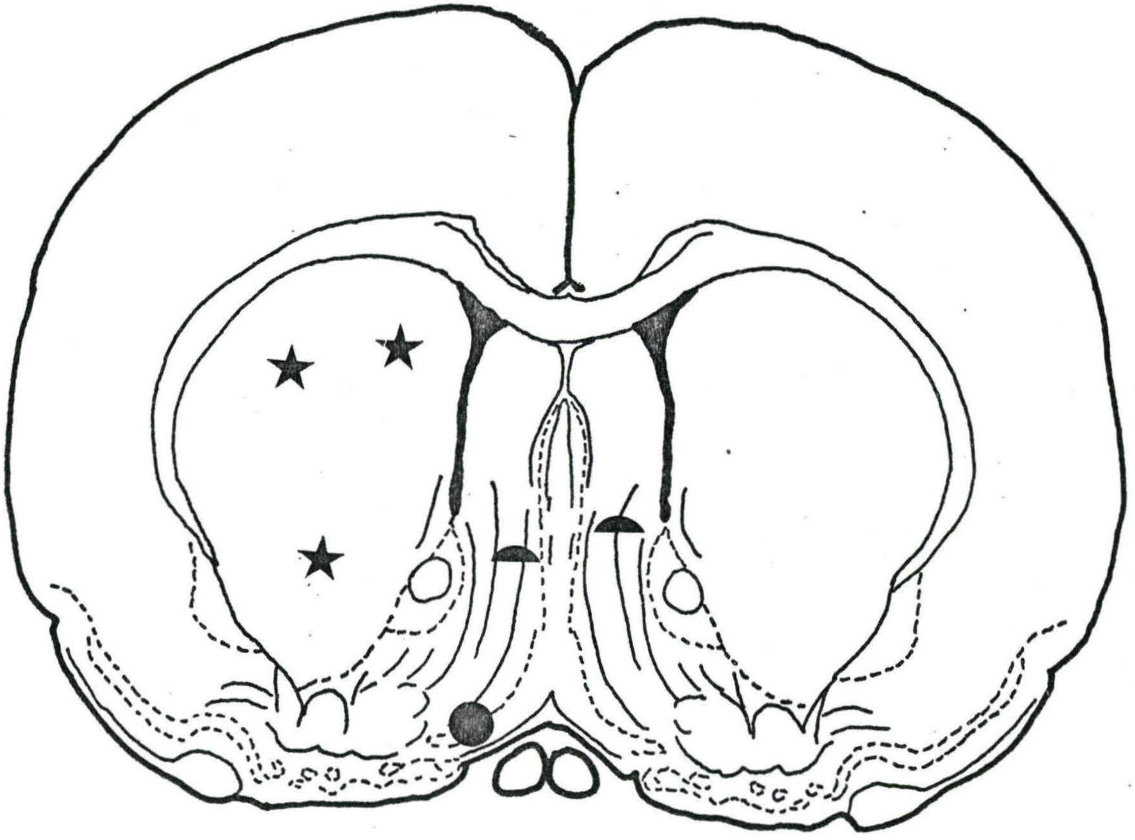
[2] Unpublished study entitled "The effects of different levels of food deprivation on grooming behavior," 1968.

Fig. 3. Composite frontal diagrams of sites from which stimulation elicited shaking or behavioral seizures. Shaking only (◓), seizures only (★), both shaking and behavioral seizures ●. The numbers below the drawings refer to the figures in Konig and Klippel (1963) on which each drawing is based.



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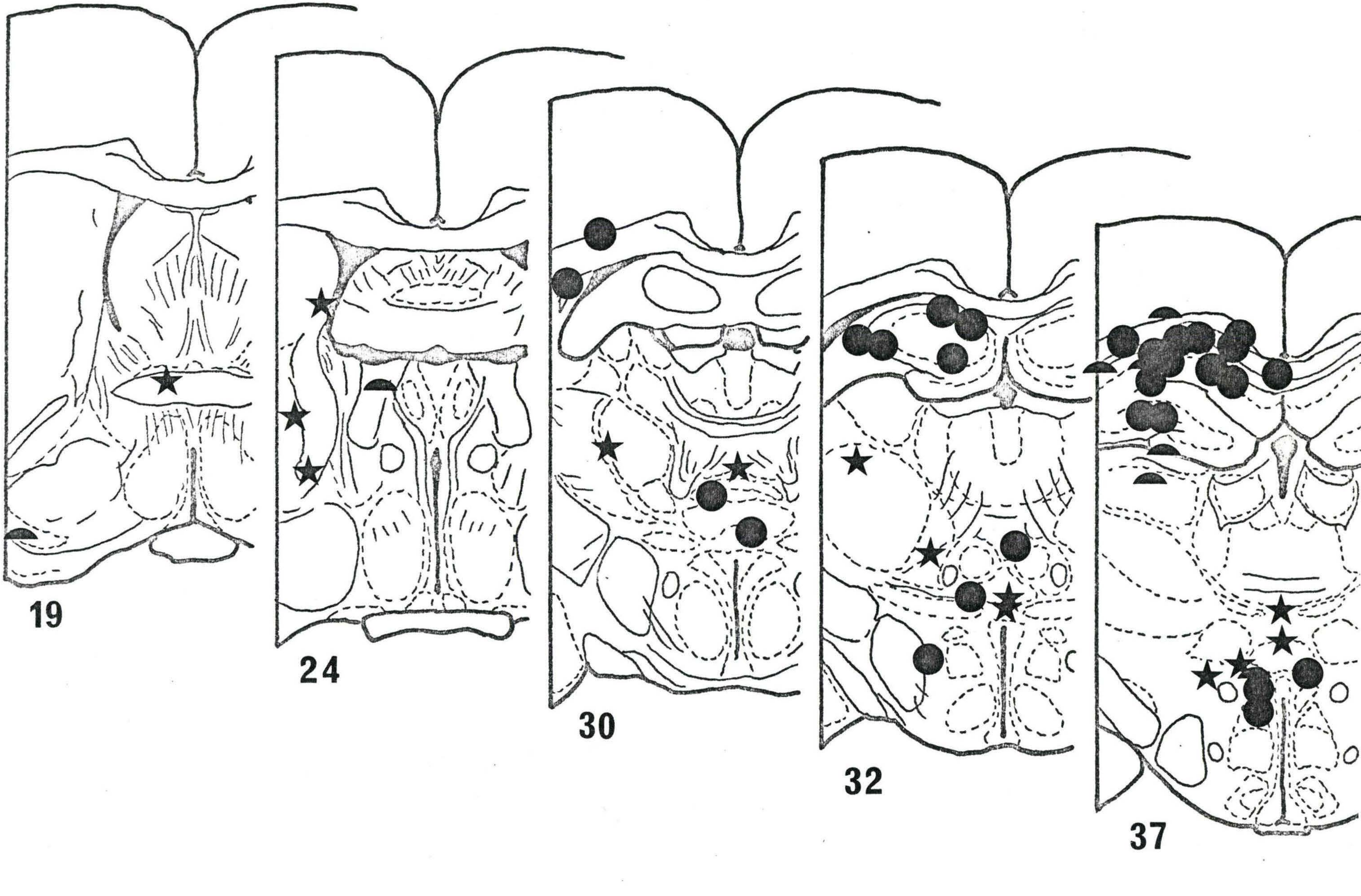
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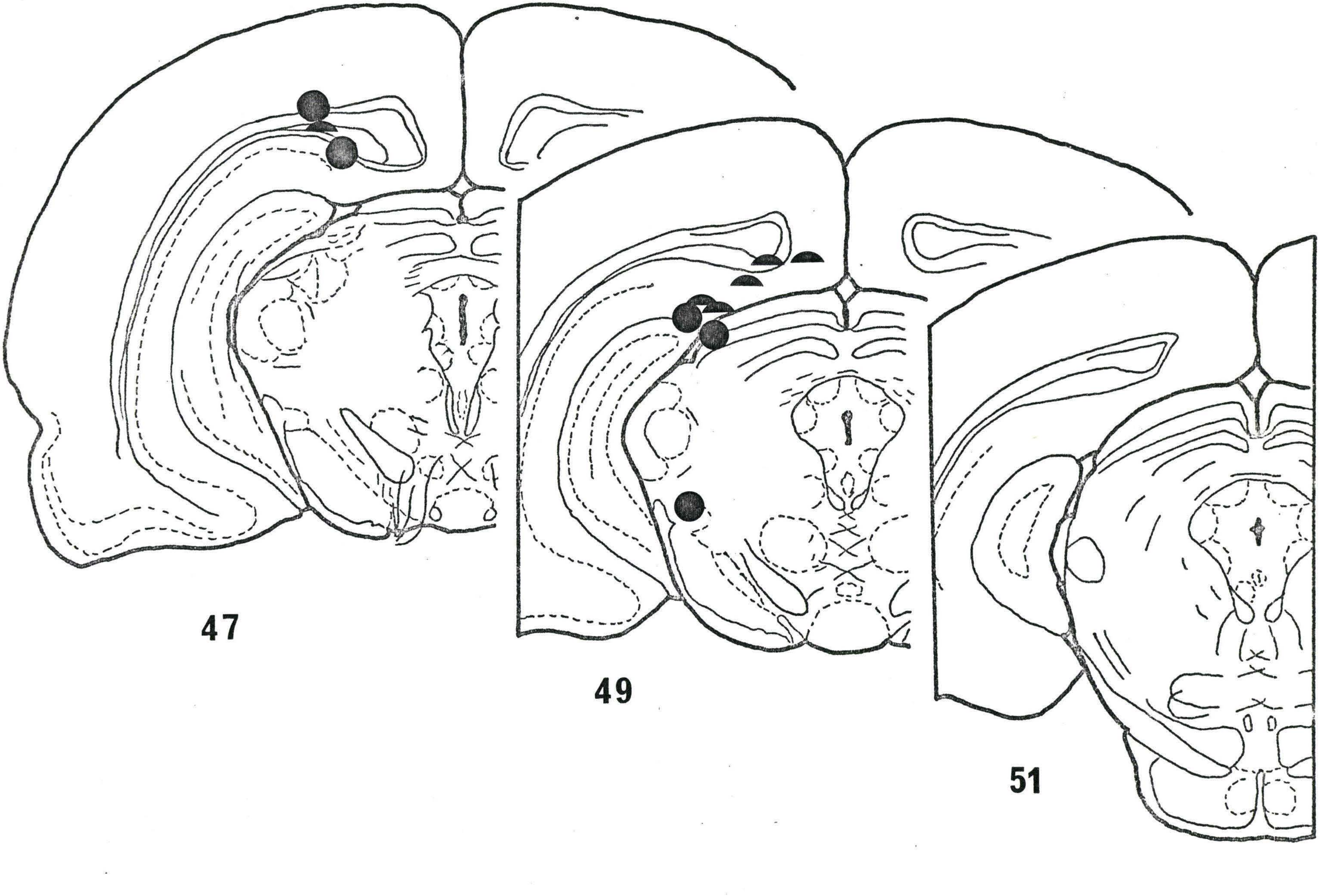
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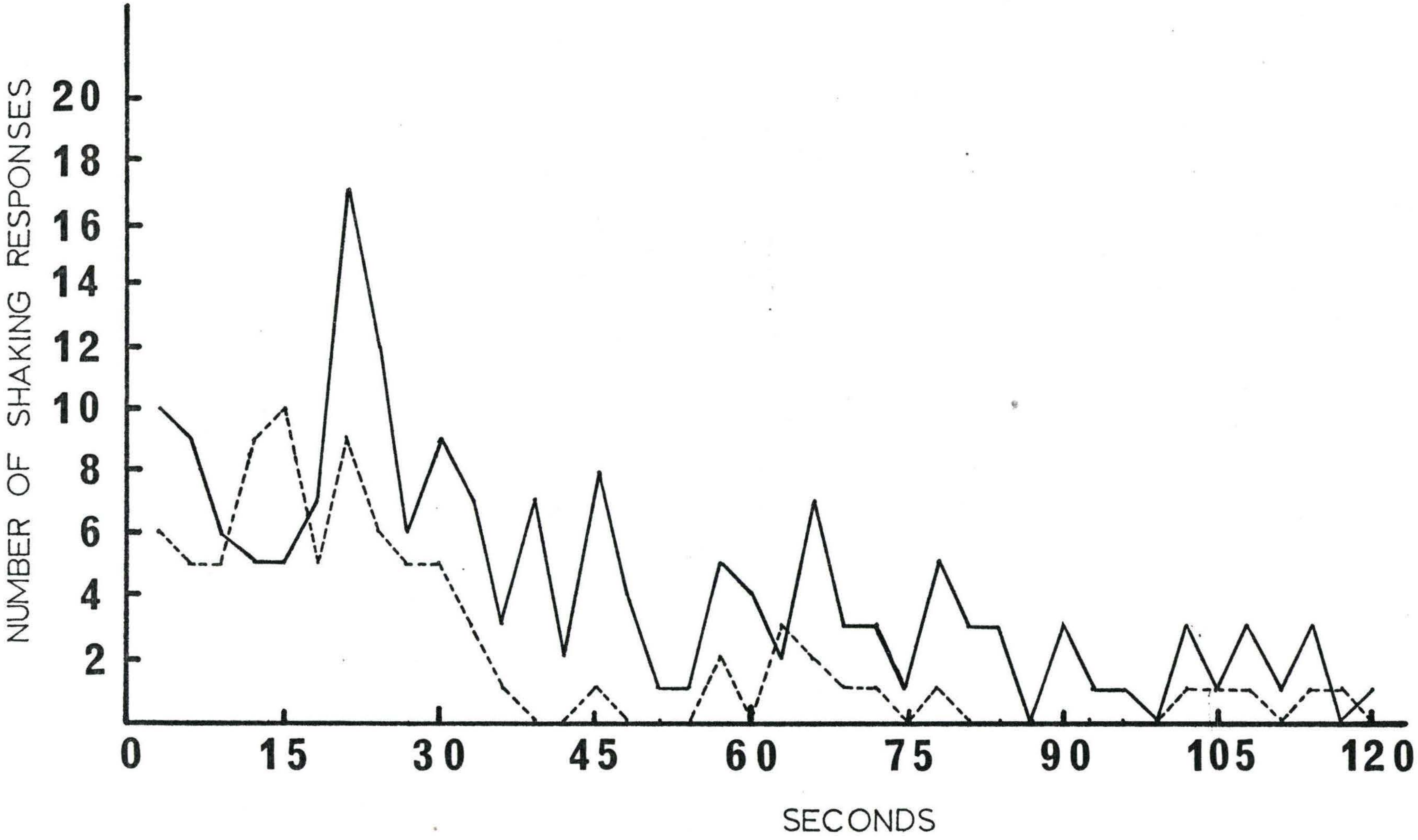
first within a few seconds of stimulation offset. Once initiated by stimulation, shaking continued intermittently for up to five minutes or more, but typically stopped within two minutes (see Figure 4).

Frame by frame analysis of 8 mm film exposed at 16 frames per second showed that the duration of evoked shaking responses of three rats ranged from 0.5 to 1.0 seconds with a mean duration of 0.75 seconds. By analysing the movement in each frame, of a black patch of fur in the center of the back of hooded rats, it was determined that the shaking occurred at a rate of four to five cycles per second. One cycle was defined as the movement of the black patch of fur, from the midline to one side, to the other side, and back to the midline.

The evoked shaking appears to be related to hippocampal seizure activity, but not necessarily to the occurrence of behavioral seizures. In two subjects, recordings of hippocampal electrical activity following stimulation confirmed the observations of Ito (1966) and MacLean (1957b) that the grooming occurred at the onset of and following seizure discharges in the hippocampal formation. Also, evoked shaking was similar whether the stimulation elicited a behavioral seizure or not. The frequency of occurrence of shaking as a function of time from stimulus offset or the end of behavioral seizure is shown for two animals in Figure 4. The response became less and less frequent as a function of time, but the character of individual responses remained the same. Stimulation of the fimbria and area CA_3 of Ammon's Horn elicited shaking after stimulation offset in subject 1-68.

Fig. 4. Occurrence of shaking responses following hippocampal stimulation without a behavioral seizure (Rat # 1-68) or with a behavioral seizure (Rat # 6-68). Solid line, Rat # 1-68, based on 38 stimulation trials. Broken line, Rat # 6-68, based on 18 trials. Individual shaking responses were cumulated within 3 sec. intervals.


NUMBER OF SHAKING RESPONSES
20
18
16
14
12
10
8
6
4
2
0
15
30
45
60
75
90
105
120
SECONDS

Stimulation of the dentate gyrus and area CA_4 of Ammon's Horn elicited a behavioral seizure followed by shaking in subject 6-68. In the latter subject, shaking was plotted as a function of time from the cessation of clonic motor activity rather than stimulation offset.

Behavioral seizures, as Figure 3 illustrates, were also elicited by stimulation of the majority of sites from which grooming was elicited. The main characteristics of the seizures were a gradual development and building up of phasic activity of the forelimbs and trunk, accompanied by falling over on the back or on one side. There tends to be a continuum of severity of behavioral seizure activity which ranges from clonic activity of the limbs and head (minor fit) to violent clonic activity accompanied by falling over, salivation, and piloerection, and followed by severe depression of reflexes and spontaneous movement (major fit).

It is possible that shaking is a sign of seizure activity in the limbic system that fails to spread widely enough to culminate in a behavioral seizure. In support of this, at 28 of 41 sites from which both shaking and behavioral seizures were elicited, shaking had a lower threshold than behavioral seizures (Sign Test, $\underline{p}<.001$). Seizures were elicited at a lower intensity in only three sites, while in the remaining 10 sites both behaviors were first evoked with the same stimulation parameters. The threshold was taken as the lowest frequency and voltage combination of stimulation parameters that first elicited shaking or seizures. There was, however, evidence that the lower thresholds for shaking were not just a matter of stimulation levels *per se*, since simply repeating stimulation that elicited shaking often led to the development of an overt seizure even after the evoked shaking had stopped. This observation indicates that there was an effect of the stimulation that carried over between stimulation trains.

The finding that stimulation of all hippocampal sites elicited shaking or shaking and behavioral seizures (see Figure 3) suggests that specific ascending and descending pathways were involved in the spread of the seizure activity. Other sites without known direct connections to the limbic system tended to yield behavioral seizures alone. Figure 3 shows that these sites were mainly in the striatum and diencephalon. Specificity is also suggested by the finding that proportionately more hippocampal-stimulated animals than subcortical-stimulated animals began shaking at a stimulation frequency of 5 pps ($\chi^2=33.0$; df=1, $\underline{p}<.001$). Moreover, the hippocampal placements required lower voltages to evoke shaking than the subcortical placements at a frequency of 5 pps (Mann-Whitney U; two-tailed $\underline{p}<.01$). Table 1 shows the thresholds for both shaking and seizures for hippocampal and subcortical sites. These differences between the hippocampal formation and subcortical structures could be a reflection of hippocampal sensitivity to low frequency stimulation, or to a lower hippocampal threshold on an intensity dimension (*i.e.*, less current per unit time is passed with stimulation at 5 pps than at 20 pps).

Finally, spontaneous behavior was more depressed following a behavioral seizure than following stimulation trains that evoked shaking. For example, poor coordination, absent placing responses, absent climbing responses, or catatonia were often observed for periods ranging up to 10

TABLE 1

Mean Stimulus Voltage at Each Frequency on Trial of First Occurrence of Shaking or Behavioral Seizure Elicited by Hippocampal or Subcortical Stimulation.

	HIPPOCAMPAL						SUBCORTICAL					
	Shaking			Seizures			Shaking			Seizures		
N[a]	38	2	0	15	15	0	7	19	2	8	26	0
Frequency	5	20	200	5	20	200	5	20	200	5	20	200
Threshold Voltage	4.7	5.0	-	6.3	5.3	-	7.0	6.6	8.5	6.5	6.9	-

---

[a] N refers to the number of sites. Sites from which both shaking and seizures were elicited are included once for each behavior.

min. or more following behavioral seizures in 28 of 62 sites, but were never observed following stimulation that elicited shaking alone. In addition, sequences of grooming were frequent following stimulation that elicited shaking (38 of 62 sites) but were less frequent following stimulation that elicited seizures (18 of 62 sites).

The Medial Hypothalamus

Stimulation of the medial hypothalamus and preoptic area of 36 subjects elicited complete sequences of vigorous stereotyped grooming lasting over 60 sec. in a two-minute stimulation train and frequently continuing after stimulation offset. Brief grooming lasting only a few seconds during two min. of stimulation was elicited by stimulation of 19 subjects. In some of these latter subjects, grooming occurred more vigorously as an aftereffect of the stimulation. Figure 5 shows frontal diagrams of the locations of sites from which stimulation elicited or did not elicit grooming. The distribution of placements shows that the most effective region was in the medial aspect of the anterior hypothalamus extending from the preoptic area to the middle hypothalamus. Stimulation in and around the paraventricular nuclei of the hypothalamus[3] was particularly effective in eliciting vigorous grooming. Figure 6 is a photomicrograph of a placement in the region of the paraventricular nucleus.

In most respects, the evoked grooming was identical to normal spontaneous grooming. However, the evoked grooming was much more

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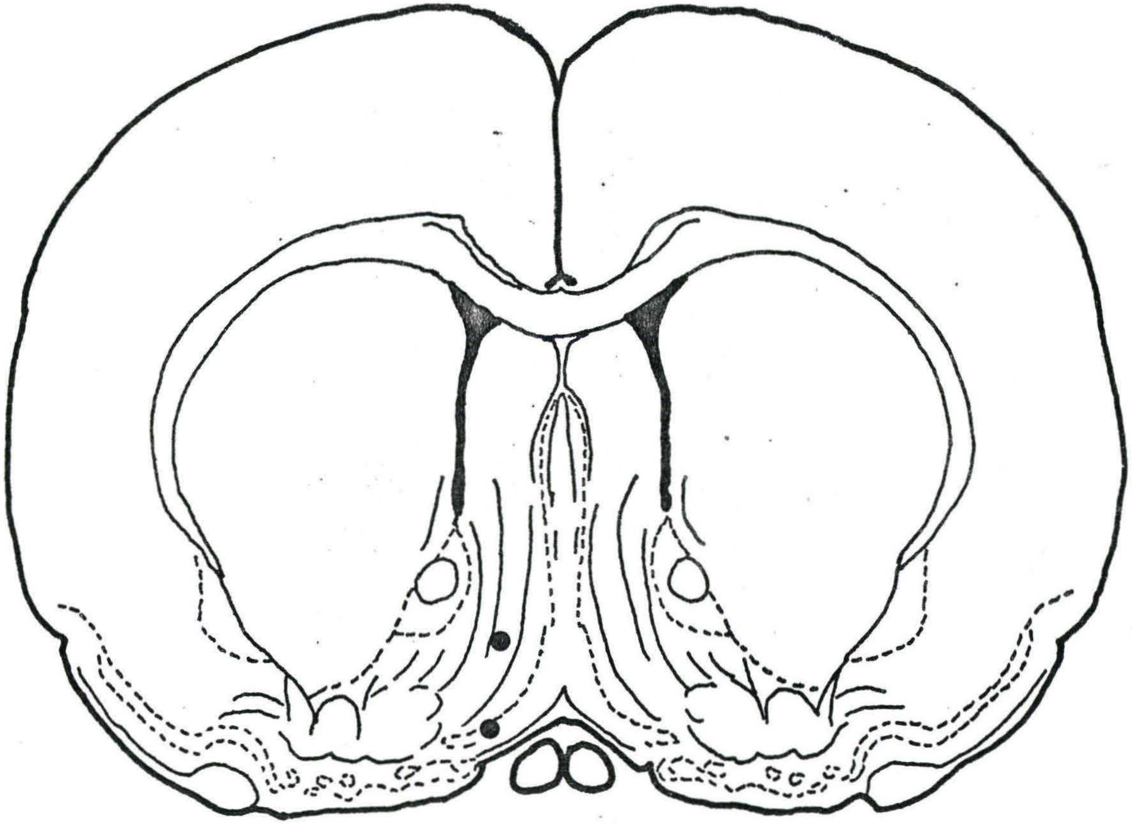
[3] Paraventricular nucleus refers to the nucleus paraventricularis (hypothalami).

Fig. 5. Composite frontal diagrams showing sites from which stimulation elicited persistent grooming (▲), brief grooming (△), and no grooming (●). Drawings based on Konig and Klippel (1963).



16

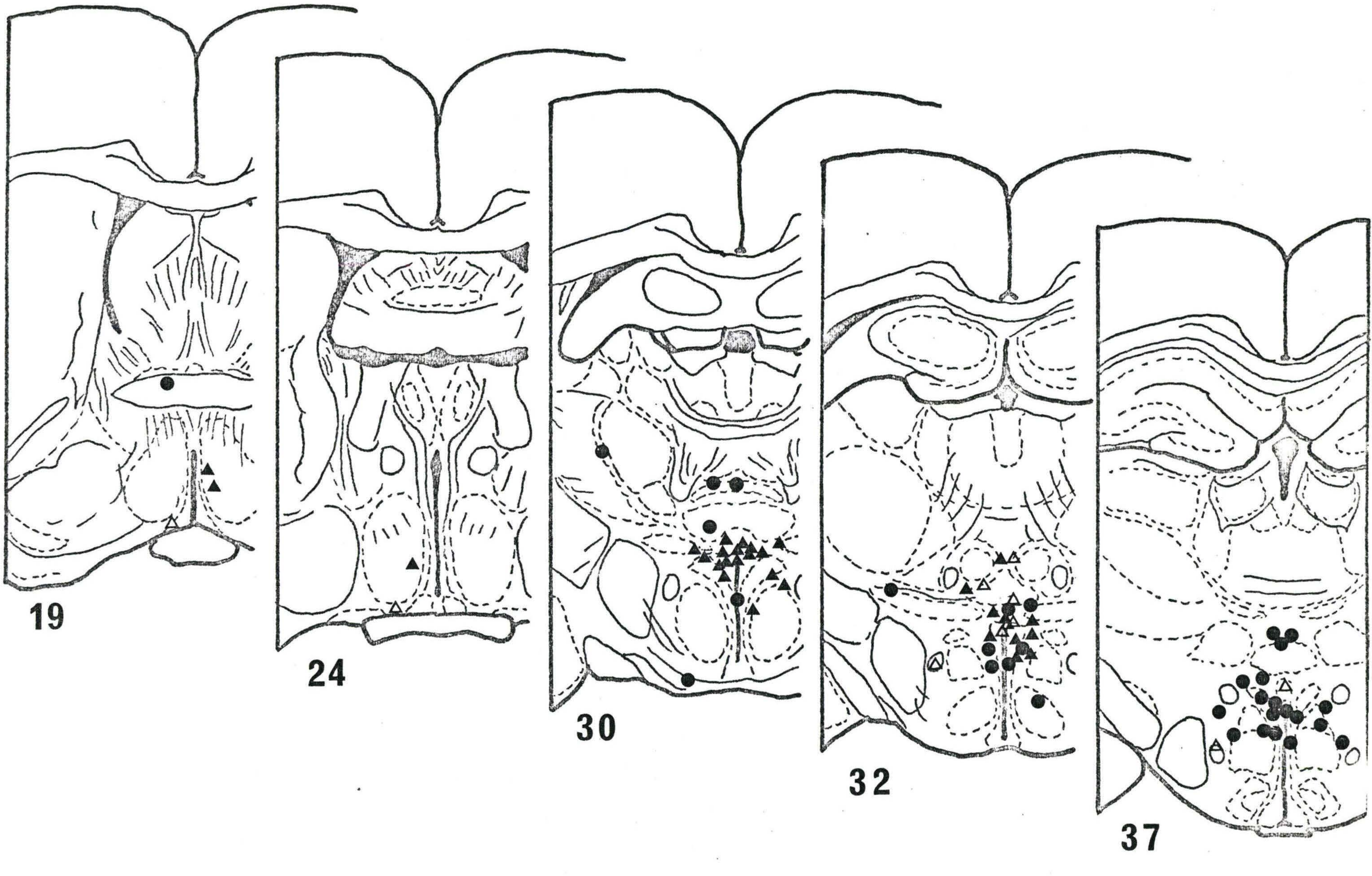

19
24
30
32
37

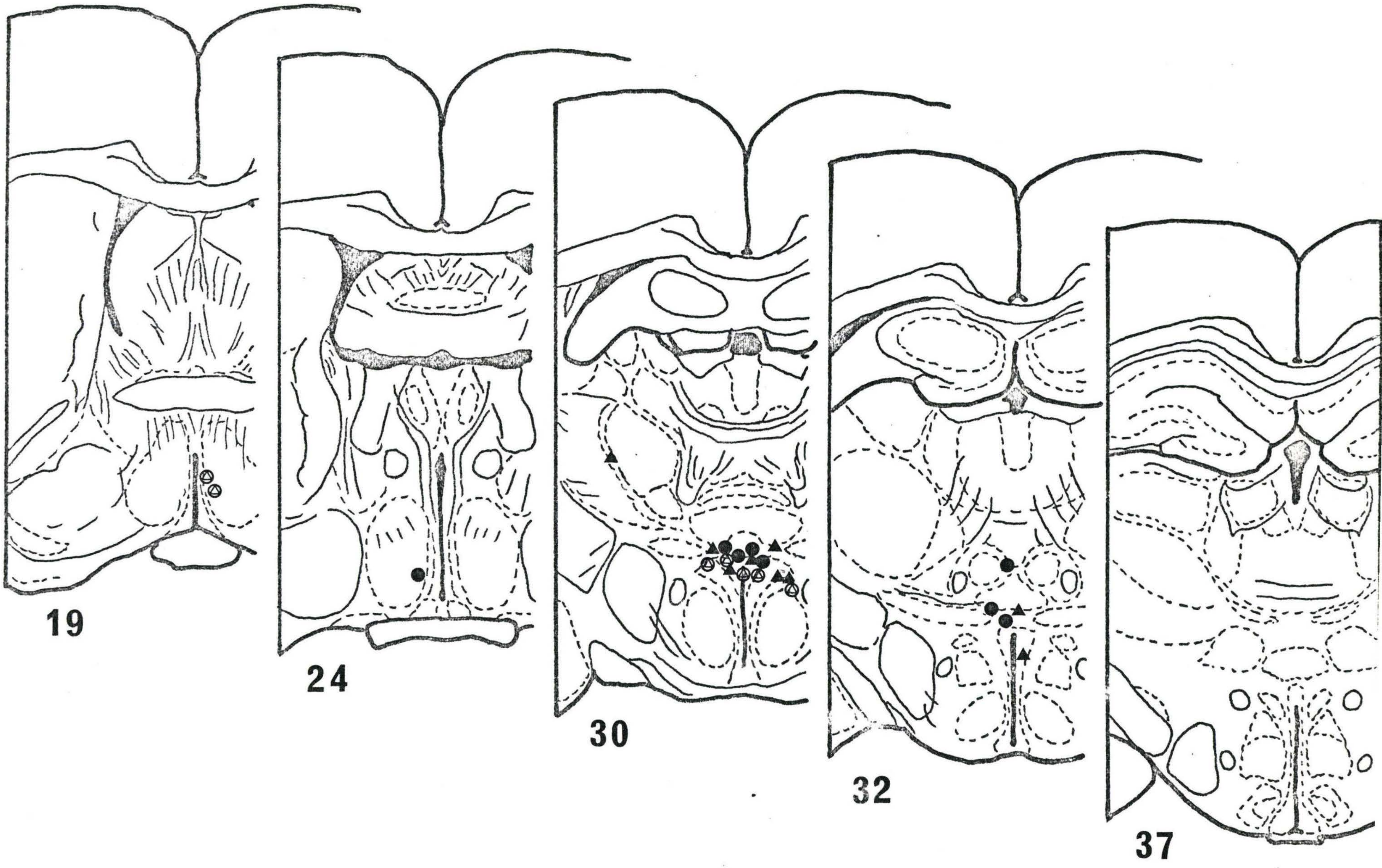
Fig. 6. Photomicrograph of a site in the paraventricular nucleus (hypothalami) from which stimulation elicited grooming (x 180).

vigorous and displayed a greater variety of components in comparable sequences. The components of grooming elicited by stimulation included face-washing (the predominant component), grooming of the back, and licking of the abdomen, penis, scrotum, hind feet, and tail. All of the subjects from which grooming was elicited showed face-washing, back-grooming, and one or more components of ventral-surface grooming. That is, stimulation elicited complete sequences of grooming and not just isolated components. Shaking, scratching, and scratching alternating with biting the toes of the active foot occurred very infrequently in the behavior tests and were not related to the stimulation in any consistent manner.

A typical sequence of evoked grooming began with a rapid repetitive shaking of the forepaws (lasting less than one sec.) followed by licking of the forepaws which were then brushed over the vibrissae, snout, and head. Next, the animal turned to its back, licking and biting the fur of the back, starting rostrally and working gradually down towards the base of the tail and the anogenital region. Frequently, the abdomen and hind feet were also licked. Finally, the animal either stopped grooming or returned to face-washing in which case a similar sequence might ensue. Sequences such as this lasted from several seconds (in which case not all the components would be evoked) to several minutes, continuing without interruption when stimulation was turned off.

Tail licking was elicited by stimulation of the 15 sites shown on the frontal diagrams of Figure 7. This response occurred within long sequences of grooming like that described above. Starting by licking the base of the tail, the rat then licked toward the tip of the

Fig. 7. Composite frontal diagrams showing sites from which stimulation elicited tail licking (●), penis licking (▲), and both tail licking and penis licking (◉). Drawings based on Konig and Klippel (1963).


19
24
30
32
37

tail. When about half way along the tail, the rat would pick it up in its forepaws and continue to lick the dorsal and ventral surfaces of the tail until the tip was reached. The rat then licked and nibbled the tip for a few seconds. The response usually lasted about 20 sec. but ranged in duration from 10 to over 60 sec. Tail licking also continued after stimulation offset and was observed on occasion to begin after offset during a sequence of grooming other body areas. The tail licking response does not appear to occur spontaneously in the type of rat used, and in three years of work has never been observed except during and following stimulation of the sites shown in Figure 7.

Penis licking was elicited by stimulation of 16 sites. Licking of the penis was associated with long sequences of grooming and occurred both during and after stimulation. The response normally was performed when the rat was sitting on its haunches. The penis licking tended to occur in several short bouts interrupted by pauses consisting of sitting up, looking about, and face-washing. The penis was apparently always erect when licking occurred and small pelvic thrusting movements often accompanied the licking. This behavior is seen relatively frequently during spontaneous grooming sequences and was similar to that which occurs following sexual activity and intromission. However, ejaculate was never observed on the floor of the testing platform during or following stimulation of the hypothalamic sites shown in Figure 7. Figure 7 also illustrates that stimulation of several of the sites elicited both penis licking and tail licking. Grooming was also elicited by stimulation of all the sites but two from which penis licking was elicited.

Other Behavior

Stimulation of the brain stem also elicited a variety of behaviors other than grooming but since the main concern of this thesis is with evoked grooming they are not described in detail.

Stimulation of the midbrain tectum elicited head movements, circling, backward walking, escape, and vocalization. Stimulation of the hippocampal formation and other limbic system structures elicited acts such as head movements, circling, and escape behavior during stimulation. Hyperactivity, exaggerated fear and startle responses, and ataxia were frequently observed as aftereffects of stimulation that elicited grooming or behavioral seizures. Other behaviors elicited by stimulation of sites in the medial hypothalamus (both "grooming" and "non-grooming" sites) included locomotion, exploratory activity, chewing, shaking, seizure activity, and escape at higher intensities of stimulation.

Summary

Of the three general anatomical subdivisions from which grooming was elicited by electrical stimulation, grooming elicited by stimulation of the preoptic/anterior hypothalamic area was most like normal, spontaneous grooming. Complete and complex sequences of grooming were elicited by stimulation of this area whereas stimulation of the tectum elicited a single, rapidly fatiguing component (back-grooming) and stimulation of the limbic system elicited grooming that was associated with electroencephalographic and behavioral seizure activity. The normalcy and richness of the grooming elicited by stimulation of the medial anterior hypothalamus encouraged further investigation of the details of its organization. Several experiments were conducted in which the organization of grooming elicited by stimulation of the hypothalamus was examined in terms of its somatic and autonomic components, its sequential organization, and its relationship to reinforcement.

CHAPTER III

The Medial Anterior Hypothalamus

Since grooming may subserve a number of functions, experiments were conducted to elucidate the nature of the evoked grooming in relation to other types of grooming. Comparisons were made among evoked grooming, spontaneous grooming, and thermoregulatory grooming in terms of the response components exhibited by each type. In different experiments, latency, duration, and relative frequency of components of evoked and spontaneous grooming were determined. The degree of stimulus control in evoked grooming was examined by comparing stimulation periods with non-stimulation periods. In further experiments, thermoregulatory responses other than grooming were investigated. Since salivation and peripheral vasodilatation of the feet and tail are major heat loss responses in the rat (Grant, 1963; Hainsworth, 1966; Thompson and Stevenson, 1965) an experiment was conducted to determine if these autonomic responses were elicited by stimulation that elicited grooming or by central warming of sites from which grooming was elicited.

With a view to assessing the specificity of the evoked grooming, the effect of stimulation on other responses (antidiuretic hormone release, micturition, and defecation) was investigated. The question of specificity with respect to these responses is important because (1) antidiuretic hormone is released during exposure to high temperatures (Collins and Weiner, 1968) and, (2) grooming, antidiuretic hormone secretion, and defecation accompanied exposure to stress in the rat (Stein and Mirsky, 1954).

METHOD

Subjects

The subjects were 70 male hooded rats. Fifty-seven animals with implanted bipolar electrodes had been tested previously in the mapping experiment (Chapter II). The remaining 13 animals were unoperated control subjects.

Stimulation Parameters

Stimulation parameters were the same as in the mapping experiment.

Apparatus

The behavior testing apparatus was the same as used in the mapping experiment. A plywood insert was used to cover the sawdust floor of the platform in some tests. With the insert in place, the walls were one inch high and the behavior testing apparatus was designated as the "open-field apparatus."

In those tests where stimulation was remotely controlled, Grason-Stadler relay equipment was used for programming. Responses were recorded on a Gerbrands 5-channel event marker and an Esterline Angus 10-channel event marker activated by microswitches operated by the experimenter. Stimulation periods were recorded automatically on the event recorders.

A 0.7 cubic foot Fisher oven with a glass panel in place of the door was used to study thermoregulatory responses in normal animals.

Air temperatures ranging from 32 to 42°C. could be controlled to within ± 1°C. of a selected temperature.

Procedure

In each of the following experiments, stimulation parameters were selected for each electrode site on the basis of whether they strongly elicited a given behavior, either grooming or other somatomotor response, in the mapping experiment (behavior testing procedure).

Open-field Test. Six operated and five control animals were observed in the open-field apparatus continuously for eight ten-minute sessions. During each session, the operated animals received continuous electrical stimulation of the brain with stimulation parameters that evoked grooming. All grooming responses were described by dictation into a Sony TC 102 M tape recorder. At the end of each session, during playback of the tape, the latency and duration of grooming responses were timed using a stopwatch and transcribed for later analysis.

Remote Control Stimulation Tests. In order to control for possible experimenter bias, 18 animals were given repeated daily sessions with stimulation onset and offset controlled by Grason-Stadler programming equipment. A subject was placed in the behavior testing apparatus and stimulation leads were attached for 30 to 60 min. before a test began. This was done so that when the testing session began, spontaneous grooming would be at a minimum since rats groom after exploring a novel environment, but have usually stopped this within 30 min. A session consisted of 20 two-minute periods arranged in a random sequence of two-minute continous stimulation and two-minute non-stimulation periods. For each condition, there was an equal number of periods, and no more than two periods of the same condition occurred in sequence.

Thirteen animals were tested daily for five days during which four categories of behavior (face-washing, back-grooming, ventral-surface grooming, and shaking) were recorded continuously on the Gerbrands event recorder. Five animals were tested daily for 6 to 10 days during which nine behaviors (face-washing, back-grooming, abdomen-licking, foot-licking, scrotum-and tail base-licking, tail-licking, scratching, shaking, and walking) were recorded on the Esterline Angus event recorder. Five operated animals were tested without stimulation being applied during testing. These animals were run with the stimulation leads attached and comprised a "pseudo-stimulation" control group.

Three subjects were tested with stimulation and non-stimulation periods arranged in alternating order for the 40-min. session.

Of the animals receiving stimulation, all but four groomed vigorously in response to stimulation in the mapping experiment. The evoked behavior shown by these four subjects included sniffing, walking, and head movements. One of these subjects showed brief grooming during stimulation and grooming after offset, but the main stimulation effect was walking. These subjects were a stimulation control group. Since tail-licking is rare as a spontaneous response in this strain of rats, the "grooming" rats were divided into two groups on the basis of whether or not they showed tail licking in the mapping experiment.

In summary, the four groups of rats tested using the remote control stimulation procedure were: (1) a no-stimulation control group (n=5) which was tested with the stimulation leads attached, (2) a stimulation control group (n=4) from which stimulation elicited responses other than grooming, (3) an experimental group (n=7) from which stimulation elicited grooming but not tail-licking, and (4) an experimental group (n=10) from which stimulation elicited grooming including the tail-licking response.

Thermoregulatory Response Tests. Eight unoperated rats were exposed to ambient temperatures of 36 to 42°C. for periods of up to three hours. Subjects were watched continuously for a total of 25 hours. Notes were made describing the components of behavioral thermoregulation so that the responses could be compared with the grooming components elicited by electrical stimulation of the medial anterior hypothalamus. In some tests, a shallow dish of water was present in the oven. In addition, five animals showing evoked tail-licking during stimulation were stimulated in the open field with the water dish present.

An increase in tail temperature, a reliable and sensitive indicator of peripheral vasodilatation in response to increased core temperature, has been used by several investigators (Grant, 1963; Johansen, 1962; Little and Stoner, 1968; Thompson and Stevenson, 1965) studying thermoregulatory responses in furred animals. Tail temperature was recorded from three subjects which showed grooming and tail-licking and one subject which showed grooming and foot-licking in the mapping experiment. Each subject was restrained and suspended in a canvas harness. A disc temperature sensor (Yellow Springs Instrument Company, Probe 421) was taped on the dorsal aspect of the tail 1.0 in. from the base. Stimulation leads were attached and tail temperature was recorded using a Yellow Springs Instrument Company telethermometer (Model 43 TA) for 5 to 30 min. before stimulation, for 5 to 30 min. during stimulation, and for 2 to 10 min. following stimulation. Behavior tests were usually conducted before and after restraint to check the efficacy of the central stimulus. Tail temperature was recorded from one animal while it moved about freely, groomed, and licked its tail.

Tail temperature was recorded in 11 sessions using electrical stimulation with parameters which elicited grooming in behavior tests and in three sessions using radio-frequency warming. Radio-frequency warming was accomplished using a Grass Model LM4 lesion maker set at maximum output. Current was controlled by a 100 KΩ variable resistor in series with the electrode. Preliminary calibration using egg white at 37°C. showed that a temperature increase of 1 to 2°C. was obtained about 1.0 mm. from the electrode tips when the resistance was set at 40 KΩ. The increase in temperature in the egg white occurred in less than 20 sec. at which time the temperature had usually stabilized at the new level.

Specificity Tests. The effect of stimulation on antidiuresis, micturition, and defecation was investigated. Animals were also tested for evoked eating and drinking responses.

Water loading was attempted in two animals. To avoid stress and antidiuresis that might result from gavage, animals were water loaded following the procedure used by Kakolewski, Cox, and Valenstein (1968). The animals were housed in individual wire cages suspended in a wooden frame. Food was always available. Their water consumption was measured for four days. Water was then removed and replaced by a saccharin and glucose solution (0.125 gms. of sodium saccharin and 3.0 gms. of d-glucose powder per 100 mls. of distilled water). The night before testing, the stimulation leads were attached to the animal's electrode. The following morning, urine output was measured for 20 min. before stimulation, during stimulation of 5 to 30 min. and for 20 min. after stimulation. When voided, the urine was collected with a syringe from Saran wrap covered cardboard under the cage. The occurrence of defecation was also noted.

Micturition and defecation were also recorded for three experimental and the five control animals tested in the open-field experiment described on page 49.

Twenty-five subjects were tested, while satiated, for eating and drinking behavior during stimulation that elicited grooming and other behaviors. In a test of seven subjects, food pellets and a water bottle were present in the behavior testing apparatus. Food and water consumption were recorded for 5 min. before stimulation, during 5 min. of continuous stimulation, and for 5 min. following stimulation. Seven animals were tested twice using this procedure. In tests of 18 animals, food only was available during behavior testing in which stimulation was delivered according to the procedure used in the mapping experiment.

RESULTS

Open-field Test. In the open-field, there were marked qualitative differences in the grooming of the stimulated and non-stimulated animals. The subjects from which grooming was elicited by stimulation groomed much more vigorously, with longer sequences, and displayed more of the components of grooming in each bout. These differences were reflected in both the latency of the first grooming responses and the duration of grooming for each group. The experimental group started grooming significantly sooner and groomed for significantly longer periods of time as shown in Table 2.

Remote Control Stimulation Tests. All 26 subjects (including the control subjects) tested in the remote control stimulation tests displayed all the grooming responses in the rats repertoire except penis-licking and tail-licking. Both control and experimental animals engaged in penis-licking but it was an infrequent response for most of them. On the other hand, tail-licking occurred only in the group which showed tail-licking in the mapping experiment and was not observed in control subjects or other subjects from which grooming was elicited. Figure 8 presents the mean percentage of time each subject spent grooming in the remote control stimulation tests. The results for the three subjects which received alternating stimulation periods are included with the results of the other subjects since inspection of individual data indicated they were essentially identical. Scratching and biting the toes of the hind feet are not included in the totals since their occurrence was not recorded for the majority of stimulated subjects. However, scratching and toe-biting were infrequent in all the stimulation groups.

A Kruskal-Wallis one-way analysis of variance (Seigel, 1956)

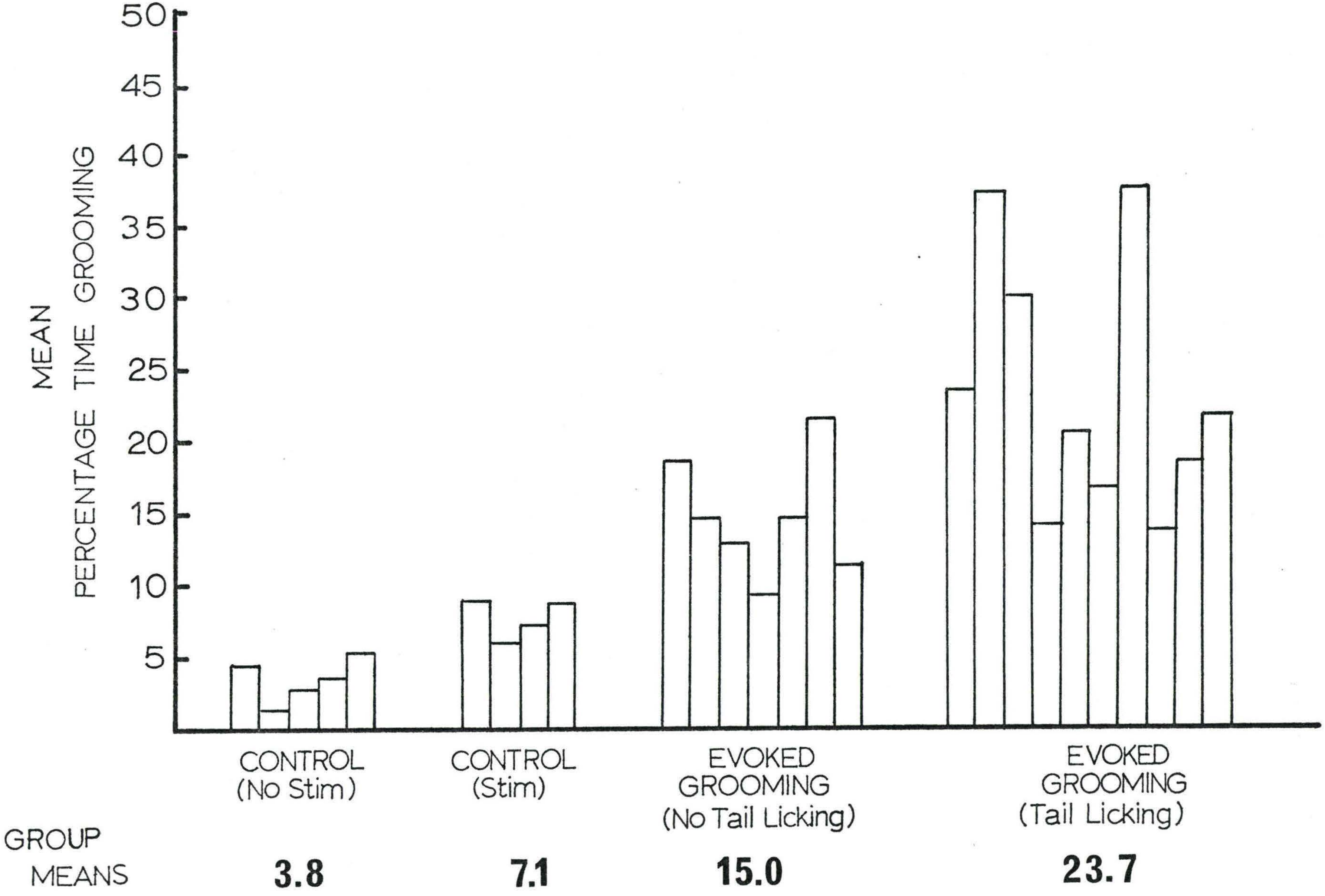
TABLE 2

Mean Latency and Duration of Grooming of Stimulated and Non-stimulated Subjects in the Open Field

GROUP	N	LATENCY (sec.)	DURATION (sec.)
Experimental	6	34.5	218.1
Control	5	213.5*	21.5*

*p=.002, Mann Whitney U Test, Two-tailed.

Fig. 8. Mean percentage of total time individual rats spent grooming in remote control stimulation tests (stimulation plus non-stimulation periods).


MEAN PERCENTAGE TIME GROOMING
50
45
40
35
30
25
20
15
10
5
CONTROL (No Stim)
CONTROL (Stim)
EVOKED GROOMING (No Tail Licking)
EVOKED GROOMING (Tail Licking)
GROUP MEANS
3.8
7.1
15.0
23.7

revealed that the groups groomed for different lengths of time ($H=20.3$, d.f.=3, $p<.001$). There was no overlap in grooming times between the two control groups and the two groups receiving stimulation that elicited grooming during the mapping experiment. Although the difference between the two control groups was not statistically significant (Mann-Whitney $U=2$, $p=.064$, two-tailed test), there was a tendency for the control group receiving stimulation to groom more. Two of these animals, which groomed mainly after stimulation offset, had electrodes in the reuniens nucleus and near the fornix respectively. These areas were found, in the mapping experiment, to be involved in the shaking behavior observed following stimulation of numerous limbic system sites. Thus, the grooming elicited from these sites in the stimulation control group could have been due to activation of limbic system seizure activity. On the other hand, in the absence of the vigorous shaking, the effect could have been due to a general facilitating effect on grooming by the stimulation evoked behavior rather than activation of the specific neural substrates for grooming. In other words, stimulation produced movement may have had a secondary effect on grooming. Finally, the difference in time spent grooming between the two evoked grooming groups was not statistically significant (Mann-Whitney, $U=19$, $p>.10$, two-tailed test).

While the mean grooming time in the remote control stimulation tests for each group shows that stimulation elicited grooming, the specific nature of the relationship between stimulation and grooming is best shown by comparison of the stimulation and non-stimulation periods. Table 3 shows that all the experimental subjects groomed more

TABLE 3

Percentage of Total Grooming Occurring During Stimulation and Non-stimulation Periods in Remote Control Stimulation Tests

GROUP	RAT	TOTAL TIME OBSERVED (min.)	PERCENTAGE (STIMULATION)	PERCENTAGE (NO STIMULATION)
Control (No stimulation)	105	200	43.6	66.4
	109	240	40.0	60.0
	114	200	57.0	43.0
	118	240	63.7	36.3
	119	200	54.3	45.7
Control (Stimulation)	67	200	10.6	89.4
	73	200	48.9	51.1
	81	200	60.4	39.6
	120	200	9.8	90.2
Grooming (No Tail-Licking)	52	200	52.4	47.6
	57	200	89.5	10.5
	60	200	52.9	47.1
	64	200	84.3	15.7
	71	200	74.9	25.1
	76	200	82.1	17.9
	78	200	83.0	17.0
Grooming (Tail-Licking)	18	200	94.3	5.7
	34	200	56.6	43.4
	48	200	57.3	42.7
	54	200	56.4	43.6
	63	200	85.2	14.8
	75	200	61.7	38.3
	106	400	73.8	26.2
	107	400	96.8	3.2
	111	240	51.4	48.6
	114	280	76.5	23.5

during stimulation than when stimulation was not on. There was, however, a great deal of variability. In some subjects, the grooming occurred mainly during stimulation periods (stimulation-bound grooming) while in other subjects the grooming was fairly evenly divided between stimulation and non-stimulation periods. In those subjects where grooming was more evenly divided between stimulation and non-stimulation periods, the grooming was not distributed randomly throughout the non-stimulation periods. Rather, the grooming occurred at the beginning and early parts of the non-stimulation periods and was a continuation of grooming induced by electrical stimulation.

Comparing stimulation and non-stimulation periods on a component by component basis for face-washing, back-grooming, and ventral surface-licking, Figure 9 shows that each component was elicited by stimulation, although, in absolute terms, face-washing contributed most to the total grooming times and the four groups present quite different profiles with this component by component analysis.

When the components are considered in relative terms, i.e., when time occupied by each component is expressed as a percentage of total grooming time, differences in total amount of grooming are removed from the analysis. Thus, a comparison of groups can be made with respect to pattern of grooming rather than total incidence. Figure 10 shows that differences between the groups are largely removed when this is done. There is, however, an overall difference in percentage of each component among the four groups (Freidman Two-way Analysis of Variance, $\underline{p}<.05$) but face-washing is seen to be only slightly facilitated with respect to the control groups, in the evoked grooming group

Fig. 9. Mean time spent grooming during remote control stimulation tests. Component by component analysis for stimulation (solid bars) and non-stimulation (open bars) periods. The abbreviations used in this and subsequent figures are: face-washing (FW), back-grooming (BG), and ventral-surface grooming (VS).

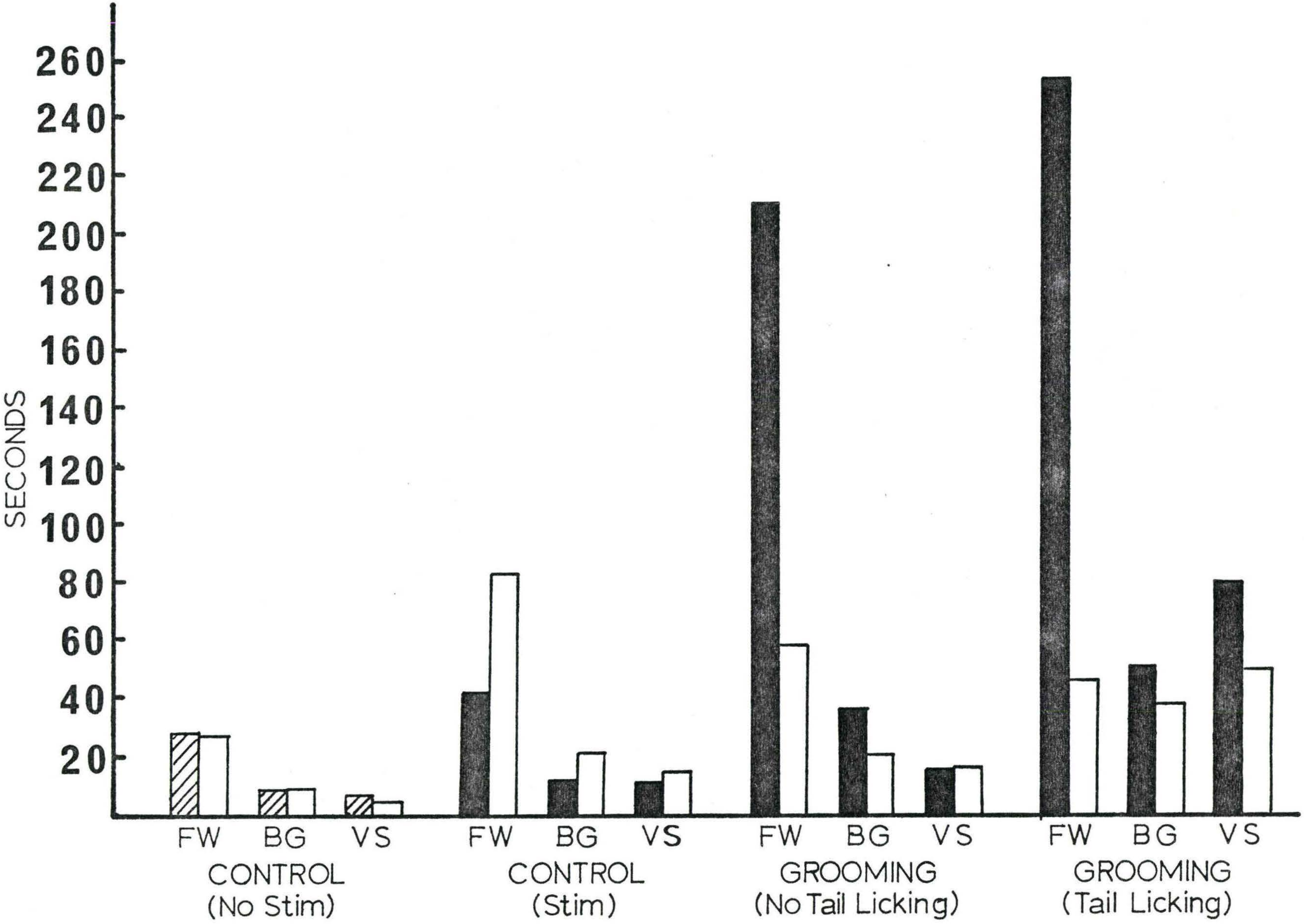
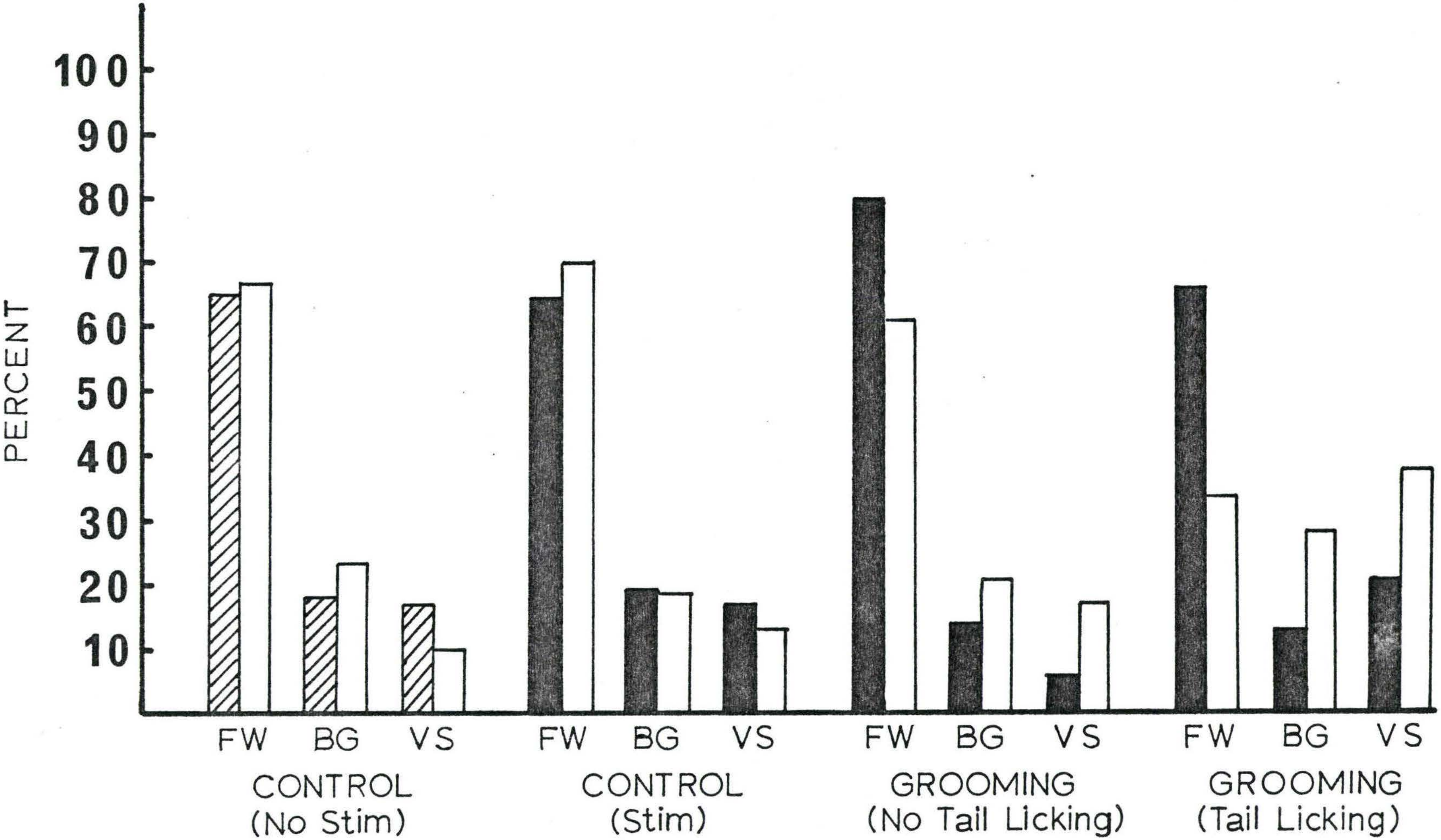

SECONDS
260
240
220
200
180
160
140
120
100
80
60
40
20
FW
BG
VS
CONTROL
(No Stim)
FW
BG
VS
CONTROL
(Stim)
FW
BG
VS
GROOMING
(No Tail Licking)
FW
BG
VS
GROOMING
(Tail Licking)

Fig. 10. Mean time occupied by each component of grooming expressed as a percentage of total grooming time during stimulation (solid bars) and non-stimulation periods (open bars) in the remote control stimulation tests.


100
90
80
70
60
50
40
30
20
10
PERCENT
FW
BG
VS
CONTROL
(No Stim)
FW
BG
VS
CONTROL
(Stim)
FW
BG
VS
GROOMING
(No Tail Licking)
FW
BG
VS
GROOMING
(Tail Licking)

that showed no tail-licking. In the group in which stimulation elicited tail-licking, the increase in ventral surface-licking was not entirely due to licking the tail. More detailed observation of some of the animals indicated that foot-licking and abdomen-licking were increased as well. When stimulation and non-stimulation periods are combined as in Table 4, there is no significant difference among the groups (Friedman Two-Way Analysis of Variance, $p > .075$). The results indicate that the groups differed more in terms of total amount of grooming elicited than in proportions of each component, again suggesting that stimulation tended to elicit normal sequences of grooming.

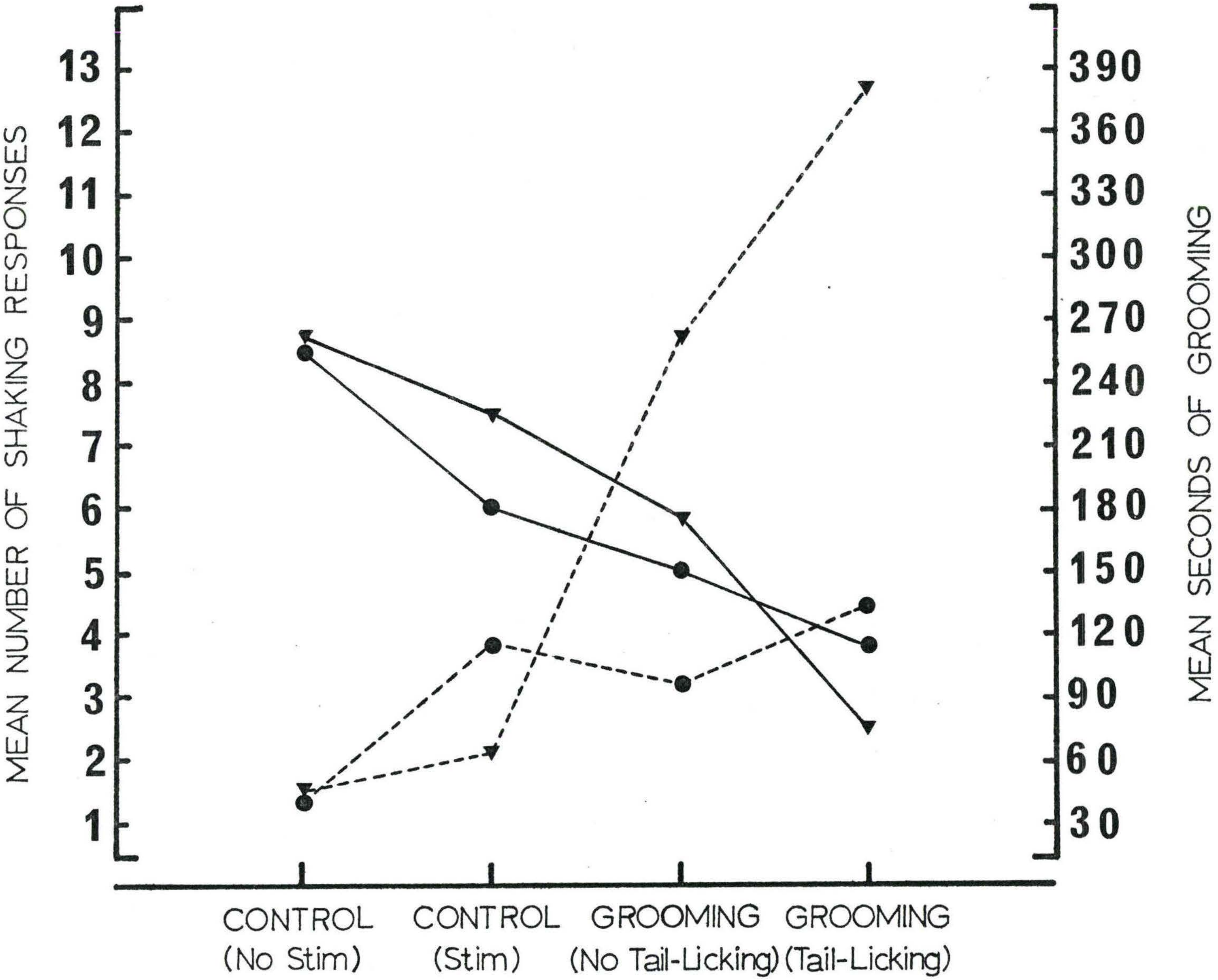
Shaking was recorded from 23 of the subjects tested in the remote control stimulation tests. In contrast to the shaking following hippocampal stimulation, the shaking response observed in this experiment was mainly head shaking, and vigorous shaking of the entire body was rare, i.e., the response resembled normal behavior. All shaking responses are included in the analysis. Unlike the other grooming responses, shaking was not related to stimulation or non-stimulation period *per se* in any of the four groups. Of the animals receiving stimulation in the remote control stimulation tests, shaking occurred more frequently during stimulation periods in 10 animals, and more frequently in non-stimulation periods in seven animals. In most instances, the difference in number of shaking responses was small. Figure 11 shows, however, that the amount of shaking was inversely related to the amount of grooming of the body that occurred and that when total grooming time is increased by stimulation, shaking is depressed in both stimulation and non-stimulation periods. It appears

TABLE 4

Mean Time Occupied by Each Component of Grooming Expressed as a Percentage of Total Grooming Time in the Remote Control Stimulation Tests (Stimulation and Non-stimulation Periods Combined)

Group	Area		
	Face and Forepaws	Back	Ventral-Surface
Control (No stimulation)	66	20	14
Control (Stimulation)	68	18	14
Grooming (No tail-licking)	75	16	09
Grooming (Tail-licking)	58	17	25

Fig. 11. Mean number of shaking responses (solid lines) and mean total time grooming (broken lines) per session of each group in the remote control stimulation tests. Triangles denote stimulation periods; circles denote non-stimulation periods.


MEAN NUMBER OF SHAKING RESPONSES
13
12
11
10
9
8
7
6
5
4
3
2
1
MEAN SECONDS OF GROOMING
390
360
330
300
270
240
210
180
150
120
90
60
30
CONTROL (No Stim)
CONTROL (Stim)
GROOMING (No Tail-Licking)
GROOMING (Tail-Licking)

that stimulation suppresses shaking behavior and that this effect continues throughout the succeeding non-stimulation period.

Finally, nine responses were recorded for the five "pseudo-stimulation" control group subjects and for four of the experimental group from which tail-licking was elicited (see Table 5). The responses of interest here were scratching and biting of the toes of the hind feet, which usually occur together in an alternating order. In the control group, scratching accounted for over 50% of that group's grooming, while scratching accounted for less than 2% of the grooming in the experimental group. This difference in percentage of grooming time spent scratching is significant (χ^2=192.8; df=1; $\underline{p}$<.001). Even in absolute terms the control group spent more time scratching in the remote control stimulation tests than did the experimental group (Mann-Whitney $\underline{U}$ = 0; $\underline{p}$ = .008). In other words, there was a depression of scratching in the experimental group as well as an enhancement of licking and biting the body.

Thermoregulatory Response Tests. The responses of the normal animals in the heat chamber consisted of thermoregulatory grooming and saliva spreading, interspersed with periods of inactivity and attempts at escape. Face-washing was frequent, back-grooming occurred, and saliva was spread on the ventral surfaces including the abdomen, scrotum, hind feet, and tail base. At no time was one of these animals observed to engage in complete tail-licking, even though the base of the tail was often licked vigorously. The presence of the water dish in some tests did not alter the animals' behavior in the heat in any obvious way. While the licking of the ventral surfaces were very similar in

TABLE 5

Mean Time Occupied by Each of Nine Response Categories Recorded During Remote Control Stimulation Tests of Non-stimulated Group and Stimulated Group (Tail-licking)

	GROUP			
	NO STIMULATION		STIMULATION	
N	N=5		N=4	
RESPONSE	Pseudo-Stim.	No Stim.	Stim.	No Stim.
Face-washing	29.2	27.6	278.4	42.9
Back-grooming	8.1	9.4	54.9	38.2
Abdomen-licking	2.6	1.4	32.0	7.0
Foot-licking	4.3	2.7	32.2	7.0
Scrotum, tail-base licking	0.8	0.1	5.9	5.5
Tail-licking	0.0	0.0	28.3	11.8
Shaking (number)	8.7	8.5	2.1	3.2
Scratching	47.9	48.1	2.8	6.5
Walking	18.8	16.9	9.5	4.5

normal rats in the oven and those which received hypothalamic stimulation, it appears that tail-licking is not an important thermoregulatory response in this strain of domestic rat. Similarly, the experimental animals did not show any change in behavior when the water dish was present in the open field during stimulation.

Profuse salivation like that observed in rats exposed to a hot environment was not observed during or following electrical stimulation or radio-frequency warming. During centrally elicited grooming, licking and slight wetting of the paws and fur occurred just as in normal grooming.

Tail temperature did not increase during or following electrical stimulation or radio-frequency warming. Tail temperature increased in one subject which struggled vigorously while being put in the harness and continued to struggle while restrained. After about three minutes in the harness (prior to stimulation) the animal's tail temperature increased sharply to 29.5°C. then gradually increased to above 30°C. where it remained for the duration of restraint. The increase can readily be attributed to increased body temperature as a result of myothermic heat production while the animal was struggling.

Finally, it is important to note that radio-frequency warming did not produce any significant behavioral effects when the animals were stimulated without restraint.

Specificity Tests. Two animals were water-loaded according to the procedure described and an attempt was made to measure any antidiuretic effects produced by hypothalamic stimulation. Although the two subjects consumed three or more times their normal intake of fluid, little or no urination was observed before stimulation. In the absence of significant urination before stimulation, there was no adequate baseline against which to assess any antidiuretic effects of stimulation. The failure of the procedure to produce a constant water diuresis was most likely due to the fact that the rats were tested 3 to 4 hours after their night period when most of the drinking occurred. Also, demonstration of an antidiuretic effect using the procedure of Kakolewski et al. (1968) may require large numbers of animals since the urine output of individual animals water loaded this way is small. Any assessment of an antidiuretic effect was further complicated by the immediate response of the subjects to the electrical stimulation. Stimulation elicited micturition and defecation in both rats. Urine (up to 6.5 mls.) and feces (up to 5 boli) were expelled simultaneously beginning at the onset of stimulation. On subsequent stimulation or during a long train of stimulation, lesser amounts of urine were sometimes excreted. The tips of the electrodes in both subjects terminated in the dorsal half of the paraventricular nucleus.

Since stimulation that elicited grooming also elicited micturition and defecation in two animals, the results of the open-field experiment were particularly interesting. No significant differences on urination and defecation counts were observed between the experimental group (which included the two animals from which stimulation elicited micturition and defecation in the above tests) and the control group of normal animals. Since merely placing the animals in the open field elicited these two responses, the experimental subjects probably had no urine or feces to eliminate when stimulation began.

Only one of the 25 animals tested in this experiment ate or drank during or following stimulation. This subject ate intermittently for about 60 sec. after stimulation offset. The evoked behavior that this animal displayed included shaking and grooming after stimulation offset. The tips of the electrode in this animal were located adjacent to the fornix at the level of the ventromedial nucleus of the hypothalamus.

Summary

The above investigations of the medial anterior hypothalamus showed that, although stimulation selectively facilitated individual components to some extent (e.g., face-washing and ventral-surface licking), the primary effect of stimulation was to elicit long sequences of grooming. Face-washing, licking, and biting were increased by stimulation, scratching and shaking were depressed.

Comparison of evoked grooming and thermoregulatory grooming revealed that electrical stimulation elicited the thermoregulatory components of licking of the hind feet, abdomen, and scrotum. However, there were important differences in the grooming produced by electrical stimulation and environmental warming. First, there was no evidence that tail licking was a thermoregulatory response in this strain of rats. Second, stimulation did not elicit profuse salivation or peripheral vasodilatation although increases in core temperature did have this affect. Thus, grooming elicited by hypothalamic stimulation is either not related to thermoregulation, or stimulation elicits only the somatic components.

At levels of stimulation that induced grooming, micturition and defecation were also elicited. Feeding and drinking were not elicited by stimulation of the medial anterior hypothalamus.

CHAPTER IV

The Sequential Organization of Grooming

In observing grooming elicited by electrical stimulation of the hypothalamus, it became apparent that not only the basic components of grooming (such as face-washing, back-grooming, and ventral-surface grooming) were stereotyped. The way in which certain components were sequentially organized was also stereotyped. Therefore, an experiment was undertaken (1) to provide quantitive data on the sequential organization of evoked grooming, and (2) to compare the sequential organization of grooming evoked by stimulation of the medial anterior hypothalamus and spontaneous grooming in normal rats.

METHOD

Subjects

The subjects were 11 male hooded rats. Six subjects had been tested previously in the mapping experiment and had bipolar electrodes implanted in the medial hypothalamus. The remaining five subjects were unoperated control subjects.

Apparatus

The open-field apparatus was the same as in the Open-field Test of Chapter III. The closed-field apparatus was a plywood box, measuring 16 x 11 in., with 11.5-in. walls and a door in the roof. The front wall of the closed-field apparatus consisted of a one-way mirror.

The back wall of the apparatus was made of 1/4-in. hardware cloth, and illuminated inside by two 60-watt light bulbs mounted outside the back wall. The floor was covered with newsprint or sawdust.

Procedure

In the open field, animals were observed for 5 to 10 sessions of 10-min. duration. During each session the operated animals received continuous stimulation using parameters which had previously been found to elicit grooming. Four of the operated animals were also observed in a single half-hour session in which they received stimulation only in the middle 10 min. All grooming responses were described by dictation into a tape recorder. At the end of each session, during playback of the tape, the responses were timed using a stopwatch and transcribed for later analysis. Ambient temperature was recorded at the beginning and end of each session.

As in the previous experiments, stimulation of the medial anterior hypothalamus elicited considerable grooming whereas normal subjects groomed very little. Therefore four of the normal subjects were observed for 10 to 13 additional sessions in the closed field in an attempt to obtain a larger number of grooming responses.

Sequential Analysis of Components of Grooming. Although all grooming responses were recorded, particular attention in analysis was paid to components of face-washing and to responses following face-washing because they showed the sequential dependencies observed previously in other experiments. On the basis of preliminary observations, three categories of face-washing were distinguished and analysed sequentially. The first was designated face-washing one (FW 1) and consisted of bilateral repetitive, but not necessarily synchronous, movements of the forepaws which touched the mouth, vibrissae, and snout. Chewing and licking of the forepaws always accompanied this response. The second component was designated face-washing one rapid (FW 1 R) and consisted of very rapid bilateral repetitive synchronous movements of the forepaws over the vibrissae. This response lasted about 1 sec. and was distinctly different from FW 1. The third component distinguished was face-washing two (FW 2). This response consisted of bringing one or both forepaws up over the top of the head and behind the ears. If only one forepaw as brought behind the ears in this way, the behavior was called unilateral FW 2. Other grooming responses are described in Appendix A. Since FW 1 R usually signalled the beginning of a sequence leading to back-grooming or ventral-surface grooming (i.e., a postural change) during evoked grooming, the sequential analysis was carried out on those components associated with FW 1 R.

RESULTS

In contrast to other grooming responses, FW 1 R was always preceded by FW 1 and never ended a sequence. The FW 1 R response was observed 146 times in the group receiving brain stimulation and 81 times in the normal subjects. One of three acts always followed FW 1 R. The animal either returned to FW 1, went on to FW 2, or changed posture (usually to back-grooming). If both FW 1 R and FW 2 occurred in sequence, a postural change (and initiation of back-grooming) usually followed immediately. All sequences containing the FW 1 R component are depicted by the tree diagram of Figure 12. Two solid lines indicate highly probable subsequent responses in the stimulation group; a broken and solid line indicate highly probable subsequent responses in the normal control group; and three lines indicate that the sequences are highly probable for both groups. The number and relative frequencies observed for each of the sequences of Figure 12 are shown in Table 6 for both groups. It can be seen from Table 6 that the patterns of components were not random; certain sequences were much more likely to occur than others. Of course, Figure 12 and Table 6 are by no means exhaustive of grooming sequences, since they do not include the numerous other grooming responses which have been described in this thesis, and back-grooming or ventral-surface grooming can also be the initial component in a bout of grooming.

In all six of the experimental rats whenever FW 1 R occurred a postural change usually followed. On the other hand, all of the five control rats usually returned to FW 1 (Table 7). This difference between the two groups is shown in Figure 13A. The strongest association of components was seen in both groups when FW 1 R and FW 2 occurred in sequence. These findings are summarized in the bottom part of Table 7 and in Figure 13B. In the stimulated rats, this sequence was followed by a postural change every time but once, and in the control group of normal animals, the sequence was followed by a postural shift more often than not.

The sequence FW 1 - FW 1 R - FW 2 - POSTURAL CHANGE itself showed a

Fig. 12. Tree diagram of grooming sequences. See text for explanation of solid and broken lines.

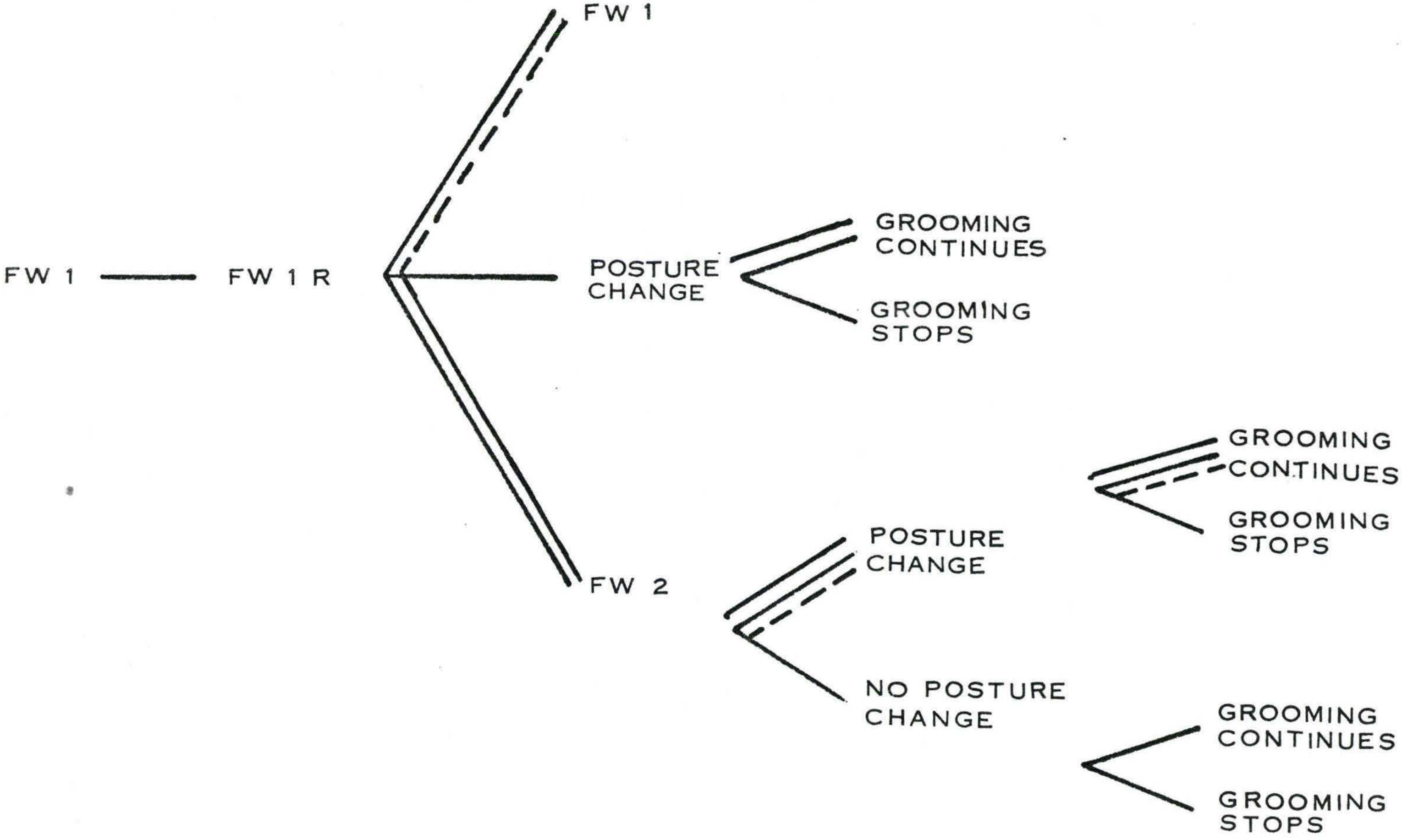

FW 1
FW 1 R
FW 1
POSTURE CHANGE
GROOMING CONTINUES
GROOMING STOPS
FW 2
POSTURE CHANGE
GROOMING CONTINUES
GROOMING STOPS
NO POSTURE CHANGE
GROOMING CONTINUES
GROOMING STOPS

TABLE 6

Number and Relative Frequency of Grooming Sequences of Figure 12 for Stimulated (E) and Normal (C) Rats.

SEQUENCE	NUMBER		RELATIVE FREQUENCY[a]	
	E	C	E	C
FW 1 - FW 1 R - FW 1	16	58	.11	.72
FW 1 - FW 1 R - POSTURE CHANGE - GROOMING CONTINUES	26	0	.18	.00
FW 1 - FW 1 R - POSTURE CHANGE - GROOMING STOPS	0	1	.00	.01
FW 1 - FW 1 R - FW 2 - POSTURE CHANGE - GROOMING CONTINUES	102	14	.70	.17
FW 1 - FW 1 R - FW 2 - POSTURE CHANGE - GROOMING STOPS	1	3	.01	.04
FW 1 - FW 1 R - FW 2 - NO POSTURE CHANGE - GROOMING CONTINUES	1	2	.01	.03
FW 1 - FW 1 R - FW 2 - NO POSTURE CHANGE - GROOMING STOPS	0	3	.00	.04
TOTAL	146	81	1.01	1.01

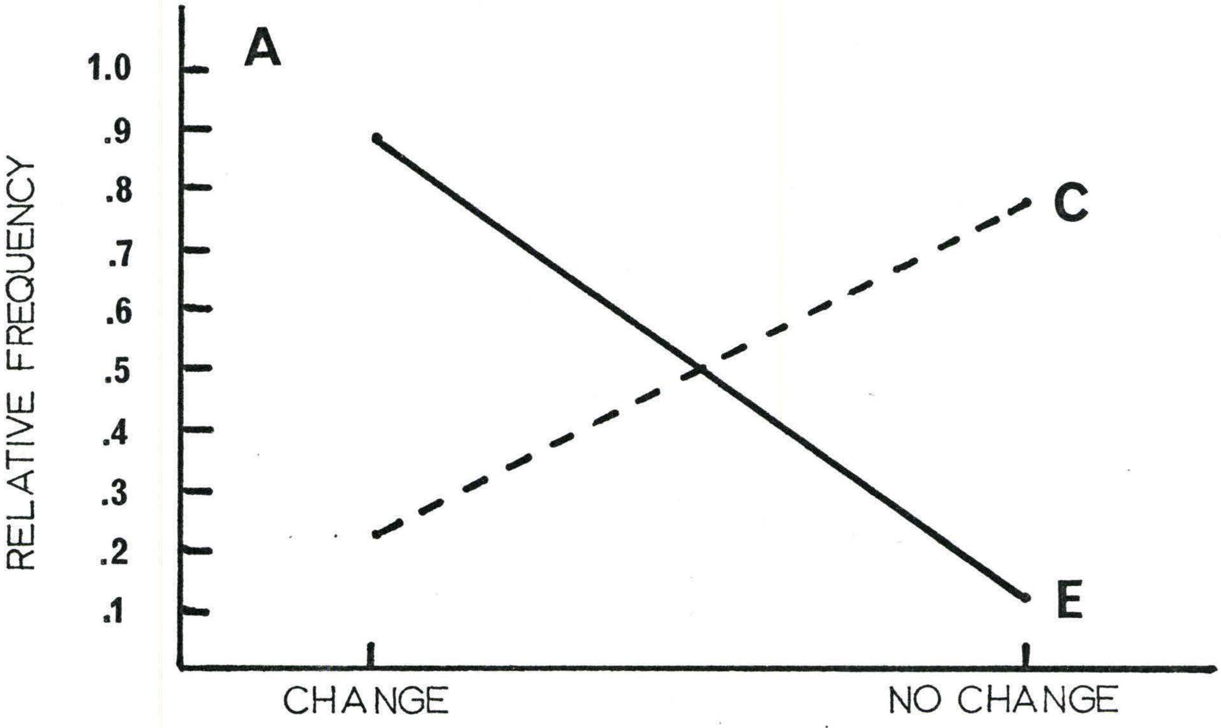
[a] The relative frequency is the number of observations of a sequence over the total number of sequences.

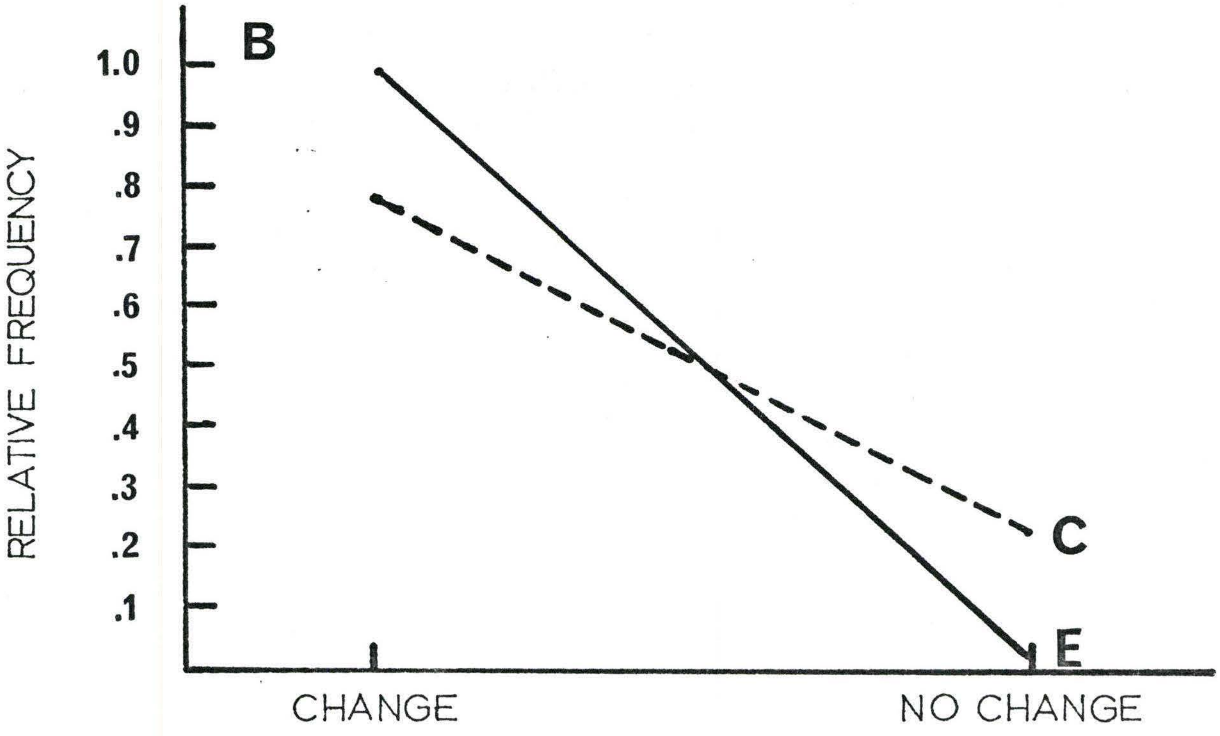
TABLE 7

Number and Relative Frequency of a Postural Change Following the Sequences FW 1 - FW 1 R and FW 1 - FW 1 R - FW 2

SEQUENCE	NUMBER		RELATIVE FREQUENCY	
	E	C	E	C
FW 1 - FW 1 R - POSTURAL CHANGE	129	18	.88	.22
FW 1 - FW 1 R - NO POSTURAL CHANGE	17	63	.12	.79
TOTAL	146	81	1.00	.99
FW 1 - FW 1 R - FW 2 - POSTURAL CHANGE	103	17	.99	.77
FW 1 - FW 1 R - FW 2 - NO POSTURAL CHANGE	1	5	.01	.23
TOTAL	104	23	1.00	1.00

Fig. 13. Relative frequency of a postural change following (A) FW 1 - FW 1 R and (B) FW 1 - FW 1 R - FW 2. Evoked grooming animals (E); normal control animals (C).


A
RELATIVE FREQUENCY
1.0
.9
.8
.7
.6
.5
.4
.3
.2
.1
C
E
CHANGE
NO CHANGE


B
RELATIVE FREQUENCY
1.0
.9
.8
.7
.6
.5
.4
.3
.2
.1
C
E
CHANGE
NO CHANGE

very interesting organization. In those sequences where FW 2 was unilateral, that is, either the right or left forepaw passed behind the right or left ear respectively, the animal usually turned to the ipsilateral side, as shown in Table 8.

Finally, it was found that, in the stimulated group, the side groomed was related to the location of the electrode and degree of preference for grooming one side was related to the distance of the electrode from the midline. This relationship is shown in Table 9. In Table 9, stimulated animals are ranked according to the distance from the midline to the center of the end of the electrode tract, as shown in histological examination. It can be seen that the side preferred was ipsilateral to the electrode and the degree of preference was dependent upon the distance of the electrode tip from the midline. All six placements were in the dorsal part of the paraventricular nucleus, as shown in Figure 14.

Summary

The results showed that, while there are many alternative patterns of response at the beginning of a sequence of grooming, as the sequence progresses to each successive stage, the pattern becomes much more fixed or stereotyped. In particular, a sequence of the three face-washing components distinguished was followed by a postural change, to grooming of the back, in virtually every case in the evoked-grooming experimental group and in the majority of cases in the spontaneously-grooming control group. Within such a sequence, it is often possible to predict, in advance, whether the right or left side of the back will be

TABLE 8

Number and Relative Frequency of Ipsilateral and Contralateral Back-Grooming (BG) Following Unilateral FW 2.

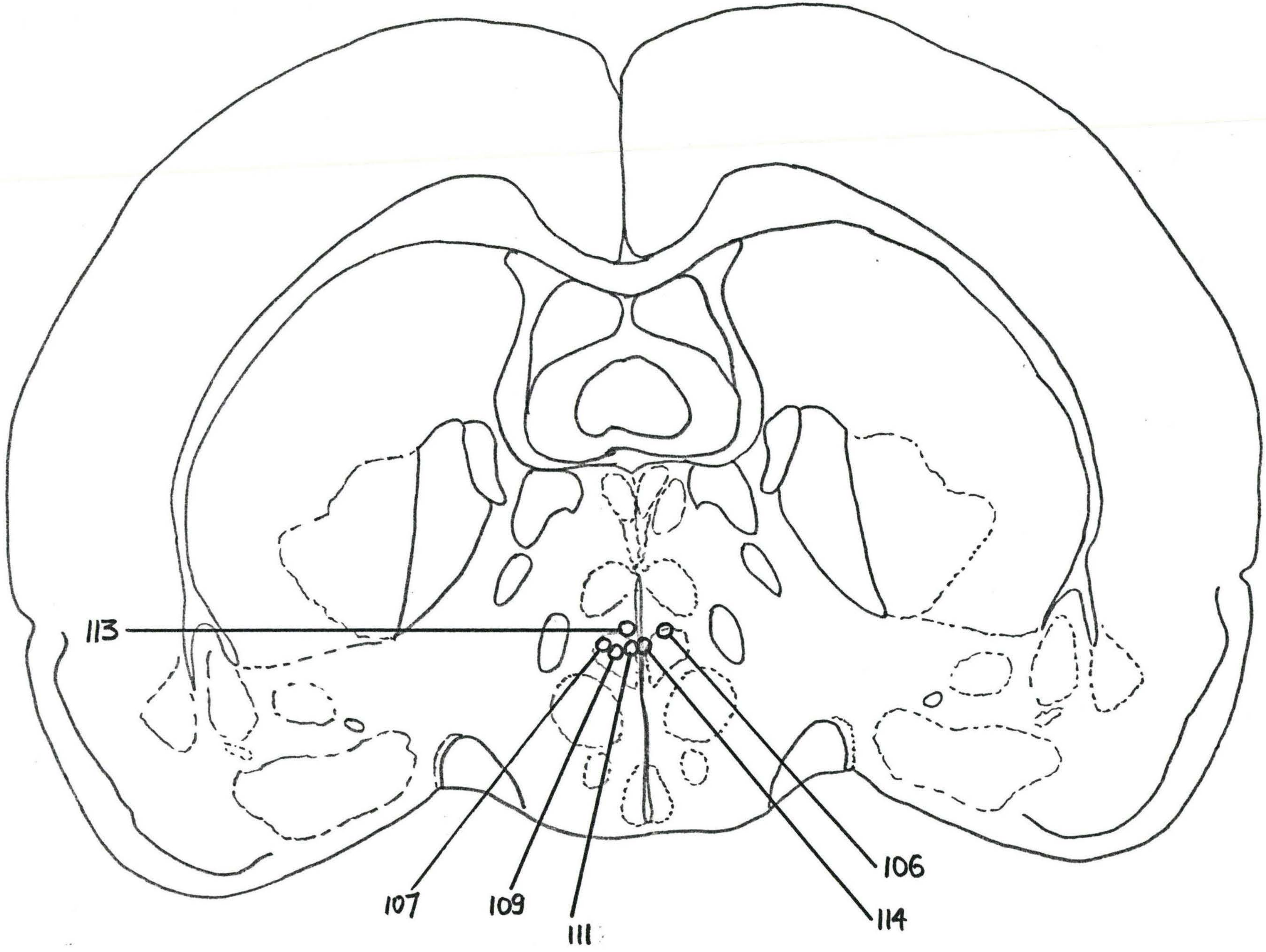
SEQUENCE	NUMBER		RELATIVE FREQUENCY	
	E	C	E	C
FW 1 - FW 1 R - FW 2 - Ipsilateral BG	51	6	.82	.85
FW 1 - FW 1 R - FW 2 - Contralateral BG	11	1	.18	.14
TOTAL	62	7	1.00	.99

TABLE 9

Duration and Side of Back-Grooming (BG) and Electrode Location of the Experimental Animals Tested in the Open-field.

RAT	SECONDS OF BACK-GROOMING		PROPORTION OF BG ON IPSILATERAL SIDE	ELECTRODE LOCATION	
	RIGHT SIDE	LEFT SIDE		SIDE	DISTANCE FROM MIDLINE (mm.)
109	66	266	.80	left	0.75
107	18	143	.89	left	0.6
106	263	13	.95	right	0.3
111	92	167	.64	left	0.25
113	177	150	.46	left	0.25
114	109	101	-	midline	0.0

Fig. 14. Location of electrode tips of experimental subjects tested in sequential analysis experiment. Frontal diagram based on DeGroot (1959). Numbers indicate individual rats.


113
106
107
109
111
114

groomed.

Histological analysis showed that the experimental subjects tended to groom the side of their body ipsilateral to the stimulation electrode.

CHAPTER V

Self-stimulation Experiments

With the possible exception of exploratory behavior, virtually all the species-typical behaviors elicited by electrical stimulation, which is also reinforcing, "are relatively infrequent, isolated events in the flow of behavior" (Nissen, 1953) and are directed towards specific external goal objects such as food (Hoebel and Teitelbaum, 1962; Margules and Olds, 1962), water (Mogenson and Stevenson, 1966), an estrous female rat (Caggiula and Hoebel, 1966), a piece of wood suitable for gnawing (Roberts and Carey, 1965), or a rat which could be attacked and killed (Roberts and Kiess, 1964). The importance of this type of correlation in understanding the neurology of reinforcement in operant conditioning has been pointed out by Glickman and Schiff (1967). In the only report relating grooming and self-stimulation, only 10 of 23 sites from which grooming was elicited also supported self-stimulation (Christopher and Butter, 1968). However, it is hard to draw firm conclusions about the relationship between evoked grooming and self-stimulation from this report because (1) the frequency of spontaneous grooming was very high, raising doubts as to whether the grooming was really a result of the stimulation and (2) the self-stimulation tests were stopped if self-stimulation was not established in two sessions. Therefore, the possibility remains that hypothalamic stimulation which produces grooming will also support self-stimulation.

In order to elucidate this important theoretical and empirical issue, experiments were conducted in which the behavioral and self-stimulation tests were more extensive.

METHOD

Subjects

The subjects were 31 male hooded rats. The experimental animals were 19 rats which had bipolar electrodes implanted in the medial hypothalamus; these animals had been tested extensively in the previous experiments. The control animals were 12 naive unoperated rats.

Apparatus

Three self-stimulation boxes (SS box) were used.

SS box 1 (the Skinner box) measured 10 x 12 in. with walls 9 in. high and with a plexiglas door and top. A metal bar, 2 1/2 x 3/4 in., projected from the midline of one side, 3 1/2 in. above the floor. A 40-watt light bulb covered by a hood was mounted, outside the box, behind the bar assembly. Pressing the bar closed a switch operating a Hunter Decade Interval Timer (Model 111-B, Series D) which operated the stimulator and relay equipment.

SS box 2 (the photorelay box) was an unpainted plywood box measuring 12 in. square and 20 in. high, with a partition, 5 in. square by 2 in. high, in the middle of one side. A light was mounted behind a small hole in the partition and a Hunter photorelay unit was located outside the box, behind a small hole in the opposite wall. Breaking the lightbeam (e.g., with the snout) operated a timer controlling the stimulator and relay equipment.

SS box 3 was a shuttlebox (Harvard Instrument Company) measuring 8 x 19 in. and 8 1/4 in. high. The floor of the box was a grid of 1/8-in. steel bars set about 3/8 in. apart. The floor was pivoted at the middle so that the subject's weight on either side of the center operated relay equipment which (1) controlled the stimulator and (2) gave a positive report on an event recorder of the subject's location in the shuttle-box.

The stimulator described in Chapter II was used. The SS boxes and stimulator were programmed with Grason-Stadler relay equipment, as described in the Procedure.

Procedure

The parameters used for self-stimulation tests of each animal had elicited behavior clearly and reliably in the behavior tests of the mapping experiment and, in many cases, in the remote control stimulation tests as well. During self-stimulation tests, the room lights were on continuously.

In the Skinner box, seven experimental animals were tested daily in 20-min. sessions. For the first two sessions, operant rates of bar-pressing (no stimulation) were recorded; in subsequent sessions, a 0.5-sec. train of electrical stimulation was delivered upon each bar press. The bar-pressing was "shaped", by the method of successive approximations, for a maximum of four sessions.

In the photorelay box, 14 animals were tested daily, in two

10-min. sessions. The control animals (n=8) received 5 to 7 sessions and the experimental animals received one operant (no stimulation) and nine stimulation sessions. In stimulation sessions, a 0.5-sec. train of electrical stimulation was delivered each time the lightbeam to the photorelay was broken.

In the shuttlebox, four unoperated-control animals and six experimental animals were tested daily in a 20-min. session. The control animals received six sessions and the experimental animals received two operant (no stimulation) and 10 to 14 stimulation sessions. In the stimulation sessions, continuous stimulation was delivered while the animal was on the positive side of the apparatus, and the positive side was alternated each session. The latency and side of the first grooming response were recorded for each animal.

In all three boxes, the number of stimulation trains and total stimulation time were recorded on counters and event markers.

RESULTS

The results of all three procedures were similar: sites at which electrical stimulation evoked grooming did not generally support self-stimulation. Of the 19 experimental animals (13 showed evoked grooming in the behavior tests), two animals showed positive self-stimulation at short durations of stimulation, the rewarding effects of stimulation were ambivalent for two subjects, and clearly negative for one subject. The behavioral and anatomical results for each animal are shown in Table 10.

None of the experimental animals tested in the Skinner box

TABLE 10

Behavioral and Anatomical Results of the Self-stimulation Experiments

RAT	BEHAVIOR		ANATOMICAL LOCATION OF ELECTRODE TIPS
	EVOKED	SELF-STIM. (Skinner box)	
52	grooming	none	paraventricular and periventricular nuclei
54	grooming	none	reuniens nucleus
57	grooming	none	reuniens and paraventricular nuclei
60	grooming	none	periventricular nucleus
63	grooming	none	paraventricular nucleus
64	grooming	none	paraventricular and periventricular nuclei
67	walking, shaking	none	reuniens nucleus
		(photorelay box)	
71	grooming	none	paraventricular nucleus, anterior hypothalamus
73	looking, sniffing	none	reuniens nucleus, zona incerta
75	grooming	positive at short durations	paraventricular nucleus, anterior hypothalamus
76	grooming	none	periventricular nucleus

TABLE 10 (continued)

RAT	BEHAVIOR		ANATOMICAL LOCATION OF ELECTRODE TIPS
	EVOKED	SELF-STIM.	
78	grooming	none	periventricular and paraventricular nuclei
81	walking back and forth	none	dorsomedial nucleus of the hypothalamus, periventricular nucleus
		(shuttlebox)	
135	grooming	neutral	medial preoptic area
137	grooming	neutral	medial preoptic area
139	grooming	ambivalent	anterior hypothalamus
136	exploratory activity	short durations positive	diagonal tract of Broca
142	circling, seizure	ambivalent	diagonal tract of Broca
143	looking, sniffing, walking	negative	optic tract, medial preoptic area

showed any self-stimulation behavior. In fact, shaping was discontinued after four sessions because no animal could be shaped even to orient towards the bar. Moreover, the animals spent most of the time near the wall opposite the bar, suggesting that the stimulation may have been slightly aversive.

Since extensive shaping may obscure self-stimulation effects at some points, if there is an aversive component associated with stimulation (L. Taylor, personal communication, February, 1969), the photorelay box was used to obtain relatively high operant rates of responding so that shaping would not be necessary. Of the six experimental animals tested in the photorelay box, only one self-stimulated. This animal showed evoked grooming in the mapping experiment and in the remote control stimulation tests. The tip of the electrode was in the anterior hypothalamus near the paraventricular nucleus. However, three animals, which had similar electrode placements and also showed evoked grooming in the mapping experiment and in the remote control stimulation tests, did not self-stimulate. Therefore, the self-stimulation cannot be related either to the anatomical location of the stimulation electrode or to the evoked grooming. In this apparatus, as well as in the Skinner box, there were indications that stimulation which evoked grooming was mildly aversive: the control animals had a mean frequency of 18.5 beam crossings while the experimental animals which did not self-stimulate had a mean frequency of only 8.6 crossings ($t=3.5$, $df=11$, $p<.01$). However, it is also possible that stimulation made the rats inactive.

Since the latency of the grooming response was considerably longer than the 0.5 sec. reinforcement used in the above tests, it was possible that the brief stimulation trains were of insufficient duration or strength to facilitate neural activity in the motor pathways controlling grooming, and thus, there would be no rewarding effect. By making stimulation continuously available, as was done in the shuttlebox, the animals could select stimulation durations long enough to elicit grooming. This procedure also provided further indications of whether or not stimulation had aversive qualities and what durations an animal would tolerate.

Both control and experimental animals showed strong position preferences, which must be taken into account in interpretation of the results. The results are shown in Figures 15 and 16 and in Table 11. Of the experimental subjects from which grooming was elicited during behavior tests (n=3), one subject (#139) minimized stimulation indicating that long durations of stimulation were aversive, but returned regularly to the positive side, suggesting that some positive rewarding effects accompanied the stimulation. However, the duration of stimulation subject 139 selected was usually less than the duration required to elicit grooming in behavior tests. The position preferences of the other two subjects were not noticeably affected by stimulation.

Although the grooming latencies of animals from which stimulation elicited grooming and the grooming latencies (spontaneous grooming) of animals from which stimulation elicited other behavior were not statistically significantly different (Mann-Whitney $\underline{U} = 2$; two-tailed test, $\underline{p} = .40$), qualitative observations made during the self-stimulation

Fig. 15. Self-stimulation behavior, in shuttlebox, of rats from which grooming was elicited in behavior tests. Dashed line, operant performance (no stimulation available); solid line performance with stimulation available. Session length 1200 sec. (20 min.).

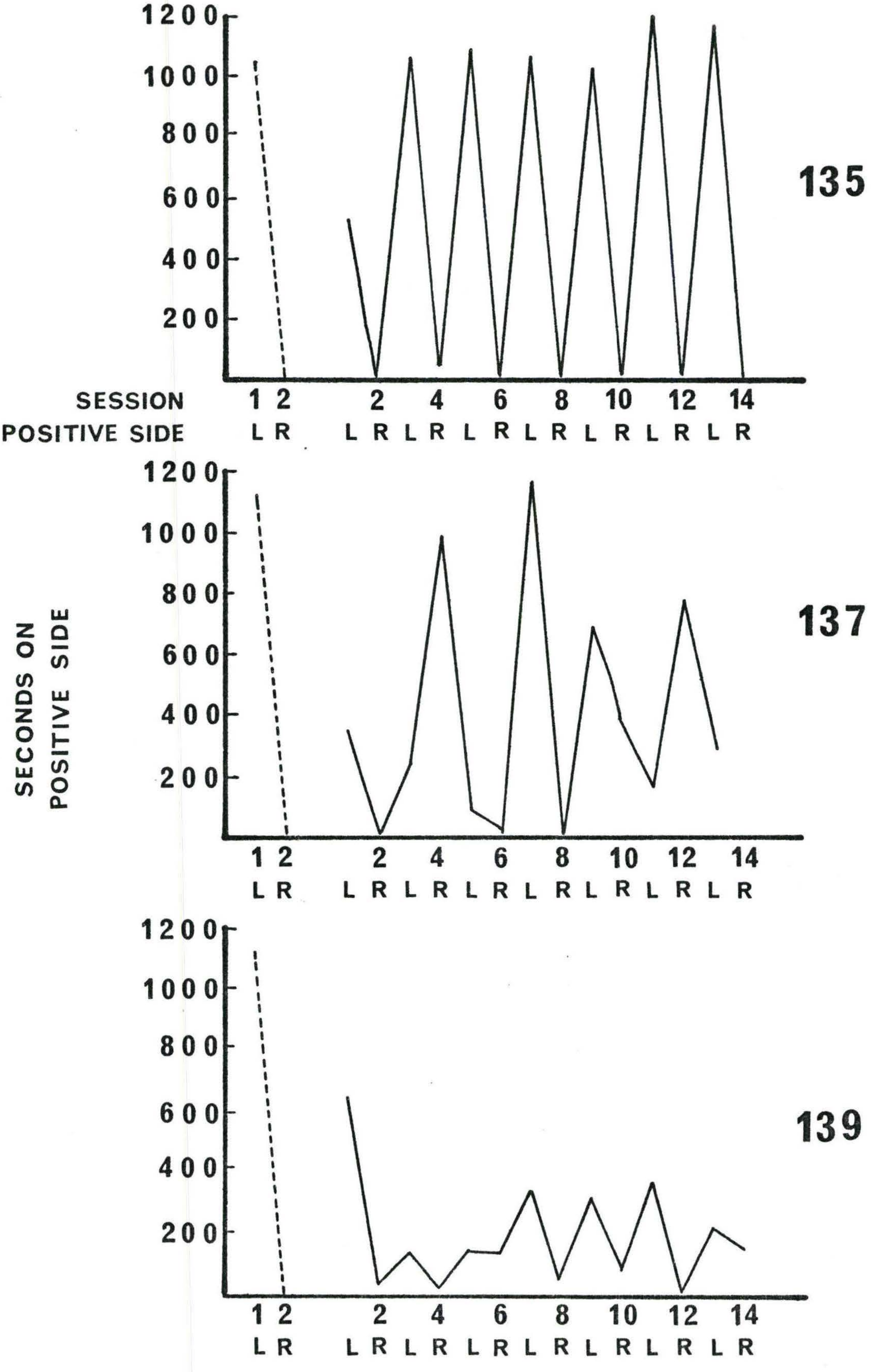
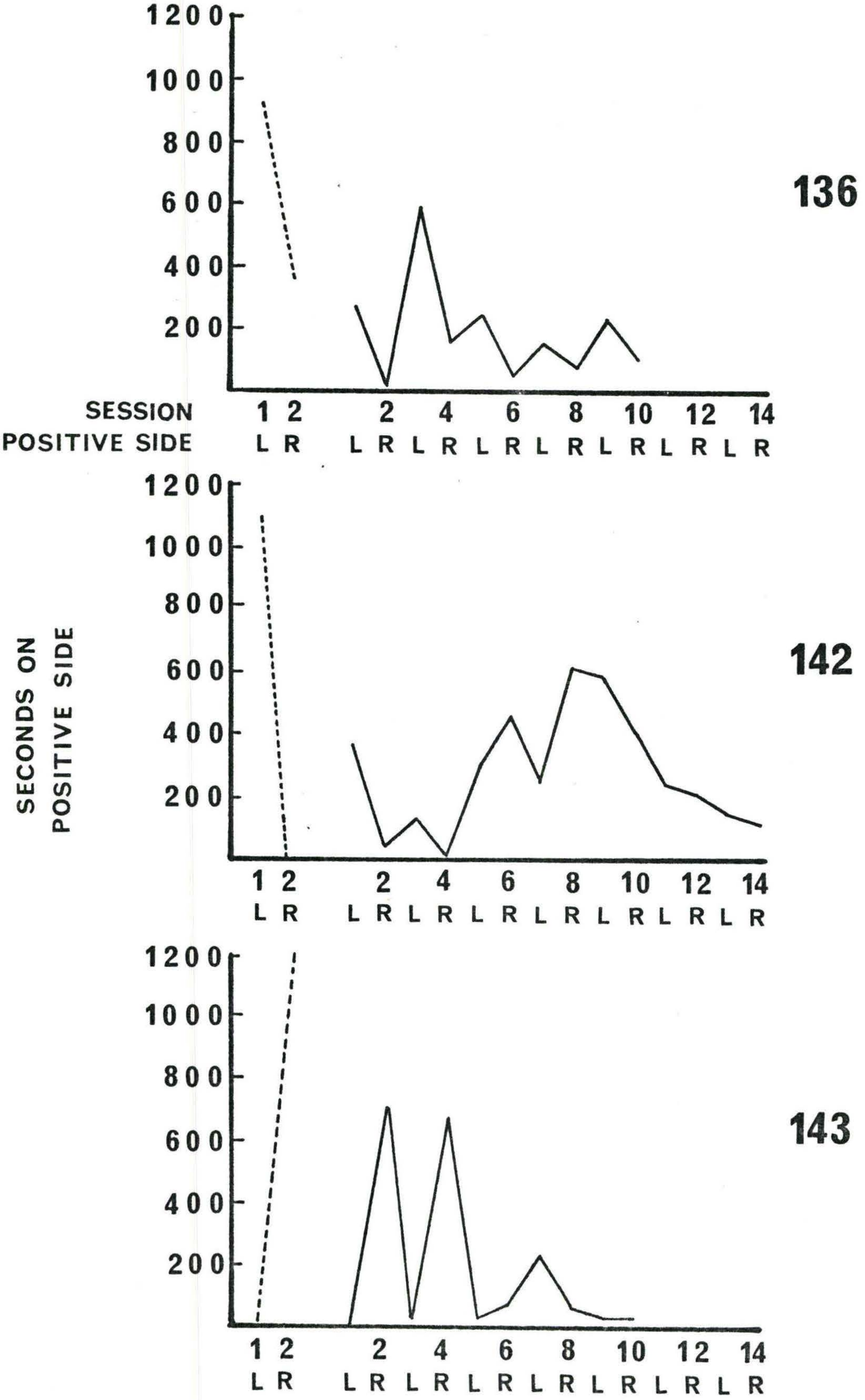

1200
1000
800
600
400
200
135
SESSION
POSITIVE SIDE
1 2 2 4 6 8 10 12 14
L R L R L R L R L R L R L R L R
137
SECONDS ON POSITIVE SIDE
139

Fig. 16. Self-stimulation behavior, in shuttlebox, of rats from which grooming was not elicited in behavior tests. Dashed line, operant performance (no stimulation available); solid line performance with stimulation available. Session length 1200 sec. (20 min.).



136
142
143
SECONDS ON POSITIVE SIDE
1200
1000
800
600
400
200
SESSION
POSITIVE SIDE
1 2
L R
2 4 6 8 10 12 14
L R L R L R L R L R L R L R

TABLE 11

Summary of results obtained in SS box 3

RAT	BEHAVIOR		Stimulation trains	MEAN GROOMING LATENCY		STIMULATION SITE
	Evoked	Self-stimulation		Positive side	Negative side	
135	Grooming	Neutral	29	55	210	medial preoptic area
137	Grooming	Neutral	30	18	56	medial preoptic area
139	Grooming	Ambivalent	90	27	25	anterior hypothalamus
136	Exploratory activity	Short durations positive	372	87	150	diagonal tract of Broca
142	Circling, seizure	Ambivalent	97	540	304	diagonal tract of Broca
143	Looking, sniffing, walking	Negative	21	183	163	optic tract, medial preoptic area

tests in the shuttlebox confirmed that the animals which showed evoked grooming in the behavior tests groomed more vigorously and for longer durations. Thus, it seems reasonable to conclude that the stimulation was activating neural elements involved in the control of grooming on an overt level during the tests in the shuttlebox.

Summary

Only one of 13 animals from which grooming was elicited in the behavior tests showed self-stimulation behavior. There were indications that stimulation which elicited grooming may also have been aversive to some animals. In one test where continuous stimulation was available, animals did not learn to select durations of stimulation that elicited grooming in the behavior tests.

CHAPTER VI

Discussion

LEVELS OF ORGANIZATION

Grooming was elicited by stimulation of three different "levels" of the neuraxis (the mapping experiment): the midbrain tectum, the limbic system, and the anterior hypothalamus. The evoked grooming responses, which differed in degree of complexity and functional integration at each level, were characteristic of that level but differed from components or sequences of grooming elicited by stimulation of the other levels. Grooming elicited by stimulation of the medbrain tectum showed a strong, specific, motor effect which fatigued rapidly. Moreover, the evoked response was a single isolated response component, grooming of the back, of the many that go to make up stereotyped sequences of grooming. The grooming, primarily shaking and brief face-washing, elicited by stimulation of the limbic system structures was associated with a disruption of normal neural activity. Finally, the grooming elicited by stimulation of the medial anterior hypothalamus consisted of complete sequences of normal, highly stereotyped grooming. In the following sections of the Discussion, each of these evoked grooming responses is considered in more detail.

The Midbrain Tectum

Grooming of the back, elicited by stimulation of the midbrain tectum, was only a "fragment" of behavior in the sense used by Delgado (1964) and, with one exception, the isolated component was not integrated with ongoing behavior. When the animal was in the act of face-washing, the postural substrate for back grooming was present and, the evoked response was facilitated. However, the grooming activity did not continue following the elicitation of back-grooming whether the animal was already grooming or engaged in some other activity (when postural adjustments were difficult for the animal) at the time stimulation was turned on. Thus, stimulation of the midbrain tectum elicited a specific motor component of grooming, but in the absence of other input, no integration with ongoing behavior occurred.

At first, a grooming response elicited from an area usually thought of as being concerned mainly with visual functions appears surprising. However, the location of the electrode tips, with which back-grooming was elicited, was in or near the stratum lemnisci of the superior colliculus, which receives fibres from the spinotectal tract. The spinotectal tract, in turn, carries sensory fibres for light touch, pressure and pain from the surface of the body (Crosby, Humphrey, and Lauer, 1962; Truex and Carpenter, 1964), so that pathways involved in somatic sensation run to the area of the superior colliculus from which grooming was elicited. There are also large motor "stellate" cells in this area (Truex and Carpenter, 1964), as well as the efferent fibres of the tecto-spinal tract (Papez and Freeman, 1930) which project to the anterior horn cells, at least as far as the cervical level (Altman and Carpenter, 1961). Thus, grooming may have been elicited by stimulation of the stratum lemnisci of the superior colliculus because this region is involved in the sorts of somatic sensations which produce grooming. Also, Zeman and Innes (1963) suggested that the superior colliculus may perform sensory-motor integrations.

In addition to this anatomically-based evidence, there is electrophysiological evidence that sensory cells in the area from which grooming was elicited have functional properties similar to those observed in the evoked grooming. In the anaesthetized rabbit, single units in the superior colliculus which responded to tactile stimulation (air puffs on the contralateral side of the body) fatigued after a few seconds of constant stimulation, and a full response could not be re-elicited afterwards for about 20 sec. (Horn & Hill, 1966). These properties correspond closely to the observations (the mapping experiment) that (1) grooming evoked by stimulation of the superior colliculus diminished and then stopped altogether after about 10 sec. and (2) the evoked grooming could not be re-elicited for a few seconds afterwards but could be re-elicited after 60 sec.

There was also another parallel between the activity of single units studied by Horn and Hill (1966) and the evoked grooming observed in the mapping experiment. In the mapping experiment, stimulation of the superior colliculus elicited grooming over large areas of the back and flank on the contralateral side of the body, and the receptive fields of many of the units studied by Horn and Hill covered about the same areas.

Finally, stimulation of the superior colliculus and dorsal midbrain elicited turning of the head and body to the contralateral side, which confirms previous observations of this effect (Hyde, 1965).

Therefore, although the midbrain tectum is usually considered a "visual" area, the observations outlined above suggest that grooming can be elicited by stimulation of this area because the area is responsive to light touch or irritation of the skin on the back region of the contralateral side, and because stimulation of the midbrain tectum can produce the sort of fragmentary motor patterns which were part of the grooming response elicited from this area.

The Hippocampal Formation and Limbic System

Stimulation of the hippocampus and subcortical limbic structures produced more complex and variable grooming than stimulation of the midbrain tectum. The initial acts of grooming elicited by the limbic stimulation were paroxysmal shaking and brief face-washing, which are also the usual responses to external stimulation of large areas of the body with water or dust. Following the shaking and face-washing, longer sequences of stereotyped grooming occurred. Similar responses have been observed previously during and following stimulation of the hippocampal formation (MacLean, 1957b), septal nuclei (Altman, 1969), prehippocampus, corpus callosum, and anterior or paraventricular nuclei of the thalamus (Coons, cited by Miller, 1961).

Hippocampal afterdischarges apparently always accompany such evoked grooming and, in fact, seem to be a requirement for grooming to occur in these cases (MacLean, 1957b), so that the grooming evoked by stimulation of the limbic system is probably actually induced by hippocampal afterdischarges or some concomitant of them (see also p. 7 ff.).

At higher intensities, limbic stimulation also produced overt behavioral seizures.

In attempting to explain the neural basis of grooming elicited by stimulation of the limbic system, MacLean (1957b) suggested that the limbic system contains neural structures which co-ordinate grooming acts, primarily because integrated sequences of grooming occur during or following stimulation (or both) of several limbic structures. However, it is unlikely that the limbic system contains the co-ordinating structures because (1) spontaneous grooming in rats is accompanied by "inactivated" hippocampal electrical activity (Vanderwolf, 1969), and (2) grooming evoked by stimulation of limbic structures is accompanied by afterdischarges, that is, an abnormal state. Thus, this interpretation will not be considered further.

The occurrence of these electrical afterdischarges might suggest a necessary relationship between the evoked grooming and behavioral seizures because (1) afterdischarges may be considered a sign of seizure activity too weak to be manifested behaviorally, and (2) hippocampal stimulation produced both behavioral seizures and grooming. However, stimulation of sites outside the limbic system in the mapping experiment (Figure 3) generally elicited neither shaking nor longer sequences of grooming. Therefore, the behavioral seizures resulting from hippocampal stimulation were probably incidental to the evoked grooming, and the hippocampal afterdischarges thus reflect some other role of the hippocampus in the neural mechanisms of grooming. For example, stimulation in the ventral hippocampus elicites a pattern of seizure activity, which spreads diffusely, but which has a distinctive character in the ventral nucleus of the thalamus, and stimulation of the dorsal hippocampus elicits distinctive afterdischarges in the intralaminar nuclei of the thalamus (Goodfellow and Neimer, 1961). There are also several other reports of selectively propagated afterdischarges (Delgado and Sevillano, 1961; Jasper and Droogleever-Fortuyn, 1947; Liberson and Akert, 1955; Morin and Green, 1953) so that selectively-spreading afterdischarges seem to be a common phenomenon in the central nervous system. Finally, the ventral nuclei of the thalamus (to which ventral-hippocampus afterdischarges spread in a distinctive pattern) are sensory relay nuclei projecting to the somatic sensory cortex (Rose and Mountcastle, 1959), so that activity which spread to these nuclei might activate the same sensory-motor sequence as widespread stimulation of the skin. This may then be why the initial grooming acts (shaking and face-washing) evoked by hippocampal stimulation resemble so strongly those produced by external stimulation of large areas of the body with water.

Another possible interpretation of the relationship between grooming and seizure discharges is that the hippocampus is rendered functionally inoperative following the afterdischarges, and thus "release" subcortical structures which control grooming more directly. The "release" interpretation is supported by the observation that hyperactivity frequently accompanied the shaking, and preceded the long sequences of grooming, which occurred when hippocampal stimulation was terminated (the mapping experiment). The observation of hyperactivity suggests that the stimulation, which elicited seizure discharges, impaired, in part, hippocampal functioning since hippocampal damage produces hyperactivity and the greater the damage, the greater the hyperactivity (Teitelbaum and Milner, 1963).

Thus, it is possible that hippocampal stimulation produces paroxysmal shaking and face-washing initially because the stimulation produces afterdischarges which spread primarily to areas involved in somesthetic sensation and thereby mimic the effect of widespread exteroceptive stimulation. The long sequences of stereotyped grooming occur subsequently because the afterdischarges culminate in a functional impairment of the hippocampus which "release" subcortical structures more directly involved in stereotyped grooming.

The Medial Anterior Hypothalamus

Unlike the grooming elicited by stimulation of the tectum and limbic system, the grooming elicited by stimulation of the medial preoptic and medial anterior hypothalamic areas consisted of long sequences of stereotyped grooming which appeared very much like "spontaneous" grooming. Congruent with the large number of autonomic functions subserved by the hypothalamic and preoptic areas (Akert, 1961; Hess, 1957), the grooming evoked from these areas in the present experiments may reflect the activation of one or more autonomic processes. For example, licking of the feet, tail, and other ventral surfaces was evoked, and Hainsworth (1967) indicated that these acts can serve a thermoregulatory function. Licking of the penis, which was also evoked, suggests that some sexual function may be activated.

Responses similar to those elicited in the present experiments by hypothalamic or preoptic stimulation were also elicited in the Virginia opossum with stimulation of the preoptic area below the anterior commissure (Roberts et al., 1967, 1969). In the present experiments, however, stimulation in and around the paraventricular nucleus of the hypothalamus was particularly effective in eliciting grooming, and elicited a large range of integrated grooming components (Figures 5 and 6), while Roberts et al. (1967) elicited grooming only from a few scattered sites in this area and, furthermore, stimulation of several of these sites elicited only a single component. Nonetheless, the grooming components evoked in both the rat and the opossum included components usually associated with behavioral temperature regulation.

At the same time, there are certain differences between thermoregulatory grooming and the grooming elicited by electrical stimulation of the hypothalamus and preoptic area (Roberts et al., 1969). For example, environmental warming and warming of the preoptic area with radio-frequency stimulation elicited similar patterns of grooming components, while electrical stimulation elicited a different pattern of grooming components, and also elicited behaviors other than grooming. Also, the most effective sites for eliciting grooming with radio-frequency stimulation were somewhat anterior to the most effective sites for electrical stimulation.

This difference indicates that the radio-frequency warming activated only the input for thermoregulatory grooming, presumably by selectively stimulating thermosensitive neurons (Wit and Wang, 1968), while electrical stimulation may have activated several different inputs (e.g., tactile, thermal, sexual) to the neural system underlying grooming. This may be why there was such an overlap in the distribution of sites at which electrical stimulation elicited both tail-licking and penis-licking in the present experiments.

The elicitation of tail- and penis-licking was also significant for other reasons. Tail-licking was particularly unusual because it occurred frequently during electrical stimulation of the anterior hypothalamus, by comparison with its "spontaneous" incidence in this strain of rat. This contrast raises questions about the functional significance of tail-licking, and about the identity between the evoked grooming and spontaneous grooming.

While spontaneous tail-licking did not occur in the present experiments, this response occurs often in other animals and other species of rats. Barnett (1956) and Bolles and Woods (1964) included this component in the descriptions of typical sequences of spontaneous grooming in the Norway rat and Sprague-Dawley albino rat, respectively. In certain species of mice it is a regular component of grooming (Eisenberg, 1962, 1963) and occurs frequently in the behavior of the gerbil (personal observations by the author). In each of these species, no special functional significance, other than self-care, has been attributed to the tail-licking response.

However, the tail is an important organ for heat loss (Thompson and Stevenson, 1965) so that tail-licking might increase the efficiency of behavioral temperature regulation by increasing heat loss through evaporation of saliva from the tail. Such a mechanism operates in the opossum (Higginbotham and Koon, 1955; Roberts et al., 1969) and may also operate in the rat since Stricker et al. (1968) observed tail-licking by a strain of Wistar rats exposed to high ambient temperatures, even though there were dishes of water in the environmental chamber, and the rats often submerged parts of their bodies (including their feet and tails) in the water. Curiously, Sprague-Dawley rats in a hot environment restricted their saliva spreading to the base of the tail, according to Hainsworth and Epstein (1966), although this was the same strain in which Bolles and Woods (1964) reported spontaneous licking of the whole tail.

Thus, tail-licking occurs spontaneously in certain strains of rats and, in some of these strains at least, it is a thermoregulatory response. The present observations indicate that well-integrated neural mechanisms for tail-licking exist in hypothalamic and preoptic areas of the hooded rat used here, even though this response is very rarely manifested behaviorally. It may be that the hypothalamic-preoptic area of the rat contains neural mechanisms for several species-typical responses which are rarely manifested behaviorally since, for example, placing small amounts of testosterone into the medial preoptic area elicits maternal behavior in male rats (Fisher, 1956).

Penis-licking occurs both in the spontaneous grooming behavior and in the sexual behavior of the hooded rat. In the present experiments, this response was elicited by stimulation of the paraventricular nucleus. The evoked penis-licking may be related to sexual behavior since electrical stimulation of the paraventricular nucleus releases oxytocin (Brooks, Ishikawa, Koizumi, and Lu, 1966; Harris, 1955), and oxytocin release is also induced by manipulation of the male sexual organs (Fitzpatrick, 1966) or seminal vesicles and ampullae (Debackere, Peeters, and Tuyttens, 1961) and by sexual activity or courtship in male animals (Fitzpatrick, 1966). Since injections of oxytocin increase the number of ejaculations in male rabbits (Melin and Kihlstrom, 1963), there may be a feedback circuit in sexual activity involving sequences of sexual organ-manipulation, paraventricular nucleus activity, oxytocin release, copulation, manipulation, etc. This may be the basis for the penis-licking elicited by stimulation of the paraventricular nucleus, although in the present research tests of sexual activity during stimulation of this nucleus were inconclusive.

THE MEDIAL ANTERIOR HYPOTHALAMUS: SPECIFICITY OF FUNCTIONS

In the remote control stimulation tests, several comparisons were made between spontaneous grooming and the grooming elicited by stimulation of the medial anterior hypothalamus. The two control groups ("non-groomers") were nearly identical in terms of the relative percentages of different components which occurred during these tests; this similarity suggests that the same neural mechanisms were activated in both groups.

In the two experimental groups ("groomers"), stimulation of the medial anterior hypothalamus elicited all the components of normal grooming in both groups and, furthermore, this stimulation very frequently elicited long sequences of stereotyped grooming which continued without interruption when the stimulation was terminated. Such long sequences of grooming which continued after stimulation offset were also reported with stimulation of the septal area of the cat (Hess and Meyer, 1956).

Nonetheless, the relative percentages of different components were different during stimulation periods than the subsequent non-stimulation periods of the remote control stimulation tests (Figure 10). In particular, more time was spent face-washing during the stimulation periods than during the subsequent non-stimulation periods, and the reverse was true for ventral-surface grooming. These results probably occurred because the stimulation initiated a sequence of grooming which very frequently continued after stimulation offset. In such a sequence, face-washing tends to occur early (Chapter II) and to occupy a long time (Table 4), while ventral-surface grooming tends to occur late in the sequence (Chapter II). A similar temporal organization of grooming components occurs in normal mice (Eisenberg, 1962, 1963). Therefore, when stimulation starts a sequence of stereotyped grooming, face-washing occupies a considerable part of the stimulation period but tends to be "completed" before stimulation offset. On the other hand, ventral-surface grooming tends to start late in the stimulation period and to continue after stimulation offset or may even start after stimulation offset; in either case, more time is thus spent in ventral-surface grooming during the non-stimulation periods than during the stimulation periods.

Finally, results from the remote control stimulation experiments and the mapping experiments indicated a dissociation between two sets of somatic components: one set consisted of face-washing, back-grooming, and ventral-surface grooming, and the other set consisted of shaking and scratching. Three results in the present experiments support this conclusion.

First, in the remote control stimulation tests, the amount of shaking within the three stimulation groups was about the same during stimulation and non-stimulation periods, and the amount of body-grooming (face-washing, back-grooming, and ventral-surface grooming) was inversely proportional to the amount of shaking indicating, perhaps, that stimulation suppresses shaking behavior and that this effect continues throughout the succeeding non-stimulation period. Second, comparisons between the experimental (tail-licking) and control (no stimulation) groups in the remote control stimulation tests showed that both the absolute amount and the proportion of scratching, relative to the other set of components, and shaking were higher in the control group than in the experimental group. Third, in the mapping experiment, stimulation of the hippocampal formation and limbic system elicited shaking which was often accompanied by vigorous scratching with the hind feet, and longer sequences of stereotyped body-grooming occurred only after the shaking had stoppped.

Thus, stimulation of the medial anterior hypothalamus in the remote control stimulation experiment elicited integrated sequences of grooming which were, however, different than "spontaneous" grooming. It seems that there are two "sets" of somatic grooming components, and that hypothalamic stimulation resulted in the more frequent occurrence of only one set (face-washing, fur-licking and biting) while the other set (shaking and scratching) occurred more frequently in spontaneous grooming and during and following limbic system stimulation.

Although stimulation of the medial anterior hypothalamus elicited grooming components which were similar to thermoregulatory grooming, it did not elicit autonomic components of thermoregulation (such as salivation and peripheral vasodilatation). This is not surprising since there is considerable evidence that the somatic and autonomic components of thermoregulation are controlled, in part, by different neural mechanisms although both components involve the hypothalamus. For example, panting (which has both autonomic and somatic aspects) and "sleep-like relaxation" can be elicited with warming of the medial anterior hypothalamus, but not by electrical stimulation of the same area, in the opossum (Roberts et al., 1969). Similarly, autonomic thermoregulatory responses (polypnea and peripheral vasodilatation) can be elicited by electrical stimulation of the hypothalamus in the goat (Anderson and Persson, 1957) and the cat (Eliasson and Strom, 1950) although thermoregulatory grooming does not occur in those animals. Nonetheless, although salivation and peripheral vasodilatation are major autonomic responses to heat loss in the rat (Grant, 1963; Hainsworth, 1967; Thompson and Stevenson, 1965), they were not evoked by stimulation of the hypothalamus which elicited somatic responses usually associated with heat loss.

The dissociation between the neural mechanisms for somatic and autonomic thermoregulation is probably due to an anatomical difference in the inputs for these two types of response; the area most sensitive to radio-frequency warming is somewhat more anterior in the hypothalamus of the opossum than the area from which electrical stimulation elicited maximum grooming (Roberts et al., 1969). Furthermore, thermally-sensitive units in the cat are located somewhat more anteriorly in the hypothalamus than the sites stimulated electrically in the present experiments (Nakayama, Hammel, Hardy, and Eisenman, 1963), which is probably why radio-frequency warming failed to elicit a response in the present experiments (Chapter III). Finally, lateral hypothalamic damage in the rat, which eliminated salivation, had no effect upon thermoregulatory grooming (Hainsworth and Epstein, 1966), suggesting an anatomical difference between the neural mechanisms for autonomic and somatic thermoregulation in the rat as well.

Based upon this evidence, it seems that a system involving the hypothalamus reacts to increased temperature in a way which integrates the appropriate autonomic and somatic responses, but that this system has somewhat different inputs (perhaps as part of a "feedback" subsystem) for the two types of responses. According to this reasoning, the hypothalamic areas stimulated in the present experiments were involved only with certain somatic components of thermoregulation, and the input for these components does not necessarily involve hypothalamic units which are themselves thermosensitive.

Micturition and Defecation

The major autonomic responses to hypothalamic stimulation in the present experiments were simultaneous micturition and defecation elicited by stimulation of the paraventricular nucleus. This reaction also occurs in unanesthetized cats when the medial anterior hypothalamus is electrically stimulated (Hess, 1957). A similar reaction occurs in anaesthetized cats

(Ranson, Kabat, and Magoun, 1935) and rabbits (Yokoyama, Ban, and Kurotsu, 1960) during acute experiments in which the hypothalamus is stimulated.

Micturition and defecation elicited by hypothalamic stimulation may be due to activation of normal eliminative mechanisms, or may be due to anxiety or fear. Hess (1957) demonstrated that flight and "affective defence" could be elicited by stimulation of the medial anterior hypothalamus in the cat. However, the grooming elicited by hypothalamic stimulation in the present experiments cannot be attributed to fear or anxiety since rats actually groom very little in fear-producing situations (Bolles, 1960; Hughes, 1968). Also, stimulation of the hypothalamus at intensities that evoked grooming did not produce flight or freezing behavior, and rats in which grooming was evoked did not usually avoid stimulation in the self-stimulation tests (Figure 15).

Eating and Drinking

The failure of medial-hypothalamic stimulation to induce eating or drinking is consistent with previous results (Grossman, 1967). The single animal from which stimulation elicited eating had an electrode in the fornix (Chapter III) and stimulation of this site also elicited vigorous shaking followed by grooming like that observed in the mapping experiment (Chapter II). Shaking and grooming occurred when eating was elicited after the end of stimulation in the hippocampal formation and septal area (Milgram, 1968; Altman, 1969), so that the limbic areas involved in eating may be similar, in part, to those involved in grooming. In the hypothalamus, however, the areas involved in eating and drinking are probably somewhat different from those involved in shaking and stereotyped grooming.

THE SEQUENTIAL ORGANIZATION OF GROOMING

The results of Chapter IV confirmed preliminary observations that grooming evoked by stimulation of the medial hypothalamus does not comprise random or haphazard occurrences of components. Rather, components of grooming occur in organized sequences, so that certain components tend to follow one another with a high probability. The longer the sequence, the higher the probability that a particular component will occur, and the culmination of this effect is a probability approaching unity that a postural change will occur if three face-washing components occur consecutively (Figure 14). A similar sequential organization of grooming was also observed in normal hooded rats (Chapter IV), in albino rats, and in rats removed four generations from the wild (personal observations by the author).

Detailed analysis of this sequential organization also disclosed that hypothalamic stimulation elicits grooming which is predominantly directed to the ipsilateral side. Similarly, Roberts et al. (1967) mentioned in passing that, when the opossum grooms one side predominantly, the side is usually ipsilateral to the electrode. The present results, moreover, indicated that the degree of preference for grooming the ipsilateral side was related to the distance of the electrode tip from the midline.

Stimulation of the ventral or medial brain stem in cats (Skultety, 1962) or rats (Hopkins, 1967) elicits ipsiversive turning primarily, while stimulation of the lateral brain stem produces primarily contraversive motor effects. Thus, ventral midline structures may exert primarily ipsilateral effects to several levels of the brain and, at least in the hypothalamus, the strength of the ipsilateral tendency depends upon the distance of the stimulation from the midline.

GROOMING AND REINFORCEMENT

The results of the self-stimulation experiments were similar in all three test situations, and were consistent with the results of Christopher and Butter (1968): self-stimulation did not generally occur at sites from which grooming was elicited. This result is not surprising since the medial hypothalamus is an area in which self-stimulation cannot be obtained, yields low rates of responding, or has ambivalent rewarding effects (Olds & Olds, 1963; Poschel, 1966; Poschel & Ninteman, 1965; Wetzel, 1968). More specifically, electrodes in the paraventricular nucleus of the hypothalamus, through which stimulation readily evoked grooming in the present experiments, failed to support self-stimulation in the cat (Wilkinson & Peele, 1963) or the goat (Persson, 1962), so that the present results confirm this effect for the hooded rat.

Nonetheless, the failure to obtain self-stimulation at sites from which grooming was elicited is theoretically significant, because it has been proposed that facilitation or elicitation of the motor activity involved in species-typical behavior is a sufficient condition for reinforcement (Glickman & Schiff, 1967). This conclusion is based, in part, upon findings that self-stimulation often occurs at sites from which eating (Margules & Olds, 1962), drinking (Mogenson & Stevenson, 1966), or copulation (Caggiula and Hoebel, 1966) can be elicited, and that animals will learn tasks that provide an opportunity to perform an evoked response such as gnawing (Roberts and Carey, 1965) or aggression (Roberts and Kiess, 1964). The present results demonstrate, in contrast, that self-stimulation does not occur at sites from which grooming can be elicited, although grooming is certainly a species-typical behavior.

SUMMARY

(1) Grooming was elicited by electrical stimulation of three different levels of the neuraxis: the midbrain tectum, the limbic system, and the medial anterior hypothalamus.

(2) There was a dissociation between classes of somatic components. Hypothalamic stimulation resulted in the more frequent occurrence of only one class (face-washing and fur-licking and biting), while the other class (shaking and scratching) occurred more frequently in spontaneous grooming during and following limbic system stimulation.

(3) Grooming elicited by anterior hypothalamic stimulation resembled thermoregulatory grooming in some respects, except that salivation and vasodilatation of the tail were absent.

(4) Components of both evoked grooming and spontaneous grooming occur in organized sequences, so that particular components tend to follow one another with a high probability.

(5) Self-stimulation did not generally occur at hypothalamic sites from which grooming was elicited.

REFERENCES

Akert, K. Diencephalon. In D. E. Sheer (Ed.), Electrical stimulation of the brain. Austin, Texas: University of Texas Press, 1961, pp. 288-310.

Altman, J. L. Motivational responses evoked by stimulation of the septal area in the rat. Unpublished M. A. Thesis, University of Western Ontario, 1969.

Altman, J. & Carpenter, M. B. Fibre projections of the superior colliculus in the cat. Journal of Comparative Neurology, 1961, 116, 157-178.

Andersson, B. & Persson, N. Pronounced hypothermia elicited by prolonged stimulation of "the heat loss centre" in unanaesthetized goats. Acta physiologica scandinavica, 1957, 41, 277-282.

Andrew, R. J. Some remarks on behaviour in conflict situations, with special reference to Emberiza Sp. British Journal of Animal Behaviour, 1956, 4, 41-45.

Bard, P. & Macht, M. B. The behavior of chronically decerebrate cats. In G. E. W. Wolstenholme and C. M. O'Connor (Eds.), Neurological basis of behavior. London: J. and A. Churchill Limited, 1958, pp. 55-71.

Barnett, S. A. The rat: A study in behavior. Chicago: Aldine, 1964.

Beach, F. A. A review of physiological and psychological studies of sexual behavior in mammals. Physiological Reviews, 1947, 27, 240-307.

Bindra, D. Motivation: A systematic reinterpretation. New York: Ronald Press, 1959.

Bindra, D. & Mendelson, J. Training, drive level, and drug effects. A temporal analysis of their combined influence on behavior. Journal of Comparative and Physiological Psychology, 1963, 56, 183-189.

Bindra, D. & Spinner, N. Response to different degrees of novelty: The incidence of various activities. Journal of the Experimental Analysis of Behavior, 1958, 1, 341-350.

Bligh, J. The thermosensitivity of the hypothalamus and thermoregulation in mammals. Biological Reviews, 1966, 41, 317-367.

Bolles, R. C. The effect of food deprivation upon the rat's behavior in its home cage. Journal of Comparative and Physiological Psychology, 1963, 56, 456-460.

Bolles, R. C. Grooming behavior in the rat. Journal of Comparative and Physiological Psychology, 1960, 53, 306-310.

Bolles, R. C. & Woods, P. J. The ontogeny of behavior in the albino rat. Animal Behaviour, 1964, 12, 427-441.

Brooks, C. McC., Ishikawa, T., Koizumi, K., & Lu, H. H. Activity of neurones in the paraventicular nucleus of the hypothalamus and its control. Journal of Physiology, 1966, 182, 217-231.

Caggiula, A. R. & Hoebel, B. G. "Copulation-reward site" in the posterior hypothalamus. Science, 1966, 153, 1284-1285.

Christopher, S. M. & Butter, C. M. Consummatory behaviors and locomotor exploration evoked from self-stimulation sites in rats. Journal of Comparative and Physiological Psychology, 1968, 66, 335-339.

Collins, K. J. & Weiner, J. S. Endocrinological aspects of exposure to high environmental temperatures. Physiological Reviews, 1968, 48, 785-839.

Crosby, E. C., Humphrey, T. and Lauer, E. W. Correlative anatomy of the nervous system. New York: Macmillan, 1962.

Debackere, M., Peeters, G. and Tuyttens, N. Reflex release of an oxytocic hormone by stimulation of genital organs in male and female sheep studied by a cross-circulation technique. Journal of Endocrinology, 1961, 22, 321-334.

de Groot, J. The rat brain in stereotaxic coordinates. Verhandelingen Konenklijke Nederlandsche Akademie van Wetenschappen, Naturkunde, 1959, 52, 1-40.

Delgado, J. M. R. Prolonged stimulation of brain in awake monkeys. Journal of Neurophysiology, 1959, 22, 458-475.

Delgado, J. M. R. Free behavior and brain stimulation. International Review of Neurobiology, 1964, 6, 349-449.

Delgado, J. M. R. Sequential behavior repeatedly induced by stimulation of the red nucleus in free monkeys. *Science*, 1965, *148*, 1361-1363.

Delgado, J. M. R. & Sevillano, M. Evolution of repeated hippocampal seizures in the cat. *Electroencephalography and Clinical Neurophysiology*, 1961, *13*, 722-733.

Denny-Brown, D. Motor mechanisms - *Introduction*: The general principles of motor integration. In J. Field, H. W. Magoun, and V. E. Hall (Eds.), *Handbook of physiology*, *Volume 2*, Washington, D. C.: American Physiological Society,1960.

Dirlam, D. K. The effects of septal, thalamic, and tegmental lesions on general activity in the hooded rat. *Canadian Journal of Psychology*, 1969, *23*, 303-314.

Doyle, G. & Yule, E. D. Grooming activities and freezing behaviour in relation to emotionality in albino rats. *Animal Behaviour*, 1959, *7*, 18-22.

Egger, M. D. & Flynn, J. P. Further studies on the effects of amygdaloid stimulation and ablation on hypothalamically elicited attack behavior in cats. In W. R. Adey & T. Tokizane (Eds.), *Progress in brain research*, *Volume 27*, Structure and function of the limbic system. Amsterdam: Elsevier, 1967. Pp. 165-182.

Eisenberg, J. F. Studies on the behaviour of *Peromyscus Maniculatus* and *Peromyscus Californicus Parasiticus*. *Behaviour*, 1962, *19*, 177-207.

Eisenberg, J. F. The behavior of heteromyid rodents. *University of California Publications in Zoology*, 1963, *69*, 1-114.

Eliasson, S. & Strom, G. On the localization in the cat of hypothalamic and cortical structures influencing cutaneous blood flow. *Acta physiologica scandinavica*, 1950, *20* (Supplementum 70), 113-118.

Fentress, J. C. Interrupted ongoing behaviour in two species of vole (*Microtus agrestis* and *Clethrionomys britannicus*). I. Response as a function of preceding activity and the context of an apparently "irrelevant" motor pattern. *Animal Behaviour*, 1968, *16*, 135-153. (a)

Fentress, J. C. Interrupted ongoing behavior in two species of vole (*Microtus agrestis* and *Clethrionomys britannicus*). II. Extended analysis of motivational variables underlying fleeing and grooming behaviour. *Animal Behaviour*, 1968, *16*, 154-167. (b)

Fernandez de Molina, A. & Hunsperger, R. W. Organization of the subcortical system governing defence and flight reactions in the cat. Journal of Physiology, 1962, 160, 200-213.

Fisher, A. E. Maternal and sexual behavior induced by intracranial chemical stimulation. Science, 1956, 124, 228-229.

Fitzpatrick, R. J. The neurohypophysis and the male reproductive tract. In G. W. Harris & B. T. Donovan (Eds.), The pituitary gland, Volume 3: Pars intermedia and neurohypophysis. London: Butterworths, 1966. Pp. 606-516.

Glickman, S. E. & Schiff, B. B. A biological theory of reinforcement. Psychological Review, 1967, 74, 81-109.

Gloor, P. Amygdala. In J. Field, H. W. Magoun, & V. E. Hall (Eds.) Handbook of physiology, Volume 2, Washington, D. C.: American Physiological Society, 1960. Pp. 1395-1420.

Goodfellow, E. F. & Niemer, W. T. The spread of after-discharge from stimulation of the rhinencephalon in the cat. Electroencephalography and Clinical Neurophysiology, 1961, 13, 710-721.

Grant, R. T. Vasodilatation and body warming in the rat. Journal of Physiology, 1963, 167, 311-317.

Grossman, S. P. A textbook of physiological psychology. New York: John Wiley & Sons, 1967.

Hainsworth, F. R. Saliva spreading, activity, and body temperature regulation in the rat. American Journal of Physiology, 1967, 212, 1288 -1292.

Hainsworth, F. R. & Epstein, A. N. Severe impairment of heat-induced saliva-spreading in rats recovered from lateral hypothalamic lesions. Science, 1966, 153, 1255-1257.

Harris, G. W. Neural control of the pituitary gland. London: Edward Arnold and Company Limited, 1955.

Herberg, L. J. Seminal ejaculation following positively reinforcing electrical stimulation of the rat hypothalamus. Journal of Comparative and Physiological Psychology, 1963, 56, 679-685.

Higginbotham, A. C. & Koon, W. E. Temperature regulation in the Virginia opossum. American Journal of Physiology, 1955, 181, 69-71.

Hinde, R. A. Unitary drives. Animal Behaviour, 1959, 7, 130-141.

Hess, W. R. The functional organization of the diencephalon. New York: Grune & Stratton, 1957.

Hess, W. R. & Meyer, A. E. Triebhafte Fellreinigung der Katze als Symptom dienchphaler Reizung. Helvetica Physiological et Pharmacologica Acta, 1956, 14, 397-410.

Hoebel, B. G. & Teitelbaum, P. Hypothalamic control of feeding and self-stimulation. Science, 1962, 135, 375-376.

Hopkins, D. A. Electrical stimulation of the brain stem of the hooded rat: Evoked behavior and rewarding effects. Unpublished M. A. Thesis, McMaster University, 1967.

Horn, G. and Hill, R. M. Responsiveness to sensory stimulation of units in the superior colliculus and subjacent tectotegmental regions of the rabbit. Experimental Neurology, 1966, 14, 199-223.

Hughes, R. N. Behaviour of male and female rats with free choice of two environments differing in novelty. Animal Behaviour, 1968, 16, 92-96.

Hunter, J. & Jasper, H. H. Effects of thalamic stimulation in unanaesthetized animals. Electroencephalography and Clinical Neurophysiology, 1949, 1, 305-324.

Hyde, J. E. Effects of simultaneous application of opposing stimuli for head turning in cats. Experimental Neurology, 1965, 11, 230-244.

Ito, M. Hippocampal electrical correlates of self-stimulation in the rat. Electroencephalography and Clinical Neurophysiology, 1966, 21, 261-268.

Jarrard, L. E. Behavior of hippocampal lesioned rats in home cage and novel situations. Physiology and Beahvior, 1968, 3, 65-70.

Jasper, H. H. and Droogleever-Fortuyn, J. Experimental studies on the functional anatomy of petit mal epilepsy. Research Publications, Association for Research in Nervous and Mental Disease, 1947, 26, 272-298.

Johansen, K. Heat exchange through the muskrat tail. Evidence for vasodilator nerves to the skin. Acta physiologica scandinavica, 1962, 55, 160-169.

Kakolewski, J. W., Cox, V. C., & Valenstein, E. S. Short-latency antidiuresis following the initiation of food ingestion. Science, 1968, 162, 458-460.

Kimble, D. P., Rogers, L., & Hendrickson, C. W. Hippocampal lesions disrupt maternal, not sexual, behavior in the albino rat. Journal of Comparative and Physiological Psychology, 1967, 63, 401-407.

Lehrman, D. S. A critique of Konrad Lorenz's theory of instinctive behavior. Quarterly Review of Biology, 1953, 28, 337-363.

Liberson, W. T. & Akert, K. Hippocampal seizure states in guinea pigs. Electroencephalography and Clinical Neurophysiology, 1955, 7, 211-222.

Little, R. A. & Stoner, H. B. The measurement of heat loss from the rat's tail. Quarterly Journal of Experimental Physiology, 1968, 53, 76-83.

MacLean, P. D. Chemical and electrical stimulation of hippocampus in unrestrained animals. I. Methods and electroencephalographic findings. Archives of Neurology and Psychiatry, 1957, 78, 113-127. (a)

MacLean, P. D. Chemical and electrical stimulation of hippocampus in unrestrained animals. II. Behavioral findings. Archives in Neurology and Psychiatry, 1957, 78, 128-142. (b)

MacLean, P. D., Dua, S. & Denniston, R. H. Cerebral localization for scratching and seminal discharge. Archives of Neurology, 1963, 9, 485-497.

MacLean, P. D. & Ploog, D. W. Cerebral representation of penile erection. Journal of Neurophysiology, 1962, 25, 30-55.

Margules, D. L. & Olds, J. Identical "feeding" and "rewarding" in the lateral hypothalamus of rats. Science, 1962, 135, 374-375.

Melin, P. & Kihlstrom, J. E. Influence of oxytocin on sexual behavior in male rabbits. Endocinology, 1963, 73, 433-435.

Milgram, W. N. Effect of hippocampal stimulation on feeding in the rat. Unpublished Ph.D. thesis, McGill University, 1968.

Miller, N. E. Learning and performance motivated by direct stimulation of the brain. In D. E. Sheer (Ed.), Electrical stimulation of the brain. Austin: University of Texas Press, 1961. Pp. 387-396.

Mogenson, G. J. & Stevenson, J. A. F. Drinking and self-stimulation with electrical stimulation of the lateral hypothalamus. Physiology and Behavior, 1966, 1, 251-254.

Morin, F. & Green, J. D. Diffuse after discharges following stimulation of the fimbria hippocampi. American Journal of Physiology, 1953, 175, 251-257.

Nakayama, T., Hammel, H. T., Hardy, J. D. & Eisenman, J. S. Thermal stimulation of electrical activity of single units of the preoptic region. American Journal of Physiology, 1963, 204, 1122-1126.

Nauta, W. J. H. Hippocampal projections and related neural pathways to the midbrain in the cat. Brain, 1958, 81, 319-340.

Nissen, H. W. Instinct as seen by a psychologist. Psychological Review, 1953, 60, 291-294.

O'Kelly, L. I. The validity of defecation as a measure of emotionality in the rat. Journal of Genetic Psychology, 1940, 23, 75-87.

Olds, M. E. & Olds, J. Approach-avoidance analysis of rat diencephalon. Journal of Comparative Neurology, 1963, 120, 259-295.

Papez, J. W. & Freeman, L. Superior colliculi and their fiber connections in the rat. Journal of Comparative Neurology, 1930, 51, 409-440.

Persson, N. Self-stimulation in the goat. Acta physiologica scandinavica, 1962, 55, 276-285.

Poschel, B. P. H. Comparison of reinforcing effects yielded by lateral versus medial hypothalamic stimulation. Journal of Comparative and Physiological Psychology, 1966, 61, 346-352.

Poschel, B. P. H. & Ninteman, F. W. Self-determined aversive thresholds from the medial hypothalamus of the rat. Psychological Reports, 1965, 16, 585-591.

Ranson, S. W., Kabat, H., & Magoun, H. W. Autonomic responses to electrical stimulation of hypothalamus, preoptic region and septum. Archives of Neurology and Psychiatry, 1935, 33, 467-477.

Roberts, W. W., Berquist, E. H. & Robinson, T. C. Thermoregulatory grooming and sleep-like relaxation induced by local warming of preoptic area and anterior hypothalamus in opossum. Journal of Comparative and Physiological Psychology, 1969, 67, 182-188.

Roberts, W. W. & Carey, R. J. Rewarding effect of performance of gnawing aroused by hypothalamic stimulation in the rat. Journal of Comparative and Physiological Psychology, 1965, 59, 317-324.

Roberts, W. W. & Kiess, H. O. Motivational properties of hypothalamic aggression in cats. Journal of Comparative and Physiological Psychology, 1964, 58, 187-193.

Roberts, W. W., Steinberg, M. L. & Means, L. W. Hypothalamic mechanisms for sexual, aggressive, and other motivational behaviors in the opossum, Didelphis Virginiana. Journal of Comparative and Physiological Psychology, 1967, 64, 1-15.

Robinson, E. Effect of amygdalectomy on fear motivated behavior in rats. Journal of Comparative and Physiological Psychology, 1963, 56, 814-820.

Robinson, K. W. & Morrison, P. R. The reactions to hot atmospheres of various species of Australian marsupials and placental animals. Journal of Cellular and Comparative Physiology, 1957, 49, 455-478.

Rose, J. E. & Mountcastle, V. B. Touch and kinesthesis. In J. Field, H. W. Magoun and V. E. Hall (Eds.), Handbook of Physiology, Neurophysiology, Volume 1. Washington, D. C.: American Physiological Society, 1959, pp. 387-429.

Rowell, C. H. F. Displacement grooming in the chaffinch. Animal Behaviour, 1961, 9, 38-63.

Ruch, T. C. & Patton, H. D. Physiology and biophysics. Philadelphia: Saunders, 1965.

Seigel, S. Nonparametric statistics for the behavioral sciences. New York: McGraw-Hill, 1956.

Sheffield, F. D., Wulff, J. J. & Backer, R. Reward value of copulation without sex drive reduction. Journal of Comparative and Physiological Psychology, 1951, 44, 3-8.

Skultety, F. M. Circus movements in cats following midbrain stimulation through chronically implanted electrodes. Journal of Neurophysiology, 1962, 25, 152-164.

Stein, M. & Mirsky, I. A. The relation between anterior and posterior hypophysis and the hypothalamus in response to stress. In W. S. Fields, R. Guillemin & C. A. Carton (Eds.), Hypothalamic-hypophysial interrelationships. Springfield, Ill.: Charles C. Thomas, 1954, pp. 58-73.

Stricker, E. M., Everett, J. C. & Porter, R. E. A. The regulation of body temperature by rats and mice in the heat: Effects of desaliviation and the presence of a water bath. Communications in Behavioral Biology, 1968, Part A, Volume 2, 113-119.

Taylor, J. Selected writings of John Hughlings Jackson. London: Staples Press, 1958.

Teitelbaum, H. & Milner, P. Activity changes following partial hippocampal lesions in rats. Journal of Comparative and Physiological Psychology, 1963, 56, 284-289.

Thompson, G. E. & Stevenson, J. A. F. The temperature response of the male rat to treadmill exercise, and the effect of anterior hypothalamic lesions. Canadian Journal of Physiology and Pharmacology; 1965, 43, 279-287.

Tinbergen, N. The study of instinct. London, Oxford University Press, 1951.

Truex, R. C. & Carpenter, M. B. Strong and Elwyn's human neuroanatomy. Baltimore: Waverly Press,Inc., 1964.

Vanderwolf, C. H. Hippocampal electrical activity and voluntary movement in the rat. Electroencephalography and Clinical Neurophysiology, 1969, 26, 407-418.

Vaughan, E. & Fisher, A. E. Male sexual behavior induced by intracranial electrical stimulation. Science, 1962, 137, 758-760.

von Holst, E. & von St. Paul, U. Electrically controlled behavior. Scientific American, 1962, 206, 50-59.

von Holst, E. & von St. Paul, U. On the functional organisation of drives. Animal Behaviour, 1963, 11, 1-20.

Wetzel, M. C. Self-stimulation's anatomy: Data needs. Brain Research, 1968, 10, 287-296.

White, R. P. & Himwich, H. E. Circus movements and excitation of the striatal and mesodiencephalic centers in rabbits. Journal of Neurophysiology, 1957, 20, 81-90.

Wilkinson, H. A. & Peele, T. L. Intracranial self-stimulation in cats. Journal of Comparative Neurology, 1963, 121, 425-440.

Wit, A. & Wang, S. C. Temperature-sensitive neurones in the preoptic/anterior hypothalamic region: Effects of increasing ambient temperature. American Journal of Physiology, 1968, 215, 1151-1159.

Woods, J. W. Behavior of chronic decerebrate rats. Journal of Neurophysiology, 1964, 27, 635-644.

Yokoyama, S., Ban, T. & Kurotsu, T. Urinary bladder responses to the electrical stimulation of the hypothalamus, preoptic, and septal areas in rabbits. Medical Journal of Osaka University, 1960, 11, 191-232.

Zeigler, H. P. Displacement activity and motivational theory: A case study in the history of ethology. Psychological Bulletin, 1964, 61, 362-376.

Zeman, W. & Innes, J. R. M. Craigie's neuroanatomy of the rat. New York: Academic Press, 1963.

APPENDIX A.

Descriptions of Grooming Responses Observed in the Various Experiments.

Face-washing one (FW 1): bilateral repetitive, but not necessarily synchronous, movements of the forepaws around the mouth, vibrissae, and snout. Chewing and licking of the forepaws was always associated with this response.

Face-washing one rapid (FW 1 R): very rapid bilateral repetitive synchronous movements of the forepaws over the snout in the region of the vibrissae. The entire response lasts approximately one second and is always preceded by FW 1.

Face-washing two (FW 2): bringing one or both forepaws up over the top of the head and behind the ears.

Face-washing (FW): includes all of the face-washing responses described above.

Back-grooming (BG): licking or biting the fur on any part of the back and flank.

Abdomen-grooming (STOM): licking or biting the fur on the abdomen.

Scrotum-licking (SCR): licking the exposed skin of the scrotal sac.

Tail-base licking (TB): licking the base of the tail and perineal area.

Foot-licking (FL): licking the dorsal and ventral surface of the hind feet. The rat generally holds the hind foot in its forepaws while licking.

Tail-licking (TL): licking the length of the tail starting from the base. The tail is licked on both the dorsal and ventral surfaces while being held in the forepaws.

Penis-licking (PL): licking the penis which is usually erect during the response.

Ventral-surface grooming (VS): includes all of the above except face-washing and back-grooming.

Scratching and toe biting (SCRATCH): scratching the head and body with the hind foot. Biting the toes of the same foot is usually alternated with the scratching movements.